



More efficient aboveground nitrogen use in more diverse Central European forest canopies



Martin T. Schwarz^{a,*}, Sebastian Bischoff^b, Stefan Blaser^c, Steffen Boch^c, Barbara Schmitt^c, Lisa Thieme^d, Markus Fischer^c, Beate Michalzik^b, Ernst-Detlef Schulze^e, Jan Siemens^d, Wolfgang Wilcke^a

^a University of Berne, Geographic Institute, Hallerstrasse 12, 3012 Berne, Switzerland

^b Friedrich Schiller University Jena, Institute of Geography, Löbdergraben 32, 07743 Jena, Germany

^c University of Berne, Institute of Plant Sciences and Botanical Garden, Altenbergrain 21, 3013 Berne, Switzerland

^d Rheinische Friedrich Wilhelms University Bonn, Institute for Crop Science and Resource Conservation, Division Soil Science and Soil Ecology, Nussallee 13, 53115 Bonn, Germany

^e Max Planck Institute for Biogeochemistry, Hans-Knöll-Strasse 10, 07745 Jena, Germany

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ABSTRACT

We hypothesized that biodiversity improves ecosystem functioning and services such as nutrient cycling because of increased complementarity. We examined N canopy budgets of 27 Central European forests of varying dominant tree species, stand density, and tree and shrub species diversity (Shannon index) in three study regions by quantifying bulk and fine particulate dry deposition and dissolved below canopy N fluxes. Average regional canopy N retention ranged from 16% to 51%, because of differences in the N status of the ecosystems. Canopy N budgets of coniferous forests differed from deciduous forest which we attribute to differences in biogeochemical N cycling, tree functional traits and canopy surface area. The canopy budgets of N were related to the Shannon index which explained 14% of the variance of the canopy budgets of N, suggesting complementary aboveground N use of trees and diverse understorey vegetation. The relationship between plant diversity and canopy N retention varied among regional site conditions and forest types. Our results suggest that the traditional view of belowground complementarity of nutrient uptake by roots in diverse plant communities can be transferred to foliar uptake in forest canopies.

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1. Introduction

Ecosystem functioning comprises processes, services, and stability (Millennium Ecosystem Assessment, 2005). Pools and fluxes of water, carbon and nutrients such as nitrogen (N) within and between ecosystems are provisioning, regulating and supporting ecosystem services, respectively, because they feed back to food production and non-food resource supply such as timber (Millennium Ecosystem Assessment, 2005). A number of studies in experimental grasslands revealed the significant influence of species richness on the cycling of N by more exhaustive belowground N use through complementarity (Tilman et al., 1996; Hooper and Vitousek, 1998; Scherer-Lorenzen et al., 2003; Kahmen et al., 2006). However, the relationships of biodiversity and ecosystem functioning are far from being understood in forests. Furthermore, the small-scale experimental results have not yet been linked with replicated large-scale observations and generalized across landscapes and different land-use systems (Symstad et al., 2003; Scherer-Lorenzen et al., 2005; Fischer et al., 2010). The latter is

necessary to adequately address spatial and functional variability of biogeochemical cycles at different scales and among various management regimes (ranging from coniferous plantations to near-native deciduous forests).

Since the beginning of industrialization, the amount of N cycling in terrestrial ecosystems has increased and N from anthropogenic sources has become an important component of the N cycle in terrestrial ecosystems (Aber et al., 1998; Galloway et al., 2004). Anthropogenic N is transported and processed in the atmosphere and ultimately deposited mainly as reactive N. Forests receive high N deposition because of the large canopy surface area and its aerosol and gas scavenging capacity (Horn et al., 1989; Lovett and Lindberg, 1993; Rothe et al., 2002). The consequences of N deposition on the stability and ecosystem services of northern temperate forests have been intensively debated in the context of N saturation (Aber et al., 1998).

Central European forests are likely under use by humans since several centuries which has resulted in changes of vegetation composition and forest structure (Sala et al., 2000; FAO, 2011) and modified plant species richness among forest types (Boch et al., 2013). Especially the introduction and the preferred cultivation of conifers has impacted biogeochemical N cycling compared to

* Corresponding author. Tel.: +41 31 631 3856; fax: +41 31 631 8511.

E-mail address: martin.schwarz@giub.unibe.ch (M.T. Schwarz).

native deciduous forests in Europe through feedbacks on the light and water passing the canopy, changes in litter quality and composition, and nutrient leaching (Augusto et al., 2002; Rothe et al., 2002; De Schrijver et al., 2007). The cultivation of conifers in areas where deciduous trees would naturally dominate represents an intensified forest management, because coniferous forests evolved from human planting and are usually managed in shorter rotation periods resulting in greater resource exploitation through harvest than in deciduous forests on the long run (BMELV, 2004). The response of biogeochemical cycles to forest management may vary substantially depending on regional site conditions, resources and ecosystem resilience.

Many findings mainly derived from stable isotope experiments highlight retention, stomatal and microbial uptake, and transformation of dissolved and gaseous N species (e.g., NH_4^+ , NO_3^- , NO_2^- , NO_x , peroxy-acetyl-nitrate, organic N) in forest canopies (e.g., Garten Jr and Hanson, 1990; Sparks et al., 2003; Gaige et al., 2007). However, the physiological capability of using the various atmospheric N species and thus canopy N uptake potential depends on plant functional traits like thinner cuticles, more pronounced leaf-wettability, higher nitrate reductase activity in deciduous than in coniferous trees. Furthermore, canopy N retention may also be governed by differences in canopy surface area and seasonality of foliage between coniferous and deciduous trees (Harrison et al., 2000; Augusto et al., 2002) or feedbacks to soil N supply (Rennenberg et al., 1998). Canopy N uptake of a Norway spruce forest in Germany was estimated to range from 15% to 42% of the annual tree N demand (Harrison et al., 2000) with the majority taken up as dissolved N (Horn et al., 1989). Therefore, canopy N retention contributes to plant nutrition and thus potentially increases productivity and carbon sequestration in N-limited forests (Sievering et al., 2007). Moreover, canopy N retention buffers negative effects of inorganic N deposition through immobilization, thus, increasing ecosystem stability and supporting ecosystem services like fresh-water supply. Canopy uptake of NH_4^+ and HNO_3 by foliage and bark is accompanied by base cation leaching (mainly K^+ to maintain a balanced charge in plant cells). Thus, excessive canopy N uptake may induce base cation leaching from foliage resulting in nutrient imbalances in trees (Horn et al., 1989).

Both, positive and negative biodiversity-ecosystem functioning relationships were reported from observational forest studies (Vila et al., 2003; Vila et al., 2007; Morin et al., 2011; Paquette and Messier, 2011), but these studies focused solely on the relationship between mature tree diversity and productivity. Hence, the existence of a complementarity effect in forests is still under debate because it can only be proven using strict experimental sampling designs to overcome the 'sampling-effect' (Wardle, 1999). Such a degree of experimental control of driving factors can hardly be reached in structurally complex ecosystems like forests because the understorey species composition in forests is not fully independent of the regional species pool, the

dominant tree species, and forest management, respectively (Boch et al., 2013). Nevertheless, the assumption that species-rich plant assemblages improve N-use efficiency through complementary use of N should also hold true for forests (Scherer-Lorenzen et al., 2005). To our knowledge, a biodiversity effect has never been evaluated with respect to aboveground nutrient use in forests via plant surfaces. Several comparative studies addressed the influence of single and admixed tree species on nutrient-use efficiency in terms of N leaching (Nordin, 1991; Kelty, 2006; Berger et al., 2009) but, to our knowledge, no study investigated the functional role of vascular plant diversity on canopy N retention including the forest understorey although the diversity of woody canopy-forming understorey plants usually exceeds tree species diversity in managed Central European forests and the understorey vegetation competes for N resources with overstorey trees (Gebauer et al., 2000).

Our objective was to quantify the canopy budget of N in a range of central European forests to determine drivers of this budget. We hypothesized that canopy N budgets are driven by (1) the type of forest system determined by tree species and management intensity (reflected by the basal area) and (2) richness and diversity of trees and shrubs forming the forest canopy.

2. Materials and methods

2.1. Study site

This study was conducted as part of the "Biodiversity Exploratories" project (www.biodiversity-exploratories.de) in three regions in Germany, Schorfheide-Chorin, Hainich-Dün, and Schwäbische Alb, where the assessments are conducted in established and actively managed forests (for details see Fischer et al., 2010). The three research regions differ in climate, geological setting and prevalent soils that are representative for large parts of Central Europe (Table 1). In each region, we investigated 9 forest plots (100 m × 100 m) comprising age-class forests (i.e. forests consisting of one or more even-aged development stages which are harvested at 80–120 year intervals by clear cut or shelterwood logging) dominated by European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) H. Karst.), and Scots pine (*Pinus sylvestris* L.), respectively, and extensively managed forests (mature forests protected for at least 60 years) dominated by European beech (Fischer et al., 2010). The dominating tree species of the studied forests (Table 2) are representative for large parts of the respective region (Fischer et al., 2010).

2.2. Sampling and chemical analysis

Fluxes of Cl^- , K, Na, total dissolved N (TN), NO_3^- -N, NH_4^+ -N, dissolved organic N (DON), and total dissolved phosphorous with

Table 1

Main environmental properties of the three study regions partly taken from Fischer et al. (2010). Soil classification according to IUSS working group WRB (2006).

	Schorfheide-Chorin	Hainich-Dün	Schwäbische Alb
Location	NE Germany (53°2' N, 13°51' E)	Central Germany (51°10' N, 10°23' E)	SW Germany (48°24' N, 9°24' E)
Altitude (m a.s.l.)	3–140	285–550	460–860
Population density (km ⁻²)	23	116	258
Mean annual temperature (°C)	8–8.5	6.5–8	6–7
Mean annual precipitation (mm)	500–600	500–800	700–1000
Bedrock	Quaternary quartzitic sand (glacial till)	Triassic lacustrine limestone/ sandstone/quaternary loess	Jurassic limestone
Soils	Cambisols Albeluvisols	Luvissols Stagnosols	Leptosols Cambisols
Common tree species	<i>Fagus sylvatica</i> L. <i>Pinus sylvestris</i> L. <i>Quercus</i> spp.	<i>Fagus sylvatica</i> L. <i>Picea abies</i> (L.) H. Karst. <i>Carpinus betulus</i> L.	<i>Fagus sylvatica</i> L. <i>Picea abies</i> (L.) H. Karst.

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