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# Nutrient dynamics along a precipitation gradient in European beech forests

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## Abstract

Precipitation as a key determinant of forest productivity influences forest ecosystems also indirectly through alteration of the nutrient status of the soil, but this interaction is not well understood. Along a steep precipitation gradient (from 970 to 520 mm yr$^{-1}$ over 150 km distance), we studied the consequences of reduced precipitation for the soil and biomass nutrient pools and dynamics in 14 mature European beech (*Fagus sylvatica* L.) forests on uniform geological substrate. We tested the hypotheses that lowered summer precipitation (1) is associated with less acid soils and a reduced accumulation of organic matter on the forest floor, and (2) reduces nutrient supply from the soil and leads to decreasing foliar and root nutrient concentrations. Soil acidity, the amount of forest floor organic matter, and the associated organic matter N and P pools decreased to about a half from wet to dry sites; the C / P and N / P ratios, but not the C / N ratio, of forest floor organic matter decreased. Net N mineralization (and nitrification) rate and the available P and K pools in the mineral soil did not change with decreasing precipitation. Foliar P and K concentrations (beech sun leaves) increased while N remained constant, resulting in decreasing foliar N / P and N / K ratios. N resorption efficiency increased toward the dry sites. We conclude that a reduction in summer rainfall significantly reduces the soil C, N and P pools but does not result in decreasing foliar N and P contents in beech. However, more effective tree-internal N cycling and the decreasing foliar N / P ratio towards the dry stands indicate that tree growth may increasingly be limited by N and not by P with decreasing precipitation.

## 1 Introduction

On a global scale, growing season length and water availability are the two most important environmental factors controlling forest productivity (Chapin et al., 2002; Gower, 2002). Soil fertility, in particular N and P availability, does covary with tree growth and stand productivity mainly at regional and local scales through its influence on leaf area

index, reflecting the variability of geological substrates and soil types. Effects of water availability on forest productivity have often been expressed by plotting yield against annual or summer precipitation, or atmospheric evaporative demand (e.g. Huxman et al., 2004; Gerten et al., 2008; Seiler et al., 2009), while influences of nutrient availability were explored by comparing yield tables of a tree species for different soil or bedrock types, or by conducting fertilization trials in planted stands (e.g. Fahey et al., 1998; Sardans et al., 2004; Ste-Marie et al., 2007). However, water availability (or as a proxy: precipitation) and nutrient availability may depend on each other through a number of short-term and long-term interactive processes (Stanford and Epstein, 1974; Matson and Vitousek, 1981). Forest sites with higher precipitation and moister soils are typically characterized by more intensive rock weathering, enhanced downward transport of humic substances, clay and other materials in the soil profile with percolating water, leaching of nutrient cations and anions and other soluble compounds to the groundwater, and a tendency for soil acidification (e.g., Moreno et al., 1996). Otherwise, moister soils provide better conditions for the supply of nutrients to the roots through mass flow and diffusion; both transport processes slow down with soil drying (Kreuzwieser and Geßler, 2010). Finally, precipitation and soil moisture act as controls of soil biological activity and thus influence decomposition rate and nutrient cycling in the soil (Meentemeyer, 1978; Swift et al., 1979; Sardans and Peñuelas, 2005, 2007; Brady and Weil, 2008). Soil moisture influences the composition of the mycorrhizal community with possible consequences for the resource uptake of the symbionts (Rillig et al., 2002). A precipitation or moisture effect on nutrient cycling may well feed back on the nutrient status of the trees and their growth rate. However, the dependence of soil chemistry and the nutrient status of temperate forest trees on precipitation are not well understood. This is unsatisfactory because summer rainfall is expected to decrease in the course of climatic warming in various regions of Central Europe and elsewhere in the temperate zone (Rowell and Jones, 2006; IPCC, 2007).

We investigated soil and biomass nutrient pools and soil acidity in mature stands of *Fagus sylvatica* L. (European beech) across a steep precipitation gradient in which

soil properties changed solely due to climatic reasons, while geological substrate, forest vegetation and soil age remained sufficiently constant. Forests built by European beech provide exceptional opportunities for conducting comparative studies along environmental gradients because this species forms monospecific stands under a very broad range of precipitation and soil fertility conditions (Ellenberg and Leuschner, 2010). In fact, this species thrives on highly acid to alkaline soils and grows in the driest (420 mm yr$^{-1}$) and wettest regions (> 2000 mm yr$^{-1}$) of Central Europe. Major goal of this study was to understand how an expected future reduction in summer rainfall would act on soil nutrient availability and the nutrient status of beech trees. By investigating a number of soil and plant parameters in 14 beech stands differing in annual precipitation (970 to 520 mm yr$^{-1}$) and summer rainfall (430 to 270 mm yr$^{-1}$), we tested the hypotheses that (i) soil acidity decreases and base saturation at the cation exchangers increases with decreasing precipitation, (ii) the accumulation of organic matter on the forest floor and the built-up of nutrient stores in the organic layers is reduced in a drier climate, and (iii) lowered precipitation reduces the foliar N and P concentration of the trees possibly through drought effects on mineralization, ion diffusivity and/or root uptake activity (compare Fotelli et al., 2004; Geßler et al., 2004).

## 2 Materials and methods

### 2.1 Study sites, geology and climate

In a transect study, we compared 14 mature European beech forest stands in a confined area of Central Germany across a steep gradient of annual precipitation (970–520 mm yr$^{-1}$ across a distance of ∼ 150 km). Important criteria of study site selection were the uniformity of the geological bedrock and the comparability of stand structure and tree species composition among the 14 stands. Of the five "ecosystem state factors" defined by Jenny (1941) – climate, relief, organisms, parent material and time – four were regarded to be approximately constant in this investigation. This allowed us to

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investigate the role of the fifth factor, climate, on soil nutrient status. Variation in parent material and relief could be reduced to a minimum by selecting suitable beech stands on Triassic sandstone (Middle Bunter, formation "Hardegsen Folge") with absent or insignificant cover layers of quaternary loess and in similar topographic positions within a limited area. Sites with significant cover layers of quaternary loess as identified by their silt content were not considered. The time factor had a similar influence at all studied sites, because all soils have developed during the Holocene since about 12 000 yr, and all beech stands were of similar age. A major strength of this study is that single-species stands of the same tree species were compared, which largely eliminates the organism factor that can have a profound influence on forest floor and mineral topsoil properties (Muys, 1995; Raulund-Rasmussen and Vejre, 1995; Vesterdal and Raulund-Rasmussen, 1998).

The 14 mono-specific mature beech forests were chosen along a 150 km-long WNW–ESE transect between the Solling Mountains and the Thuringian Basin (Central Germany). The 14 forests grow along a precipitation gradient with the western sites experiencing a moist sub-oceanic climate and the eastern ones a relatively summer-dry, sub-continental climate. Stand selection criteria were (i) closed canopy without major gaps, (ii) comparable stand age (100–140 yr old; extremes: 90 and 157 yr), (iii) no significant presence of other tree species, and (iv) similar stem densities (175–250 ha$^{-1}$; cf. Meier and Leuschner, 2008a). All study plots (30 m × 30 m in size) were placed by random in stand sections with more or less homogeneous stand structure and closed canopy. All stands were located below 450 m a.s.l. in the colline and submontane belts at level to slightly sloping terrain (1.2–9.5°; Table 1). The stands were not affected by past compensatory soil liming activities, except for stands # 3 and 6, where such a treatment had been applied at least 8–13 yr ago. The time elapsed minimizes the possibility of lasting effects on today's soil chemical state (Rehfuess, 1990).

All 14 stands are growing on soils derived from the geological bedrock "Middle Bunter", a Triassic sandstone formation which stretches as a belt from the Solling Mountains in the west to the Ziegelroda Plateau in the east. The sandstone con-

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sists of sandy particles (mostly quartz, but also silicates) which are cemented by silty and clayey material to concrete rocks colored red by its content of hematite (Fiedler and Hunger, 1970; Scheffer and Schachtschabel, 2009). Weathering leads to sandy silicate-poor soils with moderate to high acidity and a relatively low base saturation at the cation exchangers. The soils in the study region were mainly Cambisols, or Umbrisols in the moister stands, with a variety of subtypes (Table 1). None of the sites was influenced by groundwater. The humus forms on the forest floor were mainly mullmoders (only L and F horizons present) or leptomoders (L, F and H horizons).

Mean annual temperature was 7.8 °C, with a tendency for slightly higher temperatures in the eastern, more continental section of the gradient (Table 1). The long-term means of annual precipitation decreased from the west (970 mm yr$^{-1}$) to the east (520 mm yr$^{-1}$), reflecting the transition from a more sub-oceanic to a more sub-continental climate in the rain shadow of the Solling and Harz mountains. The corresponding summer rainfall (May to September) decreased from 430 to 270 mm yr$^{-1}$. In the years 2003 to 2006, annual precipitation (mean of 4 yr) decreased from 920 mm yr$^{-1}$ in the west to 460 mm yr$^{-1}$ in the east of the transect, with a mean coefficient of variation (CV) of 12 % between the 4 yr. Calculation of potential evapotranspiration (ET$_p$) at the 14 sites was not possible due to missing data on relative air humidity and wind speed at most locations. Instead, we used climatological data from nearby weather stations and calculated a correlation function relating measured ET$_p$ to the corresponding annual precipitation at these reference stations ($r = -0.91$, $p < 0.001$). Based on this equation, we derived local estimates of ET$_p$ for all 14 sites from the precipitation data. The annual water balance, i.e., the difference between annual precipitation and potential evapotranspiration, decreased from +480 mm yr$^{-1}$ in the west to +110 mm yr$^{-1}$ in the east of the transect revealing a large decrease in annual water surplus. Consequently, at the moister sites, about 50 % of annual precipitation is percolating through the profile or is lost as runoff, while more than 75 % is lost by evapotranspiration at the drier sites. This hydrological gradient is supported by a

trend to larger $\delta^{13}$C-values in sun leaf dry mass indicating a reduced leaf conductance in low-rainfall stands (Table 1; cf. Meier and Leuschner, 2008a).

## 2.2   Soil sampling and chemical analyses

At every study site, a soil profile examination was carried out in a soil pit in the centre
5  of the plot following the protocol given by "Arbeitskreis Standortskartierung" (1996). The humus forms on the forest floor were classified according to Green et al. (1993), soil types after IUSS-ISRIC-FAO (2006). Soil samples were taken in April 2004 at five randomly chosen locations within the 30 m × 30 m study plot in both the organic layers and the mineral soil (0–10 and 10–20 cm depth, where the main pool of nutrients and
10  the majority of fine roots thrive, cf. Meier and Leuschner, 2008b). To account for small-scale soil variability, each of the five samples per horizon consisted of four sub-samples that were taken at random locations within a 50 cm radius around the respective sampling point. These sub-samples were mixed and used for a single analysis. Sample preparation and chemical analyses mainly followed the protocol given by "Bundesweite
15  Bodenzustandserhebung im Wald" (BMELF, 1994). In May and August 2011, net N mineralization rate was measured by field incubation for about five weeks of eight intact soil cores (upper 10 cm of the profile where 70 % of the fine roots thrive) that were carefully enveloped in a plastic bag for preserving soil structure and reburied in the soil hole where they had been extracted (modified in situ buried-bag method; Eno,
20  1960). Inorganic N was extracted immediately after soil collection by shaking with 0.5 M $K_2SO_4$ (1 : 4) and photometrical measurement with an autoanalyzer (Cenco/Skalar Instruments, Breda, Netherlands). Net N mineralization rate was calculated as the difference between the initial and final concentrations of $NH_4^+$ plus $NO_3^-$, net nitrification rate as the difference between initial and final nitrate concentrations. The fraction of
25  "plant-available phosphorus" according to Bowman and Cole (1978) was determined by resin bag extraction (anion exchange gel; Dowex 1 × 8–50; Dow Water & Process Solutions, USA). The resin was placed for 16 h in a solution of 1 g soil material sus-

pended in 30 mL water (Sibbesen, 1977). P was re-exchanged by 10 % NaCl and 2 % NaOH solutions and analyzed by blue-dyeing with 5 mM hexaammonium heptamolybdate (Murphy and Riley, 1962) and photometric measurement at 712 nm against water (spectrophotometer; Libra S 21, Biochrom, UK). We calculated nutrient pools for the 0–20 cm topsoil from bulk soil density and the corresponding nutrient concentrations (unit: $mol\,m^{-2}\,20\,cm^{-1}$).

## 2.3 Leaf and fine root sampling and chemical analyses

Leaves of the upper sun canopy were harvested by crossbow shots in July/August 2005 and 2006 in ten (2005: seven) of the 14 stands. Eight (2005: six) branches per stand from different trees with a total of 30 (2005: 180) leaves were randomly collected in every campaign. Leaf litter was collected by litter trapping in ten litter buckets (aperture: 0.28 $m^2$) per plot in autumn 2003 in all 14 stands (for measuring details, see Meier and Leuschner, 2008a). Fine roots were collected with a soil corer in the densely rooted organic layers and the mineral soil to 10 cm soil depth in summer 2005 and sorted into live and dead fine root mass under a stereomicroscope (for measuring details, see Meier and Leuschner, 2008b). A total of eight (2005: six) fresh leaf samples, ten leaf litter samples and four (necromass: three) fine root samples per stand were used for chemical analysis. Leaf and fine root samples were dried (70 °C, 48 h) and ground. The concentrations of total carbon and nitrogen of the samples were determined by elemental analysis, total phosphorus after digestion with 65 % $HNO_3$ at 195 °C by yellow-dyeing with vanadate-molybdate and photometric measurement at 440 nm. The concentrations of Ca, Mg, K, Fe, Mn, and Al in the biomass were analyzed by atomic absorption spectroscopy (AAS vario 6, analytik jena, Jena, Germany) after $HNO_3$ digestion. Nutrient resorption efficiency was calculated as the percentage of the foliar nutrient pool that is withdrawn before leaf abscission. For obtaining hints on nitrogen sources and soil N supply, the nitrogen isotope signature of sun leaf dry mass (mid-summer samples) was analyzed by mass spectroscopy (Delta plus, ThermoFinnigan, USA) in the Centre for Stable Isotope Research and Analysis (KOSI) of the University of Göttingen.

## 2.4 Statistical analyses

Means and standard errors of the soil chemical data were calculated from each five replicate samples per study site and soil horizon. Statistical analyses were conducted with the package SAS, version 9.2 (Statistical Analyses System, SAS Institute Inc., Cary, NC, USA). Probability of fit to normal distribution was tested by a Shapiro–Wilk test. In the case of Gaussian distribution, mean values of the study sites were compared by a one-factorial analysis of variance followed by a Scheffé test. We employed linear regression analyses to quantify the influence of precipitation, temperature and various soil chemical factors on each other. Multiple regression analyses with backward variable elimination were calculated to test for the significance of the effects of climate, stem basal area and N availability on nutrient pools and N mineralization in the soil. Significance was determined at $p < 0.05$ in all tests.

## 3 Results

### 3.1 Changes in soil chemical properties across the precipitation gradient

In our transect study in 14 mature beech stands growing on similar bedrock, a large decrease of annual precipitation from 970 to 520 mm yr$^{-1}$ significantly decreased soil acidity in the mineral topsoil (0–20 cm; Table 2). Stands with less than 600 mm of annual precipitation had proton concentrations in a soil suspension of about $5.8 \times 10^{-5}$ mol L$^{-1}$, while forests with more than 900 mm yr$^{-1}$ reached about twice as high concentrations ($1.1 \times 10^{-4}$ mol L$^{-1}$, corresponding to pH(KCl) values of 4.47 and 3.98). The acid/base buffer system of the soil was constituted by cation exchange buffering at the dry end of the transect (consumption of the cation exchange capacity) and changed to Al-buffering at the moist end (dissolution of siliceous Al and protolysis of Al hydroxides; sensu Ulrich, 1981). A multiple regression analysis showed that soil temperature was an additional factor influencing soil acidity (Table 3). With higher elevation (and higher pre-

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cipitation) and reduced soil temperature, soil pH decreased. The increase in acidity did not result in a significant reduction of the base saturation at the cation exchangers, even though a tendency of a decrease from the driest to the moistest sites appeared ($p = 0.15$; Table 2). Forest floor organic matter (L, F, H layers) accumulation increased with increasing growing season precipitation, while neither soil temperature nor elevation influenced the organic matter pool significantly (Tables 2 and 3). We found the largest amounts in stands with $> 900\,\mathrm{mm\,yr^{-1}}$ (mean: $4.0\,\mathrm{kg\,m^{-2}}$), while less organic matter was recorded in stands with $< 800\,\mathrm{mm\,yr^{-1}}$ (mean: $3.0\,\mathrm{kg\,m^{-2}}$; Table 2). The increase in forest floor organic matter toward the moister sites was closely linked to a marked shift in soil types from profiles with more eutric properties to more podzolic soils which prevailed in the moister stands (Table 1). Similarly, the humus profile types changed from mullmoders to leptomoders in this sequence. Mainly as a consequence of increasing amounts of organic matter, the pools of organic carbon (66 vs. $130\,\mathrm{mol\,C_{org}\,m^{-2}}$), total nitrogen (2.5 vs. $5.6\,\mathrm{mol\,N_t\,m^{-2}}$) and total phosphorus (126 vs. $191\,\mathrm{mmol\,P_t\,m^{-2}}$) in the forest floor roughly doubled with an increase in precipitation from $< 600$ to $> 900\,\mathrm{mm\,yr^{-1}}$ (Table 5). The growing stocks of nitrogen in the organic layers with increasing rainfall were closely related to the accumulation of organic carbon and total phosphorus ($N_t : C_{org}$ relationship: $r^2 = 0.997$, $p < 0.001$; $N_t : P_t$ relationship: $r^2 = 0.93$, $p < 0.001$). However, the C / N ratio of the organic layers showed a small, but significant decrease from about $27\,\mathrm{mol\,mol^{-1}}$ at $< 600\,\mathrm{mm\,yr^{-1}}$ to $25\,\mathrm{mol\,mol^{-1}}$ at $> 900\,\mathrm{mm\,yr^{-1}}$, whereas organic layer C / P ($528$ to $646\,\mathrm{mol\,mol^{-1}}$), N / P (20 to $26\,\mathrm{mol\,mol^{-1}}$), and N / K ratios (10 to $22\,\mathrm{mol\,mol^{-1}}$) significantly increased toward the moister sites (Fig. 1b). Total nitrogen in the organic layers increased exponentially with decreasing pH(KCl) in the mineral soil when the pH was $< 3.2$ ($r^2 = 0.61$, $p = 0.002$).

While the amount of summer rainfall exerted a significant influence on major nutrient pools in the organic layers, the precipitation effect was less distinct in the mineral soil. Decreasing rainfall was associated with a significant decrease of organic carbon in the mineral topsoil, ranging from $1450\,\mathrm{mol\,C_{org}\,m^{-2}\,20\,cm^{-1}}$ in stands with more than

900 mm yr$^{-1}$ to 1050 mol m$^{-2}$ in stands with less than 600 mm yr$^{-1}$ (Fig. 1a). The pool of total N in the mineral soil was by 35 % smaller in low-precipitation stands than in moister stands (Table 5) and changed in parallel with the SOC pool as evidenced by a remarkably uniform C / N ratio across the precipitation gradient (mean: 21.3 mol mol$^{-1}$). The pool of extractable NO$_3^-$ decreased significantly toward the moist end of the transect (from 980 to 341 g N m$^{-2}$ 10 cm$^{-1}$; $r^2 = 0.37$, $p = 0.03$) (average of measurements in May and August 2011), while that of NH$_4^+$ was not significantly influenced by precipitation. N-pool-specific net N mineralization and net nitrification rates in the topsoil (upper 10 cm; mineral N release per N$_t$ pool size; Fig. 2a) and mineralization and nitrification expressed per ground area showed no trend along the transect (Fig. 2b). Net nitrification rate was influenced by altitude (Table 3), while soil moisture exerted a positive and the soil ammonium pool a negative effect on net N mineralization per ground area (Table 4). The plant-available phosphorus (resin-exchangeable P: P$_a$) and exchangeable potassium (K$_{exch}$) pools in the mineral soil were highly variable among the investigated stands (8fold and 6fold difference between lowest and highest values, respectively; Fig. 1c). Significant correlations of P$_a$ or K$_{exch}$ availability with annual rainfall were not found; nevertheless, a tendency for higher K$_{exch}$ pools in low-precipitation stands (1.2 mol K$_{exch}$ m$^{-2}$ 20 cm$^{-1}$) as compared to high-precipitation stands (0.6 mol K$_{exch}$ m$^{-2}$ 20 cm$^{-1}$) was observed (compare Table 5). Plant-available phosphorus was not significantly related to any of the other investigated soil chemical parameters (not shown).

## 3.2 Nutrient compartmentalization to organic layers, mineral soil and tree biomass

Except for the pool in wood biomass, which is turned over very slowly, our investigation covered all nutrient pools that are relevant for plant nutrition: mineral topsoil (0–20 cm), organic layers, leaf biomass, and fine root biomass and necromass. Of these nutrient pools, the largest proportion was for all nutrients contained in the mineral topsoil (0–

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20 cm), which stored on average 87 % of the ecosystem stock of an element (Table 5). In the organic L, F H layers, another 10 % were contained, while leaf biomass and the living and dead fine root fractions each stored about 1 % only. However, this compartmentalization was slightly different in phosphorus, for which only about 80 % was stored in the mineral topsoil (plant-available fraction), but 15 % in the organic layers and 2 % in the fine root necromass. The less $P_a$ was stored in the mineral soil, the more was accumulated in the organic layers on the forest floor. The precipitation regime tended to influence P compartmentalization by shifting P storage from the organic layers to the mineral soil in drier stands.

When comparing the nutrient pools in leaves and fine roots, more basic (non-hydrolyzing) cations (and N) were stored in leaf mass than in fine root mass, while the P pools had equal size (Table 5). The precipitation decrease along the transect was associated with a significant increase in the Ca, K and Mg pools in leaf biomass, while the corresponding pools in fine root mass decreased. Similarly, the pools of P and acid (hydrolyzing) cations (Al, Fe, and Mn) in leaf mass increased toward stands with lower annual precipitation, but the corresponding fine root pools remained stable.

### 3.3  N pools and N dynamics across the precipitation gradient

When comparing the driest and wettest stands, the nitrogen pool in stand leaf biomass was by 23 % larger in the driest stands, despite smaller N pools in the organic layers and mineral soil: beech forests with more than 900 mm had accumulated about 452 mmol $N_t$ m$^{-2}$ in their leaf mass, while those with less than 600 mm yr$^{-1}$ contained 557 mmol m$^{-2}$ (mean of all stands: 537; Table 5). This difference is mostly caused by a similarly high or even larger (and not smaller) stand leaf biomass at the drier sites of the transect (Fig. 3), while the foliar N concentration remained more or less invariant across the precipitation gradient (Fig. 4c). In contrast to fresh leaf biomass, the N pool in fallen leaf litter was more uniform across the 14 stands and not significantly different between high- and low-precipitation sites (mean: 254 mmol N m$^{-2}$). Thus, N resorption efficiency prior to litterfall significantly increased with decreasing summer rainfall in

the beech stands (Fig. 4f). Stands with more than 900 mm of annual rainfall resorbed $\sim 47\%$ of their N stored in live leaf biomass prior to leaf abscission, while in stands with less than 600 mm yr$^{-1}$, approximately 57% were re-translocated. The resorption efficiencies of P and K, in contrast, were not related to precipitation: on average, the investigated beech stands resorbed 29% of leaf P and 59% of leaf K prior to litterfall. The concentrations of P and K in green leaves were significantly higher in drier than wetter stands (0.15 vs. 0.11 % P, 0.74 vs. 0.44 % K).

The $\delta^{15}$N signature of sun-canopy leaves decreased in both study years along the transect from the high- to the low-precipitation stands (Fig. 4c; decrease significant in 2006). The values ranged between −4.5 and −7.5 ‰ in 2005, and between −4.0 and −7.6 ‰ in 2006. Beech trees growing with less than 550 mm of annual precipitation had, on average, by 1.6 and 1.0 ‰ more negative $\delta^{15}$N signatures in their leaf biomass in the years 2005 and 2006, respectively, than trees growing with more than 850 mm yr$^{-1}$.

The amount of summer rainfall had a significant influence on the N / P ratio of sun leaf mass, with a steep decrease from about 44 mol mol$^{-1}$ in the moister stands to 33 mol mol$^{-1}$ in the drier ones (Fig. 4d). Similarly, the N / K ratio decreased from about 14 mol mol$^{-1}$ to 8 mol mol$^{-1}$ in the drier stands. Thus, with a lowering of summer rainfall, green leaves contained relatively more P and K and fewer N in their dry mass.

## 4 Discussion

### 4.1 Dependence of soil acidity and SOM accumulation on precipitation

When important site factors such as geology, atmospheric evaporative demand and vegetation remain constant, higher precipitation may influence soil chemistry and soil nutrient status via several pathways, first through a higher water surplus in the climatic water balance, thereby accelerating the leaching of nutrients with percolating water (Johnson et al., 1998), second through soil moisture effects on soil biological activity

and the decomposition rate of plant litter (Swift et al., 1979; Freckmann, 1986; Aerts, 1997; Liski et al., 2003), and third through effects of water availability on plant productivity and the related nutrient return with litter fall (Aerts, 1997; Cunningham et al., 1999; Aerts and Chapin, 2000; González and Seastedt, 2001). Our study in 14 mature mono-specific *Fagus sylvatica* forests differs from other biogeochemical studies along rainfall gradients by the uniformity of vegetation (no tree species turnover) and geology (Triassic sandstone of Middle Bunter, "Hardegsen Folge" throughout) across all sites, thereby facilitating the separation of precipitation effects from other environmental influences on soil chemical status.

One of the most conspicuous changes along the transect was the substantial decrease in soil acidity with a decrease in precipitation and increase in temperature. Beech stands with $> 950\,\mathrm{mm\,yr^{-1}}$ of annual precipitation had a 90 % higher proton concentration in the mineral topsoil (0–20 cm) than stands with less than $550\,\mathrm{mm\,yr^{-1}}$. Our study indicated an increase by 0.1 pH(KCl) units with a decrease in annual precipitation by $100\,\mathrm{mm\,yr^{-1}}$. With a decrease in annual precipitation from 970 to $520\,\mathrm{mm\,yr^{-1}}$, the climatic water balance showed a surplus that decreased from $480\,\mathrm{mm\,yr^{-1}}$ at the moistest sites to $110\,\mathrm{mm\,yr^{-1}}$ at the driest ones. More percolating water and generally higher soil moisture are favoring the wash out of ions with low bond strength to ion exchangers (such as $K^+$ and $NO_3^-$). The water surplus may also accelerate the chemical weathering of minerals. In a rainfall gradient study on volcanic rock in Hawaii, higher rainfall greatly increased the loss of exchangeably-bound basic cations, thereby increasing soil acidification, while the precipitation effect on nutrient release through weathering was secondary (Austin and Vitousek, 1998).

In our transect, the high-precipitation sites ($> 900\,\mathrm{mm\,yr^{-1}}$) tended to have a lower percent base saturation at the cation exchangers of the mineral soil (about 35 %) and reduced absolute amounts of exchangeable basic cations (Ca, K, Mg) per soil volume ($8.2\,\mathrm{mol\,m^{-2}}$ per 20 cm) than the low-precipitation sites (about 50 %, $10.4\,\mathrm{mol\,m^{-2}}$ $20\,\mathrm{cm^{-1}}$). However, a significant trend over the precipitation gradient did not exist (Table 2).

The precipitation effect on soil acidity and base cation leaching is likely to affect other ecosystem properties as well, which feed back on soil chemistry and nutrient status. Except for sites with high atmospheric nutrient deposition, high precipitation is likely to reduce the plant-availability of Ca, K and Mg directly and thus may change the foliar nutrient concentrations of the trees and consequently litter decomposability. Similarly important could be the water availability effect on decomposition rate and thus the indirect influence on plant nutrient availability. Typically, soils with higher pH and base saturation have higher litter decomposition rates (Reich et al., 2005), as is evident when comparing the fast decomposing mull-type humus forms in beech forests on calcareous soils with the slowly degrading mor humus profiles in acidic beech forests (Ellenberg and Leuschner, 2010).

In our transect study, the amount of organic matter in the L, F, H layers on the forest floor significantly decreased from the high- to the low-precipitation stands indicating a marked increase in decomposition rate, because annual leaf litter mass remained unchanged or even increased (Fig. 2). Most likely, lower litter decomposability at the wetter sites was primarily caused by lowered pH (and partly also by the change in base saturation), but other factors may have been influential as well. First, decomposition rate is influenced by soil moisture itself, but one should expect a stimulation, rather than an inhibition, of decomposition with an increase in precipitation from 520 to 970 mm yr$^{-1}$ in the transect. Thus, a significant precipitation effect on decomposition and organic matter accumulation is unlikely in our study. Second, the quality of beech litter might have changed across the precipitation gradient. While we have no data on leaf litter lignin content, we did not find a significant change in the N concentrations of leaf and fine root litter (root necromass) from lower to higher precipitation. Thus, a litter quality effect seems to be similarly unlikely as is a direct precipitation effect on the decomposition rate.

The build-up of thick organic layers on top of the mineral soil in moister climates has important consequences for tree growth: at the high-precipitation sites, the organic L, F and H layers are the places of most N mineralization activity in the soil profile (Runge,

1974) and they thus contain the bulk of tree fine root biomass (Leuschner et al., 2001) resulting in a very superficial root system of beech with considerable vulnerability to summer drought even at sites with a generally moist climate.

## 4.2 Nitrogen pools and nitrogen cycling across the precipitation gradient

Higher precipitation led to thicker organic L, F, H layers on the forest floor with larger organic $N_t$ pools, but the organic layer C / N ratio showed a slight decrease from the driest to the moistest stand (27 to 25 mol mol$^{-1}$). A decreasing C / N ratio with increasing soil acidity towards the moister sites seems to contradict a fundamental relationship often observed in studies on forest biogeochemistry, i.e., that soils with thicker mor-type organic layers have higher C / N ratios in the organic material than mull-type humus forms (Brumme and Khanna, 2008). However, long-term monitoring of the N stocks of Central European forest soils has revealed that atmospheric deposition of oxidized and reduced nitrogen compounds, which increases with precipitation, most likely has reduced the C / N ratio at the high-precipitation forest sites during the past decades (Meiwes et al., 2002), masking possible trends in soil N availability across this precipitation gradient.

We hypothesized that a climate with drier summers and slightly higher summer temperatures as in the eastern part of the transect imposes drought-induced restrictions on N mineralization in summer, while temperature stimulation of decomposer activity is of minor importance. In accordance, we found markedly lower nitrification and N mineralization activities per soil mass in the drier beech stands (data not shown). This result might be interpreted as support for the N limitation hypothesis of Fotelli et al. (2004) and Geßler et al. (2004) who postulated that beech growth may be significantly limited by N shortage in drier climates. However, N mineralization per ground area (upper 10 cm) remained unchanged along the gradient because the decrease in mass-specific N mineralization rate was counteracted by an increase in soil density (decreasing humus mass) from the wet to the dry sites. Moreover, the release of mineral N per unit total N in the soil (N-specific mineralization rate) did not change from moist to dry

sites. This matches with the unchanged N concentration in fresh sun leaves across the transect, a result contradicting our third hypothesis. Other authors working on precipitation gradients found a more pronounced increase in canopy carbon gain than in N mineralization with increasing precipitation, suggesting that N limitation of plant growth should become increasingly important in moister climates, despite increasing soil N pools (Buamscha et al., 1998); this would contradict the hypothesis of N limitation in drier climates. Our data show a significantly smaller N pool in stand leaf biomass (and a larger in stand fine root biomass) at moist than at dry sites which is due to the smaller stand leaf mass. This result points to preferential N investment of beech into roots under conditions of ample water supply, while leaves were apparently favored in N allocation under drier conditions. Based on the optimal resource partitioning theory, this unexpected result could be interpreted as indication of increasing N deficiency at moist and not at dry sites. However, the total N pool in leaf mass may not be a good indicator of the N supply status which may be better reflected by qualitative shifts in the foliar pool of organic N compounds (Hu et al., 2013). Whether N limitation of beech growth increases or decreases with a reduction in precipitation is also dependent on drought-induced changes in carbon acquisition rate.

The foliar $\delta^{15}$N signature may provide valuable additional information on N availability and N cycling in forest ecosystems. Discrimination against $^{15}$N-labelled nitrogen compounds may occur, for example, under conditions of ample N supply with nitrate uptake (Kohl and Shearer, 1980; Mariotti et al., 1982), with the transfer from mycorrhizal hyphae to the roots (Taylor et al., 2000; Hobbie and Colpaert, 2003), and during nitrate reduction in the plant (Handley and Raven, 1992; Yoneyama et al., 1993). However, it is not clear whether within-plant fractionation does significantly change along precipitation gradients (Craine et al., 2009).

In our transect, $\delta^{15}$N in sun leaf mass was positively correlated with annual precipitation (in one of the two study years, the trend was only marginally significant). In contrast, in several other studies along precipitation gradients and also in global meta-analyses, a decrease of $\delta^{15}$N values from dry to moist environments was reported

for plant dry mass and also for SOM (Evans and Ehleringer, 1993, 1994; Austin and Vitousek, 1998; Schuur and Matson, 2001; Aranibar et al., 2004; Wang et al., 2007; Craine et al., 2009). However, these studies in most cases encompassed much more arid ecosystems than were included in our transect which only covered sites with a positive climatic water balance. In desert ecosystems, N supply through mineralization and plant uptake often occur non-synchronously with the consequence that N losses may be larger than ecosystem turnover (Tamm, 1991; Aranibar et al., 2004; Swap et al., 2004). This reduces the importance of physiological isotope-fractionating processes. Another possible explanation of our deviating $\delta^{15}$N results is that the moister soils were richer in total N and the N cycle likely was more open, which typically would lead to higher $\delta^{15}$N values in plant mass (Craine et al., 2009). Finally, across our precipitation gradient, soils were by trend richer in $NH_4^+$ at the moist end and richer in $NO_3^-$ at the dry end. Since nitrate nutrition typically results in greater discrimination against $^{15}$N, this would offer a possible explanation of the pattern found in our study. However, alternative explanations may also be possible.

In our transect, N resorption efficiency (i.e. the percent of foliar N re-translocated before leaf abscission; cf. Staaf, 1982; Chapin and Kedrowski, 1983) slightly decreased with increasing rainfall indicating that tree-internal N cycling gained in importance towards drier climates, leaving the trees less dependent on soil-borne N sources.

## 4.3 Phosphorus availability across the precipitation gradient

Even more than nitrogen, phosphorus availability for plants is dependent on soil acidity and the amount of organic matter in the soil. Both soil acidity and the amount of organic matter were found to be strongly influenced by precipitation in our transect. Generally, P availability is highest at pH 6–6.5 and decreases toward more acid and more alkaline soils due to pH-dependent salt precipitation processes (Blume et al., 2010). In addition, soil moisture conditions have been found to control the relative pool sizes of the different P fractions either through regulation of organic matter cycling or through the formation and destruction of soil minerals (Sanyal and De Datta, 1991; Schlesinger,

1997; De Mello et al., 1998). In our transect, we did not find a relationship between $P_a$ (resin-bag method) in the mineral soil and annual precipitation indicating that the pH decrease from the drier to the moister sites had no significant influence on P availability. Similarly, there was no relationship between exchangeable potassium in the mineral soil and annual precipitation.

In later stages of soil development with primary minerals depleted, most soil P exists in recalcitrant mineral or organic fractions; thus, ecosystem productivity depends on efficient P cycling between organic matter and organisms (Smeck, 1985; Lajtha and Schlesinger, 1988; Crews et al., 1995; Schlesinger et al., 1998). Even though P (and K) mineralization data do not exist for the 14 stands, we assume that P (and K) release from organic fractions in the thick mor-type organic L, F, H layers of the moist stands is slower than N mineralization since their $N/P$ and $N/K$ ratios are higher. The marked decrease in foliar P concentration (18 vs. $10\,\mathrm{mmol\,m^{-2}}$) and increase in the foliar $N/P$ ratio (33 vs. $44\,\mathrm{mol\,mol^{-1}}$) from the dry to the moist sites supports our assumption that P limitation of plant growth increases rapidly with increasing precipitation. Similarly, foliar K concentration decreased (66 vs. $31\,\mathrm{mmol\,m^{-2}}$) and the $N/K$ ratio increased (8 vs. $14\,\mathrm{mol\,mol^{-1}}$) with increasing precipitation, pointing at associated K limitation of plant growth at moist sites. We found no increase in P or K resorption efficiency from the drier to the moister sites which would represent a possible response of beech to increasing P and K limitation. Miller et al. (2001) demonstrated that, as annual rainfall and reducing conditions increased in Hawaiian montane forest soils, total phosphorus in the soil declined by nearly two thirds, but organically bound P increased and accounted for an increasing fraction of total P. Thus, it appears that the precipitation effect on soil organic matter build up is a key factor regulating the plant availability of P and K across precipitation gradients.

## 5 Conclusions

Provided that other site factors are constant, lowered summer precipitation decreases soil acidity and tends to increase base saturation in beech forest soils with the consequence that decomposer activity is stimulated and the carbon and nutrient pools in forest floor, and partly also in the mineral soil, are reduced. Increased N resorption before litter fall and lower foliar N / P and N / K ratios point to a growing importance of N over P or K limitation of beech growth in the more continental, summer-drier climates of Central Europe. Nevertheless, our data show that summer rainfall reduction by more than 30 % (from c. 430 to c. 270 mm yr$^{-1}$) does not negatively affect the foliar N concentration of mature beech trees, thereby contradicting our third hypothesis. Foliar P and K even increased toward the drier stands. Possible reasons are a higher nitrate availability (likely due to reduced soil leaching) and more effective tree-internal N cycling under drier climates. We conclude that substantial reduction in summer rainfall, as predicted for various parts of Europe in the course of climate change, should primarily affect the carbon gain and/or hydraulic functioning of beech trees, before drought-induced impairment of nutrient supply may harm beech vitality and growth.

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**Table 1.** Topographic, edaphic, and climatic parameters, as well as the $\delta^{13}$C signature of sun leaf biomass in 14 beech stands on Triassic sandstone along a precipitation gradient in central Germany. Mean annual temperature and mean annual or growing season (GS, May–September) precipitation were derived from weather station data that was corrected for altitude. The climatic water balance was calculated using potential evapotranspiration (PET). n/a = not applicable.

| Site # | Altitude [m a.s.l.] | Inclination [°] | Humus form | Organic matter [kg m$^{-2}$] | Soil type | Temperature (annual) [°C] | Temperature (GS) [°C] | Precipitation (annual) [mm yr$^{-1}$] | Precipitation (GS) [mm yr$^{-1}$] | Precipitation (2003–2006) [mm yr$^{-1}$] | Precipitation CV (2003–2006) [%] | Water balance [mm yr$^{-1}$] | $\delta^{13}$C (sun leaves) [‰] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 400 | 9.1 | lm | 3.0 | pU | 7.3 | 13.9 | 970 | 430 | 920 | 13 | 480 | −28.5 |
| 2 | 380 | 4.0 | lm | 6.2 | U-L (p) | 7.4 | 14.0 | 950 | 420 | 900 | 14 | 460 | n/a |
| 3 | 340 | 4.3 | lm | 2.7 | U (p) | 7.7 | 14.2 | 910 | 400 | 860 | 13 | 420 | −27.8 |
| 4 | 250 | 7.4 | lm | 6.2 | L-U (p) | 8.2 | 14.8 | 860 | 410 | 800 | 16 | 370 | −29.4 |
| 5 | 410 | 1.6 | m | 7.6 | L-C | 7.3 | 13.8 | 820 | 400 | 720 | 15 | 330 | n/a |
| 6 | 440 | 6.7 | vm | 2.0 | L | 7.1 | 13.6 | 800 | 370 | 740 | 15 | 310 | −27.7 |
| 7 | 250 | 1.2 | m | 1.9 | C | 8.2 | 14.4 | 680 | 330 | 650 | 13 | 210 | −28.1 |
| 8 | 340 | 9.5 | m | 1.7 | C | 7.7 | 14.8 | 670 | 290 | 620 | 13 | 200 | −27.0 |
| 9 | 320 | 4.3 | vm | 1.7 | L-C | 7.8 | 14.2 | 650 | 300 | 690 | 12 | 190 | −27.9 |
| 10 | 320 | 4.8 | vm | 2.4 | L-C | 7.8 | 14.4 | 580 | 280 | 570 | 15 | 140 | −27.9 |
| 11 | 280 | 2.3 | m | 3.2 | C | 8.0 | 14.6 | 580 | 310 | 550 | 9 | 140 | n/a |
| 12 | 230 | 5.2 | m | 3.4 | C-eL | 8.3 | 14.9 | 550 | 290 | 480 | 7 | 120 | −27.9 |
| 13 | 240 | 3.0 | m | 2.9 | C-L | 8.3 | 14.9 | 550 | 290 | 480 | 7 | 120 | n/a |
| 14 | 280 | 1.3 | m | 3.3 | C | 8.0 | 14.6 | 520 | 270 | 460 | 6 | 110 | −26.7 |

Humus forms according to Green et al. (1993): lm = leptomoder; m = mullmoder; vm = vermimull.
Soil types (WRB): C = Cambisol, e = eutric, L = Leptosol, p = podzolic, U = Umbrisol

.

**Table 2.** Pearson correlation coefficients for relationships between precipitation, soil temperature or forest floor organic matter and 16 edaphic parameters of the organic layers (forest floor) or the mineral soil (0–20 cm depth) of 14 beech forests on Triassic sandstone along the precipitation gradient. Significant correlations ($p \leq 0.05$) are in bold type. GS = growing season. Rates of net nitrification and net N mineralization are for 0–10 cm.

| | | Precipitation (annual) | (GS) | Soil temp. | Org. matter |
|---|---|---|---|---|---|
| **Organic layer** | | | | | |
| Org. matter | [kg m$^{-2}$] | 0.41 | **0.56** | −0.39 | |
| C$_{org}$ | [mol m$^{-2}$] | 0.52 | **0.63** | −0.52 | **0.95** |
| N$_t$ | [mol m$^{-2}$] | 0.52 | **0.63** | −0.54 | **0.94** |
| C / N | [mol mol$^{-1}$] | −0.41 | **-0.55** | **0.67** | −0.53 |
| P$_t$ | [mol m$^{-2}$] | 0.46 | **0.58** | −0.48 | **0.92** |
| C / P | [mol mol$^{-1}$] | 0.52 | 0.52 | −0.37 | 0.44 |
| N / P | [mol mol$^{-1}$] | **0.59** | **0.63** | −0.54 | **0.57** |
| N / K | [mol mol$^{-1}$] | **0.69** | **0.68** | **-0.66** | **0.55** |
| **Mineral soil (0–20 cm)** | | | | | |
| pH | | **-0.69** | **-0.79** | **0.67** | **-0.77** |
| C$_{org}$ | [mol m$^{-2}$] | **0.60** | **0.54** | −0.41 | 0.03 |
| N$_t$ | [mol m$^{-2}$] | 0.44 | 0.30 | −0.30 | −0.46 |
| Net Nitrification | [mg N m$^{-2}$ wk$^{-1}$] | −0.31 | −0.30 | 0.46 | −0.43 |
| Net N Min | [mg N m$^{-2}$ wk$^{-1}$] | −0.08 | −0.02 | −0.02 | −0.04 |
| P$_a$ | [mol m$^{-2}$] | −0.24 | −0.21 | −0.11 | −0.23 |
| K$_{exch}$ | [mol m$^{-2}$] | −0.43 | −0.44 | 0.32 | −0.13 |
| Base saturation | [%] | −0.29 | −0.46 | 0.33 | **-0.58** |

a = plant-available fraction, org = organic fraction, t = total element content.

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**Table 3.** Multiple regression analysis with backward variable elimination on the effects of summer precipitation ($P$), soil temperature ($T$), altitude ($A$), and stem basal area ($BA$) on the amount of organic matter, the organic layer N and P pools, available P, net N mineralization or pH in the mineral soil in the 14 stands. Values given are the determination coefficient $r^2$ and the probability of error $p$ for the model and the $F$ value and probability of error $p$ for the selected predictors. The + or − signs at the predictor variables indicate positive or negative relationships.

| | Model | | | | |
| Y | $r^2$ | $p$ | Predictor | $F$ | $p$ |
| --- | --- | --- | --- | --- | --- |
| Organic matter | 0.31 | 0.05 | $+P$ | 5.0 | 0.05 |
| $N_t$ (org. layer) | 0.39 | 0.02 | $+P$ | 7.1 | 0.02 |
| Net Nitrification | 0.52 | 0.02 | $-A$ | 8.5 | 0.02 |
| Net N Mineralization | | n.s. | | | |
| $P_t$ (org. layer) | 0.33 | 0.04 | $+P$ | 5.5 | 0.04 |
| $P_a$ (min.) | | n.s. | | | |
| pH (min.) | 0.78 | 0.002 | $+T$ | 6.6 | 0.03 |
| | | | $+A$ | 6.5 | 0.03 |
| | | | $-P$ | 6.2 | 0.03 |

**Table 4.** Multiple regression analysis with backward variable elimination on the effects of soil moisture ($M$), soil temperature ($T$), litter N concentration ($N_{Litter}$), and soil ammonium ($NH_4^+$) and nitrate pools ($NO_3^-$) on net nitrification and net N mineralization rate. Values given are the determination coefficient $r^2$ and the probability of error $p$ for the model and the $F$ value and probability of error $p$ for the selected predictors. The + or − signs at the predictor variables indicate positive or negative relationships.

| Y | Model $r^2$ | $p$ | Predictor | $F$ | $p$ |
|---|---|---|---|---|---|
| Net Nitrification | | n.s. | | | |
| Net N Mineralization | 0.72 | 0.02 | $-NH_4^+$ | 15.7 | 0.01 |
| | | | $+M$ | 7.2 | 0.04 |

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**Table 5.** Pools of major plant nutrients and of aluminum in stand leaf biomass (fresh leaves measured in July/August or senesced leaves measured after litter fall), in stand fine root biomass, and in the organic layers and the mineral soil (0–20 cm depth) of beech stands with more than 900 mm yr$^{-1}$ (high precipitation amount) or less than 600 mm yr$^{-1}$ (low precipitation amount) in central Germany. Nitrogen stocks refer to total pools, while phosphorus, base (Ca + Mg + K) and acid (Al + Mn + Fe) cation stocks are given as total pools for leaves, fine roots, and organic matter, or as plant-available pools for the mineral soil. * = significant differences between stands with high and low precipitation amount. n/a = not applicable.

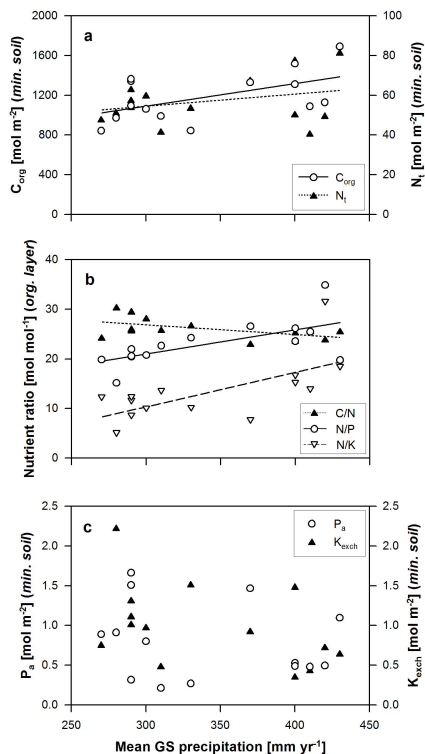| | Precipitation amount | N high | N low | P high | P low | (Ca + Mg + K) high | (Ca + Mg + K) low | (Al + Mn + Fe) high | (Al + Mn + Fe) low |
|---|---|---|---|---|---|---|---|---|---|
| Leaves (mmol m$^{-2}$) | fresh | 452 | 557* | 10 | 18* | 97 | 152* | 5 | 9* |
| | senescent | 279 | 250 | 12 | 10 | 124 | 138 | n/a | n/a |
| Fine roots (mmol m$^{-2}$) | live | 305* | 151 | 15 | 18 | 48* | 34 | 18 | 20 |
| | dead | 246 | 187 | 13 | 38 | 62 | 56 | 53 | 55 |
| Organic layers (mol m$^{-2}$) | | 5.6* | 2.5 | 0.2* | 0.1 | 0.8 | 0.8 | 1.0 | 1.3* |
| Min. soil (0–20 cm) (mol m$^{-2}$) | | 70.3* | 50.8 | 0.7 | 1.0 | 8.2 | 10.4 | 12.1 | 9.5 |

**Fig. 1.** Relationships between mean growing season (GS; May–September) precipitation and **(a)** organic carbon and total nitrogen content in the mineral soil (0–20 cm), **(b)** the C / N, N / P and N / K ratios in the organic layers, and **(c)** plant-available P and exchangeable K contents (0–20 cm mineral soil) in 14 beech forests on Triassic sandstone along the precipitation gradient in central Germany (mean of $n = 5$ soil samples per study site; net N min: $r^2 = 0.75$, $p < 0.001$; net nitrification: $r^2 = 0.46$, $p = 0.02$; $P_a$: $r^2 = 0.04$, $p = 0.24$; $K_{exch}$: $r^2 = 0.19$, $p = 0.06$; $C_{org}$: $r^2 = 0.29$, $p = 0.02$; $N_t$: $r^2 = 0.09$, $p = 0.15$; C / N: $r^2 = 0.30$, $p = 0.02$; N / P: $r^2 = 0.40$, $p = 0.01$; N / K: $r^2 = 0.43$, $p = 0.01$).
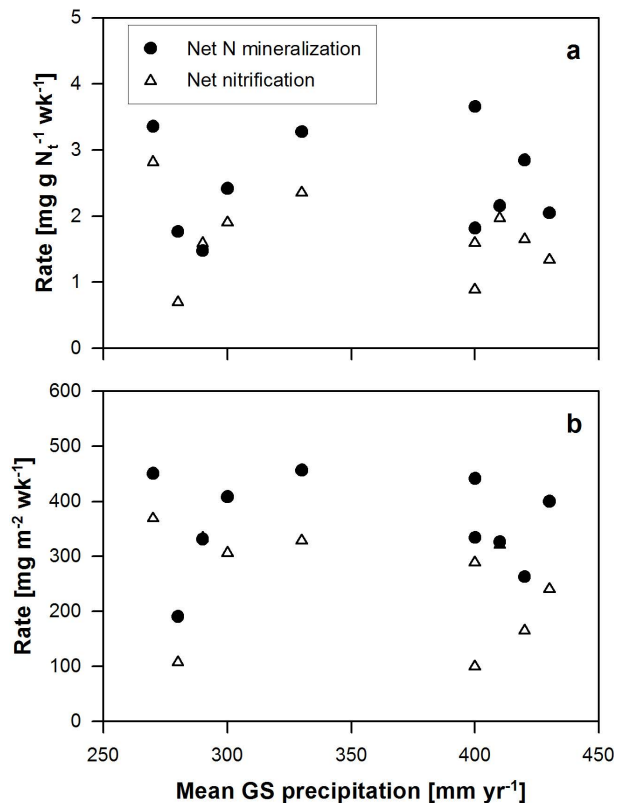
**Fig. 2.** Relationships between mean growing season (GS) precipitation and **(a)** N-pool-related net N mineralization and net nitrification rates and **(b)** ground area-related net N mineralization and net nitrification rates in the topsoil (upper 10 cm) in 10 beech forests on Triassic sandstone along the precipitation gradient in central Germany (mean of $n = 8$ soil samples per study site; net N min (per N): $r^2 = 0.003$, $p = 0.44$; net nitrification (per N): $r^2 = 0.07$, $p = 0.23$; net N min (per area): $r^2 < 0.001$, $p = 0.48$; net nitrification (per area): $r^2 = 0.09$, $p = 0.20$).

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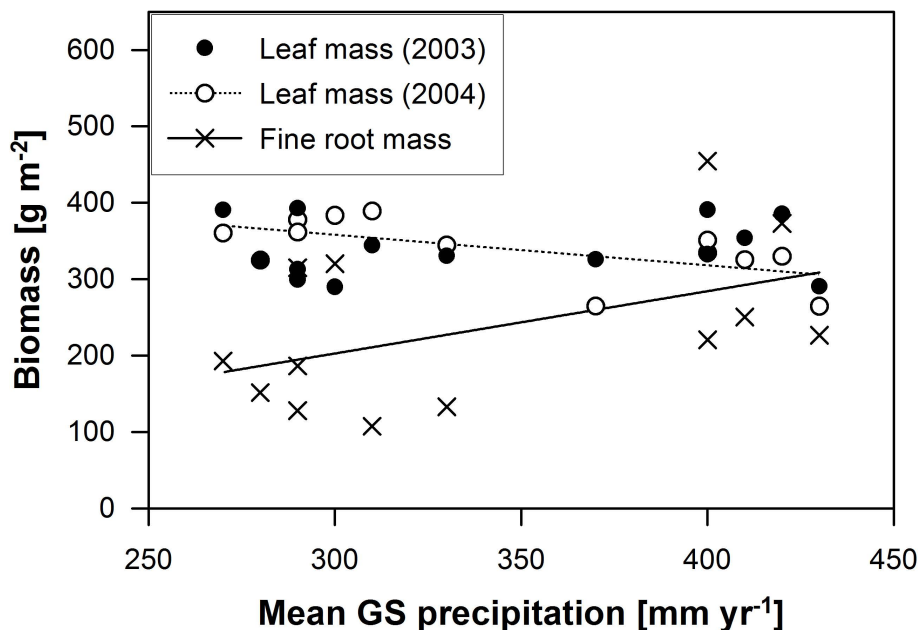Printer-friendly Version

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**Fig. 3.** Relationships between mean growing season (GS) precipitation and stand leaf mass or fine root biomass in the organic layers and mineral soil to 20 cm depth (FRB) in 14 beech stands along a precipitation gradient in central Germany (leaf mass: $n = 10$ buckets per site; 2003: $r^2 = 0.01$, $p = 0.38$; 2004: $r^2 = 0.37$, $p = 0.01$; FRB: $n = 12$ profiles per site; $r^2 = 0.23$, $p < 0.05$; leaf mass data according to Meier and Leuschner, 2008a, data for fine root mass according to Meier and Leuschner, 2008b).
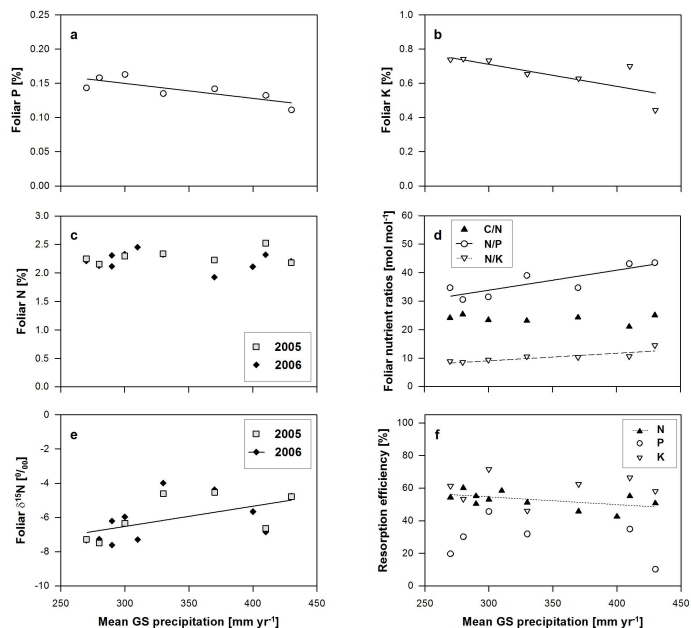
**Fig. 4.** Relationships between mean growing season (GS) precipitation and **(a)** foliar P concentration, **(b)** foliar K concentration, **(c)** foliar N concentration, **(d)** foliar C / N, N / P and N / K ratios, **(e)** $\delta^{15}$N signature in living sun leaves, and **(f)** nutrient resorption efficiencies before leaf litterfall in beech forests on Triassic sandstone along a precipitation gradient in central Germany (P: $r^2 = 0.65$, $p = 0.01$; K: $r^2 = 0.59$, $p = 0.02$; N (2005): $r^2 = 0.10$, $p = 0.25$; N (2006): $r^2 = 0.03$, $p = 0.30$; C / N ratio: $r^2 = 0.09$, $p = 0.72$; N / P ratio: $r^2 = 0.72$, $p = 0.01$; N / K ratio: $r^2 = 0.72$, $p = 0.01$; $\delta^{15}$N signature (2005): $r^2 = 0.22$, $p = 0.17$; $\delta^{15}$N signature (2006): $r^2 = 0.28$, $p < 0.05$; N resorption: $r^2 = 0.28$, $p = 0.04$; P resorption: $r^2 = 0.11$, $p = 0.24$; K resorption: $r^2 = 0.01$, $p = 0.41$; data for 2006 according to Fritz, unpubl.). $n = 7$ sites in 2005, 11 sites in 2006.

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