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Cycling and retention of nitrogen in European beech (Fagus sylvatica L.) ecosystems under elevated fructification frequency

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Abstract. Atmospheric deposition of nitrogen (N) has exceeded its demand for plant increment in forest ecosystems in Germany. High N inputs increased plant growth, the internal N cycling within the ecosystem, the retention of N in soil~~s~~ and plant compartments, and the N output by seepage water. But the processes involved are not fully understood, ~~especially~~notably the ~~role~~effect of fructification ~~which~~in European beech (*Fagus sylvatica* L.) on N fluxes. The frequency of fructification has increased ~~in~~together with air temperature and N deposition but its ~~frequency.~~impact on N fluxes and the sequestration of C and N in soils was hardly studied. A field experiment using ^{15}N labelled leaf litter exchange was carried out over a 5.5 years~~'~~ period at seven long-term monitoring on European beech (*Fagus sylvatica* L.) sites~~ with European beech (Fagus sylvatica L.) ecosystems~~ to study the impact of current mast frequency on N cycling. Mean annual leaf litterfall contained 35 kg N ha^{-1}, but about one half of that was recovered in the soil 5.5 years after the establishment of the leaf litter ^{15}N exchange experiment. ~~Retention of leaf litter N in the soil was more closely related to the production of total litterfall than to the leaf litterfall indicating the role of fructification of beech trees in the amount of leaf N retained in the soil.~~ In these forests, fructification occurred commonly ~~in~~at intervals of 5 to 10 years, which has now changed to every two~~ to three~~ years as observed during this study period. Seed cupules contributed 51 % to the additional litterfall in mast years which ~~caused~~put a high nutrient demand during their decomposition due to the~~ir~~ very high carbon (C) to N and C to phosphorus (P) ratios. Retention of leaf litter ^{15}N in the soil was more closely related to the production of total litterfall than to the leaf litterfall, indicating the role of seed cupules in the amount of leaf N retained in the soil. Higher mast frequency increased the mass of mean annual litterfall by about 0.5 Mg ha^{-1} and of litterfall N by 8.7 kg ha^{-1}. Mean net primary production (NPP) increased by about 4 %. Mean total N retention in soils calculated by input and output fluxes was unrelated to total litterfall indicating that mast events were not the primary factor controlling total N retention in soils. Despite reduced N deposition since the 1990s about 5.7 kg N ha^{-1} out of 20.7 kg N ha^{-1} deposited annually between 1994 and 2008, were retained in soils notably at acid sites with high N/P and C/P ratios in the organic layers and mineral soils~~. Ongoing N retention increased the N/P ratios in acid soils with moder type humus forms and reduced the availability of P for plant growth and~~, indicating P limitation for litter decomposition. Trees retained twice as much N compared to soils by biomass increment particularly in less acid stands where the mineral soils had low C/N ratios. These results have major implications for our understanding of the C and N cycling and N retention in forest ecosystems. Especially the role of mast products for N retention needs more research in the future.

1 Introduction

Nitrogen (N) ~~is~~was commonly a limiting nutrient in the pristine temperate forests. However, several decades of elevated atmospheric deposition of N and acidity ~~have~~ changed biogeochemical N cycles in temperate forest ecosystems in large regions of the northern hemisphere. ~~Acid deposition~~Atmospheric depositions decreased soil pH (Hallbäcken and Tamm, 1986) and affected the N cycling through reduced ~~litter~~ decomposition ~~(~~across a wide range of forest ecosystems (Persson and Wirén, 1993; Janssens et al., 2010). Carbon (C)/N ratios in the organic layers were reduced, and C sequestration in forest soils increased (De Vries et al., 2006; Hyvönen et al., 2008; Meiwes et al., 2009). High atmospheric deposition of N ~~has~~ removed N deficiency in forests ecosystems (LeBauer and Treseder, 2008~~) and~~), increased foliar N contents ~~but has~~and reduced the contents of foliar phosphorus (P) (Braun et al., 2010; Talkner et al., 2015). Probably in combination with high inputs of base cations (Meesenburg et al., 2009), N deposition accelerated forest growth to a certain degree (~~de~~De Vries et al., 2014; Etzold et al., 2020). ~~Carbon (C)/N ratios in the organic layers have been~~Despite reduced~~, and C sequestration in forest soils has been increased (de Vries~~ sulphur emission since the beginning of the 1980s (Engardt et al., ~~2006; Hyvönen~~2017) N deposition still exceeds the N demand for forest growth in unmanaged and most managed forests (Meesenburg et al., ~~2008; Meiwes~~2016; Fleck et al., 20~~0~~19).

Leaf litterfall plays a key role in the internal N cycle of temperate beech forests by adding a large amount of rapidly mineralisable N annually to the soil (Meier et al., 2005; Neumann et al., 2018). However, the amount of N transferred to the soil with total litterfall is regulated to a large extent by the amount and frequency of fructification (Khanna et al., 2009). There is an increasing evidence that the frequency of fructification in beech forests has increased when compared to that in the past decades~~.~~: It was well known from the older literature that the fruiting of beech trees was periodic and the heavy fructification happened once every 5 to 10 years in the past. For example, Hase (1964) calculated the return of a full-mast every 10 years and of a half- and full-mast every 5 years over 240 years of mast protocols (1721 – 1960) in Schleswig-Holstein, Germany. Mast protocols were used to calculate the number of hogs allowed to drive into the forests, which was economically important until the 1930s. Övergaard et al. (2007) calculated by using literature data from the end of the seventeenth century up to the 1960s that ~~a~~ mast ~~occurred~~frequency in Sweden was every 4 to 6 years~~ in Sweden~~. A review by Wachter (1964), and extended by Paar et al. (2011), summarized the observations of mast events between 1839 and 1987 in Germany and calculated a recurrence interval of heavy fructification (full-mast and half-mast) of 4.7 years. When comparing older studies, it should be ~~considered~~mentioned that the definition of a mast year was not based on uniform protocols in the past.

The classification of fructification in full-, half-, “spreng”-mast (sprinkle amount) and missing mast are based on litter trap measurements during the ~~most recent~~last three decades ~~and~~which allowed ~~the~~a better quantification of mast events. According to the classification given by Burschel (1966), which is based on the numbers of seeds in litterfall, a full-mast has more than 150 seeds per m^2, half-mast 100 – 150 seeds, and “spreng”-mast 50 – 100 seeds. Based on this protocol, Paar et al. (2011) calculated that full-masts occurred every 2.6 years during 1988 and 2010 in 10 monitoring plots in Hesse and Lower Saxony, Germany. A similar mast interval was reported for 1981 to 2004 period by Schmidt (2006) and Khanna et al. (2009) and for 2000 to 2012 by Reil et al. (2015) for beech sites in ~~the same area in~~ Germany. For southern Sweden, a mast interval of 2.5 years was reported by Övergaard et al. (2007) for the period between 1974 and 2006, which was based on a threshold value of 50 seeds per m^2 for a mast year. A fruit-bearing cycle with a two-year return period appeared in 20 European beech stands from 1994 to 2007 in France which was based on collecting leaves and nuts in litter traps (Lebourgeois et al., 2018).

Differences in summer temperature between the two years preceding mast may affect the ~~amount of~~ fruit produc~~ed~~tion (Kelly et al., 2013; Vacchiano et al~~.~~., 2017; Lebourgeois et al., 2018; Nussbaumer et al., 2018). Mund et al. (2020) reported that a positive effect of summer precipitation two years prior to fruit production was observed at a beech forest in Thuringia, Germany. ~~A detailed analysis~~A requirement for mast production is the availability of N because nuts are rich in N (Bogdziewicz et al., 2017). The demand for N in the mast years was doubled that of ~~litterfall at three~~ non-mast years in beech forests in Germany ~~between 1991 and 2003 indicated a higher N transfer to the soil organic layer during mast years as compared to years without mast~~ (Khanna et al., 2009). High N concentrations in leaves of beech trees are not related to the soil fertility in different parent materials (Meier et al., 2005), and the frequent fruitification in large areas of Europe (Nussbaumer et al., 2016) point to a high N availability in these forests after several decades of high N deposition (Galloway et al., 2008). Several studies focused on the role of litter quality on N fluxes and N retention in forest ecosystems (e.g. Berg and McClaugherty, 2020). To what extend a higher mast frequency ~~was involved in the observed accumulation of nitrogen in the~~changes soil ~~was not~~biota, decomposition processes, N fluxes and N retention in forest soils, has been hardly studied.

The objective of our study was to determine the influence of a high frequency of fructification on ~~the~~ N fluxes in European beech ecosystems (*Fagus sylvatica* L.). ~~Results of~~To achieve this objective, we used seven European beech stands of Level II sites, where a number of input-output N fluxes and internal N fluxes were monitored for 15 years to assess the effect of mast production on N fluxes. In addition to the standard regular monitoring programme we carried out a ^{15}N labelled leaf litter exchange experiment ~~on~~at these sites to study the retention of leaf litter N in the soil ~~at seven long-term monitoring beech sites have been included. On these sites a number of fluxes were monitored for 15 years to assess the effects of dry mass and N fluxes on leaf litter ^{15}N retention in~~under the ~~soil. In addition, site, stand~~different frequencies of fructification and ~~soil specific factors were studied, which potentially influenced litterfall, N retention by trees and in the soil, and N output with seepage water~~site conditions.

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2 Material and Methods

2.1 Study sites

Seven long-term monitoring sites with European beech (*Fagus sylvatica* L.) as the dominant deciduous tree species in Germany were selected for the study. The study sites are Level II plots of the ICP Forests Intensive Monitoring ~~Program (De Vries et al. 2003). Three~~Programme established under the UNECE Convention on Long-Range Transboundary Air Pollution (De Vries et al., 2003a). The Level II Intensive Forest Monitoring is carried out at about 800 selected forest ecosystems representative of the major European forest types with the aim to study the relationships between stress factors such as air pollution and forest ecosystem responses. The Level I monitoring is based on a systematic 16 x 16 km grid and covers around 6000 plots, where annual crown condition assessments are carried out. So far, two forest soil condition surveys were conducted from 1985 to 1996 and 2004 to 2008, respectively (Cools and de Vos 2011).

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Three of our sites are located in Bavaria at Bad Brückenau (BBR, Level II plot 903), Freising (FRE, 919), and Ebrach (EBR, 907), two sites in Lower Saxony at Solling (SOB, 304), and Göttinger Wald (GW, 306), ~~and~~ one site ~~each~~ in Hesse at Homberg (HOM, 607), and three sites in Rhineland-Palatinate, one at Neuhäusel (NHB, 704~~).~~) and two other sites (Kirchheimbolanden, KHB, and Neuhäusel Quarz, NHQ). KHB and NHQ were evaluated with respect to the litterfall fractions in order to disentangle the different properties of seeds and seed cupules (Table 4). The plots are located at 375 to 850 m above sea level (Table 1). The slope of the sites ranges from almost flat to a maximum inclination of 7.4°. Mean temperature ranged from 6.0 to 8.3°C and mean annual precipitation from 712 to 1209 mm. Soil pH (H_2O) in 0~~-~~ – 10 cm depth ranged from 3.6 to 6.1. ~~Forest floor~~The organic layers on these sites varied from mull type humus with 4 Mg C ha^{-1} to moder type humus with 34 Mg C ha^{-1} (Table 2). Clay content in 0~~-~~ – 10 cm soil depth ranged from 12 – 40 % and sand content from 3 – 39 %. Detailed information on soil properties can be ~~found~~obtained in Fleck et al. (2016). All forest sites are stocked with mature beech stands with mean stand ages of 94 to 163 years (2010) and stand densities of 140 to 452 trees ha^{-1}.

2.2 Methods

2.2.1 Measurements and calculations of ~~nitrogen~~N fluxes

Changes of the soil N pools (ΔN_S) were calculated for managed forests with a closed N cycling between plants and soil by input and output fluxes as follows (all values given in kg ha^{-1} yr^{-1}):

$$\Delta \cancel{S} N_S = N_D + N_F - N_L - N_E - N_U; \quad (1)$$

where N_D is the total N deposition ~~with atmospheric deposition, NF the N input~~ from the atmosphere~~-~~, N_F the N input by biological fixation, N_L the seepage ~~N~~ output of N below the root zone, N_E the net gaseous N exchange, and N_U the net N uptake for tree increment.

We are aware that there is a high degree of uncertainty associated with the estimates of N inputs and outputs for the N balance (e.g. Ahrends et al., 2020, De Vries et al., 2003b). However the N balance is a useful tool for determining small changes in soil N pools and is much more sensitive than the repeated soil inventories (De Vries et al., 2006; Brumme et al., 2008; Fleck et al., 2019).

The terms in equation (1) were quantified as follows for the period from 1994 to 2008 ~~as follows~~:

Total N deposition (N_D) was calculated from open-field deposition, throughfall deposition and stemflow inputs by using a canopy budget model as described by Ulrich (1994). Sampling design was very similar for all sites. Precipitation was sampled with funnel-flask samplers, 3~~-~~ - 6 samplers were used for open-field and 15 for throughfall deposition (Clarke et al., 2016). At the Bavarian sites throughfall samplers were reduced to ~~5 replicates~~five samplers in winter times. Stemflow was sampled by fixing polyurethane spirals around the stems, which were coated with paraffin. At each site 3 to 10 ~~replicates~~trees were ~~installed~~selected for stemflow measurement. Seepage N output (N_L) was estimated by multiplication of soil solution concentration and seepage water flux which was obtained by using a hydrological model. Soil solution was collected with suction cups (tension lysimeters, 2 to 9 ~~replicates~~collectors at each site) at 90 or 100 cm depth of the mineral soil (Nieminen et al., 2016). At the BBR site, lysimeters were installed at 60 cm soil depth due to the shallow nature of the soil, and at EBR and FRE sites they were installed at 120 cm and 140 cm depths, respectively. Soil solution and precipitation samples were collected weekly or fortnightly (at Bavarian sites a 3-week interval was used), and were pooled to monthly samples for chemical analysis. Analytical methods as described by König et al. (2009) and UNECE ICP Forests (2016) were followed.

The water budget model LWF-Brook90 (Version 3.4; Hammel and Kennel, 2001) was used to simulate soil water fluxes for all study sites except NHB site, for which the CoupModel (Jansson and Karlberg, 2004) was applied. Both models demonstrated their potential in simulating unsaturated soil water fluxes using the Richard's equation in many studies (Panferov et al~~.~~., 2009; Baumgarten et al~~.~~., 2014; Thiele et al~~.~~., 2017; Schmidt-Walter et al~~.~~., 2019). Due to a better fit between observed and modelled matrix potentials with CoupModel, we decided to choose the water fluxes from this model for the NHB site (Karl et al~~. 2012).~~., 2012). With regard to the maximum slope inclination and the estimated infiltration capacities, we assumed that N losses from the plots through surface runoff are of subordinate importance. Due to permanently formed macropores and low bulk density providing complete infiltration of precipitation surface runoff is generally rare in forest ecosystems (Jankiewicz et al., 2005; Neary et al., 2009). Meteorological data (precipitation, air temperature, humidity, global radiation, and wind speed) were obtained from observations at the respective sites (Raspe et al., 2013) or regionalized from climate stations of the German Weather Service. For more methodical details and evaluation of model performance of regionalized climate data see Ahrends et al. (2018).

The stand characteristics (e.g. stem diameter at 1.3 m DBH; tree height; number of trees) were obtained for all trees with a DBH > 7 cm by using forest inventories which were repeated at least every ~~5~~five years during the observation period and involved standardized silvicultural methods (Dobbertin and Neumann, 2016). We calculated the net N uptake for the aboveground tree increment (N_U) by multiplying the actual growth increment for each plant compartment (solid timber over

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bark above 7 cm diameter) with the content of nutrients in the respective compartment assuming that woody biomass is completely exported from the sites. Where site-specific N contents of tree compartments were missing, data from Jacobsen et al. (2003) were used. Biomass growth of each tree compartment was calculated as the sum of increment of standing trees between two forest inventory's plus biomass losses due to logging. The biomass at each site and inventory was calculated from tree diameter, tree height and number of standing and harvested trees using allometric biomass functions (e.g. Wutzler et al., 2008).

Net Primary Production (NPP) was estimated as a sum of annual biomass increase in wood and bark and total litterfall.

Net gaseous N exchange (NE) were ~~observed~~measured with the closed chamber technique at three of the seven sites (Brumme and Borken, 2009; Eickenscheidt and Brumme, 2013). The SOB site was one of the few sites in Germany where high seas~~onnu~~onal N_2O emissions (1.92 ± 0.63 kg N ha^{-1} yr^{-1} Brumme and Borken, 2009) were observed. GW site had low N_2O emissions (0.16 ± 0.002 kg N ha^{-1}) and NHB site showed negative N_2O emissions (-0.10 kg N ha^{-1}, Eickenscheidt and Brumme, 2013). Annual NO_x fluxes were also low at NHB (0.34 kg N ha^{-1}) and SOB (0.07 kg N ha^{-1}) sites (Eickenscheidt and Brumme, 2013). Mean annual emission of N_2O from deciduous forests with background emissions in Germany of 0.37 kg N ha^{-1} were estimated by Schulte-Bisping et al. (2003). We assume that annual gaseous N output of N_2O and NO_x from deciduous forests with background emissions of 0.58 kg N ha^{-1} (0.37 + (0.34 + 0.07)/2) equals ~~biological N fixation~~N_F (Posch et al., 2015). Thus net gaseous N ~~exchange~~emission (N_E-N_F) is assumed to be negligible for all sites except at the SOB site where high seasonal N_2O emissions were observed. For this site the annual emission of N_2O and NO_x equals 1.99 kg N ha^{-1} and after correcting for ~~N fixation~~N_F a value of 1.41 kg N ha^{-1} (1.99 – 0.58 kg ha^{-1}) was used for net gaseous N emission.

Litterfall was collected from 1995 – 2005 at the site NHB in Rhineland-Palatinate, from 1995 - 2008 at Lower Saxonian sites, from 1998-2008 at sites in Bavaria, and from 1997 - 2008 at the Hessian site ~~and included leaf litter, seeds, seed cupules, twigs and residual~~. Leaf litter included all tree species; in most cases it was beech only (Table 1). Eight to 12 litter traps, each with a surface area of 0.25 to 2 m^2, were used (Ukonmaanaho et al., 2016). Litter was sorted differently at the different sites. At Lower Saxonian and Hessian sites, litterfall was separated in leaf litter, seeds and a residual fraction which consists of cupules, twigs and other small pieces. At Bavarian sites, litter was separated into ~~3~~three fractions, namely leaves, fruit components (seeds + cupules), and twigs. A residual fraction was included in the fruit fraction. At the stand NHB in Rhineland-Palatinate, and two other ~~forest sites~~stands with European beech, ~~Kirchheimbolanden~~ KHB and ~~Neuhäusel Quarz~~ NHQ, ~~a~~ detailed fractionations and analyses of leaves, seeds, seed cupules, twigs, and residual of small pieces were conducted.

The numbers of seeds were used to distinguish fructification intensity according to Burschel (1966). Years with more than 150 seeds per m^2 were classified as a mast year and those with 100 to 150 seeds as a half-mast. The numbers of seeds were only available for the sites in Rhineland-Palatinate. For the ~~other~~Hessian and Lower Saxonian study sites we calculated the number of seeds from the measured dry weight (g DW m² $year^{-1}$) of annual seed litterfall flux by assuming a one single seed weight of 0.22 g~~. The seed~~ (cv = 13%). This weight was determined by using a subsample of 300 ~~seeds which~~seed from these sites. The calculated value showed a good agreement with other studies (Kaliniewicz et al., 2015; Bezdeckova and Matejka 2015). For Bavarian sites the seed mass was calculated by using a mean ratio between seeds and the sum of seeds + seed cupules of 0.14 for years without mast (n = 22), and a ratio of 0.37 (n = 11) for mast years. These ratios were derived from Rhineland-Palatinate (NHN, KHB, and NHQ sites) where the mass of seeds and cupules were separately measured between 1995 and 2005.

Foliar analyses were performed annually to characterize tree nutrition. Samples from ~~6~~six to 18 beech trees were taken from the light-exposed crown during full foliation and analysed for all major nutrients (Rautio et al., 2016). In order to characterize soil nutrient availability and acid-base status, soil samples were collected about every 10 years at the monitoring sites. Procedures of soil sampling, transport, and storage as well as analytical methods were adapted from Cools and De Vos (2016).

2.2.1 ^{15}N-labelled leaf litter exchange experiment

The ^{15}N-labelled litter exchange experiment was established in May 2006 at the study sites. Leaf litter from the beech forests was exchanged by ^{15}N labelled litter (1.3 - 6.9 ~~atom~~% ^{15}N~~)~~), collected from beech trees grown in a greenhouse ~~which~~that received ^{15}N enriched solution in the irrigation water. PVC rings (diameter of 26.6 cm) were ~~inserted~~fixed at the soil surface~~.~~ to create the plots. After removing the loose L litter inside each ring, it was replaced with 17 g of ^{15}N-labelled litter~~ at each ring~~. A wire netting was used to keep the leaves in the PVC rings until the following litterfall. At the end of the exposure ~~the~~5.5 years after the start of the experiment in November 2011 the number of PVC rings sampled were: two at the BBR and HOM sites, four at the EBR, FRE and GW sites, five at the NHB and SOB sites. The litter layers were collected separately from each PVC ring (L layer sample). Soil samples were taken from inside the PVC ring using a stainless steel tube (diameter 8 cm) down to 20 cm depth and a soil corer (diameter 2 cm) from 20 to 40 cm soil depth. Soil columns were ~~cut~~divided into ~~slices~~layers of 1 to 10 cm thickness. Individual samples from each site were mixed for each soil layer. Additional soil samples were taken at the sites for all depth to determine the natural ^{15}N abundance of N ($^{15}N_{na}$). All soil samples were sieved to ~~2~~two mm, gr~~i~~ound~~ed~~, and analysed for total N, total C and ^{15}N with an Element Analyser coupled with an IRMS (Isotopic Ratio Mass Spectrometer, Finnigan MAT, Bremen, Germany) at KOSI Laboratory, Göttingen.

Nitrogen consist of two stable atoms, ^{14}N (99,634 %) and ^{15}N (0,366 %). During N transformation processes, the ratio $^{14}N/^{15}N$ may change due to isotopic discrimination. For an accurate estimation of the recovery of added ^{15}N in labelling experiments, $^{15}N_{na}$ is needed. The $^{15}N_{na}$ of the samples of the sites ranged from 0.365 % in the L layer to 0.368 % in 30 – 40 cm soil. The recovery of the added ^{15}N in a labelling experiment $^{15}N_{ex}$ (%) is calculated by subtracting $^{15}N_{na}$ from the measured enrichment of $^{15}N_S$ in the samples ($^{15}N_{ex} = {}^{15}N_S - {}^{15}N_{na}$ (%)).

~~The ^{15}N-labelled litter exchange experiment was established in May 2006 at the study sites. The soils were sampled in November 2011 (5.5 years after the start of the experiment). Numbers of PVC rings sampled were: two at BBR and HOM, four at EBR, FRE and GW, five at NHB, and SOB sites. Individual samples from each site were mixed for each soil layer. Additional soil samples were taken at the sites to determine the natural abundance of ^{15}N to calculate the excess of ^{15}N ($^{15}N_{excess}$) over the natural abundance in the samples. ^{15}N natural abundance ranged from 0.365 atom% ^{15}N in the L layer to 0.368 atom% ^{15}N in 30 – 40 cm soil.~~

2.3 ~~Data~~Statistical analysis

The relationships between two variables were tested by using Spearman correlation coefficients (r_{Spear}) because this measure makes no assumption about the distribution of the variables and the linearity of the relations (Rhodes et al., 2009). For graphical presentation of the relationship between recovery of leaf litter N and some variables (e.g. litterfall) linear regression functions were calculated. In order to confirm the results ~~from~~of linear regression analyses, which are assumed to be quite uncertain ~~given~~due to the small sample sizes, ~~additionally~~ r_{Spear} values were calculated as well. In addition, the coefficient of variation (cv %) was estimated as ratio of standard deviation and arithmetic mean. All statistical analyses were performed using R version 3.5.2 (R Development Core Team, 2017).

~~2.4 Declaration~~

~~The field studies did not involve endangered or protected species and no specific permission was required for these locations/activities.~~

3 Results

3.1 Biomass production, foliar nutri~~tio~~ents, and ~~N cycling~~litterfall

~~Annual~~Mean annual aboveground net primary production (NPP) of the seven sites amounted to 11.8 Mg dry mass ha^{-1} (cv 25 %) out of which 57 % was contributed by tree increment and 43 % by total litterfall (Table 3). Tree N increment showed a negative correlation with the C/N ratio of the mineral soil (0 – 10 cm) (r_{Spear} = -0.82, $p < 0.05$) (Fig. 5). Mean annual leaf litterfall of the stands ~~ranged from 2.76 to~~ was 3.~~88~~12 Mg ha^{-1} (cv 13 %) and contributed 61 % to the mean annual total litterfall of 5.11 Mg ha^{-1}~~.~~ (cv 11%). Leaf litterfall was closely related to tree increment and total litterfall (Table ~~7~~6; Fig. 5). The recurrence interval of mast production was 2.0 years if half-masts were included. Years with a full-mast occurred once every 2.7 years. Particularly in the years 2000, 2002, 2004, and 2006 full- ~~plus~~and half-mast was synchronous in almost ~~each~~every stand (Fig. 1). No mast event occurred in 1996, 1997, 2005 and 2008. Mast frequency was highest at the FRE and EBR sites~~, the highest~~. The biggest increase in total litterfall due to mast ~~was~~occurred at the HOM site (+101 %). In the mast years mean annual litter production increased by 2.01 Mg ha^{-1} to an average of 6.1 Mg ha^{-1} (cv 15 %) when compared to the non-mast years. The difference in the amount of total litterfall between years with and without mast ~~is a~~was the result of seed and seed cupule production as well as of the changes in other fractions induced by fructification. ~~Mean~~The mean changes in the leaf fraction was +1.3 % (Table 3). Detailed fractionation and analysis of leaves, seeds, seed cupules, twigs, and residual of small pieces at three sites in Rhineland-Palatinate ~~revealed~~indicated a change of +3.3 % in the leaf fraction, +11 % in the twig fraction, and a ~~very high~~big change of +32 % in the residual fraction ~~indicates~~pointing to an increase in the production of ~~components like pollen and flowers~~small pieces in the mast (Table 4).

The mean annual N flux with total litterfall amounted to 58.6 kg ha^{-1} ~~from~~(cv 8 %) of which 34.6 kg ha^{-1} (cv 10 %) were contributed by leaf litter (Table 3). In mast years total litterfall N increased to 74.2 kg ha^{-1} in contrast to leaf litterfall, which contributed almost the same amount of N (36.3 kg ha^{-1}). Mast increased the total litterfall N by 32.4 kg ha^{-1} when~~ mast years were~~ compared with non-mast years. In a similar way as dry mass, mean annual N fluxes with leaf, twig and residual fractions increased by 11 – 11~~,~~.7 %, 14 %, and 49 %, respectively, in the mast years (Table 3, 4).

Dry mass of seed cupules was twice that of seeds for an observation period of 11 years (Table 4). Despite a higher mass of seed cupules, fluxes of N, P and sulfur (S) with seed cupules were low. Due to their low N content, seed cupules contributed only 2 kg ha^{-1} yr^{-1} of N to total litterfall when compared with seeds (8 kg N ha^{-1} yr^{-1}). The low N content of seed cupules resulted in very high mean C/N ratio of 144 when compared to a mean C/N ratio of 19 in seeds. Seed cupules had also very high C/P and C/S ratios.

~~Foliar~~On all the study sites foliar N concentrations of beech trees were similar~~ on all study sites~~, whereas P concentrations differed (Table 2). Beech stands on unconsolidated sandy substrates, limestone, and pumice stone (Table 1) with low soil P contents showed lower foliar P and higher foliar N/P ratios than ~~stands~~those on basaltic rock or loess.

3.2 Recovery of ^{15}N labelled leaf litter ~~exchange experiment~~N in the soil

The highest enrichment of ~~$^{15}N_{excess}$~~the added ^{15}N labelled leaf litter in the soil profiles of seven beech forests after 5.5 years of litter exchange was found in 2 - 4 cm depth of the organic layers in soils with moder type humus (BBR, NHB, SOB) and in 3 - 10 cm in the mineral soils with mull type humus (FRE, EBR, GW, HOM) (~~Table 5~~Fig. 2). In the 0 to 1 cm and 30 to 40 cm layers the enrichment was lower than 1 %. No ~~$^{15}N_{excess}$~~labelled ^{15}N was found in the L layers except at the HOM site. The recovery of ~~$^{15}N_{excess}$~~labelled ^{15}N ranged from 32 to 72 % in the upper 40 cm depth of the soils (mean value 48 % ± 5 %). This equals to an average recovery of leaf litter N of 17 kg ~~N~~ ha^{-1} after 5.5 years, ~~estimated by using~~about half of the ~~percentage ^{15}N recovery X~~mean annual leaf ~~litter N flux. Recovery in the organic layer increased with increasing carbon stock in the organic layer (Fig. 2a).~~litterfall-N of the seven sites (34.6 kg N ha^{-1}, Table 3). Sites with a low recovery ~~rate~~of

^{15}N in the organic layer exhibited higher recovery in the mineral soil and vice versa (Fig. ~~2b~~2). The ~~recovery of~~recovered leaf litter N significantly increased with total litterfall dry mass and total litterfall N but not with leaf litterfall dry mass and leaf litterfall N (Fig. 3; Table ~~7~~6).

3.3 N fluxes and N budgets

Total N deposition (N_D) was quite similar at ~~measured~~all sites, whereas net uptake for aboveground tree N increment (N_U) and seepage N output (N_L) differed considerably (Table ~~6~~5). Annual total N deposition ranged from 18 to 24 kg ha^{-1} during 1994 to 2008 and annual tree N increment between 4.4 and 14.2 kg N ha^{-1}. The mean annual total N deposition of 20.7 kg ha^{-1} (cv 9 %) was about twice as high as for tree N increment (10.1 kg N ha^{-1}) (cv 34 %). Annual seepage N output was relatively low (4.8 kg ha^{-1}; cv 83%) with values ranging from 0.8 to 6.6 kg ha^{-1} except at the BBR site, where 12 kg N ha^{-1} yr^{-1} ~~were lost with seepage water. Mean annual total N deposition of 20.7 kg ha^{-1} was about twice as high as for tree N increment (10.1 kg N ha^{-1}). Calculated soil N pool change by input-output analysis (ΔS, Eq. 1) revealed an annual soil N retention of 2.9 kg to 12.7 kg ha^{-1} in six soils and an N loss from the soil of 0.9 kg ha^{-1} at BBR site. On average 5.7 kg N ha^{-1} were retained annually in soils.~~ was~~N retention in the soil increased with the N/P ratio in the organic layer and the C/P ratio of the upper mineral soil (0 – 10 cm) (Fig. 4, Fig. 5). In total 15.8 kg N ha^{-1} of the 20.7 kg N ha^{-1} deposited were retained by trees and soil annually and 4.8 kg ha^{-1} were~~ lost with seepage water. Seepage N output from the soil was positively correlated with C (r_{Spear} = 0.93, $p < 0.01$), N (r_{Spear} = 0.96, $p < 0.01$), and P content (r_{Spear} = 0.86, $p < 0.05$) ~~and also~~as well as with the clay content in the mineral soil (0 – 10 cm) (r_{Spear} = 0.96, $p < 0.01$) (Fig. 5). The clay content was also positively related to the C (r_{Spear} = 0.86, $p < 0.05$), N (r_{Spear} = 0.89, $p < 0.01$), and P content (r_{Spear} = 0.82, $p < 0.01$) of the mineral soil.

Changes in the soil N pool which was calculated by input-output analysis (ΔN_S, Eq. 1) indicated an annual soil N retention of 2.9 kg to 12.7 kg ha^{-1} in six soils and a loss of N from the soil of 0.9 kg ha^{-1} at the BBR site. On an average 5.7 kg N ha^{-1} (cv 86%) were retained annually in soils. N retention in the soil increased with the N/P ratio in the organic layer and the C/P ratio of the upper mineral soil (0 – 10 cm) (Fig. 4, Fig. 5). In total 15.8 kg N ha^{-1} were annually retained by trees and soils in the European beech ecosystems.

4 Discussion

4.1 Frequency of fructification, biomass production and N demand

~~A~~The production of seeds on the experimental sites was highly synchronized among different years (Fig. 1) as was observed by several authors (e.g. Wachter, 1964; Nussbaumer et al., 2016; Reil et al., 2015). It may be related to the self-incompatibility of beech which therefore depends on cross wind pollination to produce seeds (Nielsen and De Muckadeli, 1954). A high frequency of a heavy mast (full- and half-mast) every 1.4 to 3.0 years (mean 2.0) in seven ~~German~~study beech forests during ~~the study period from~~ 1995 to 2008 (Table 3) confirmed the prior reports by Paar at al. (2011) for Germany, ~~by~~of Övergaard et al. (2007) for Sweden, and by Lebourgeois et al. (2018) for France. They reported that the mast occurred every two to three years between 1974 and 2009. Visual ratings of fruiting at plots of the ICP Forest Level I and Level II ~~network revealed~~networks showed a mast frequency of 2.6 to 5.5 years in Great Britain, Switzerland, Denmark, Germany, and Belgium (Nussbaumer et al., 2016). Such short mast intervals were not observed ~~in~~before the ~~past~~1960s. Most authors reported mast frequencies of 5 to 10 years during the end of the seventeenth century up to the 1960s (Hase, 1964; Wachter, 1964; Övergaard et al., 2007; Paar et al., 2011). Two of such studies using historic data and litterfall measurements indicated ~~a decrease~~an increase in the frequency of fructification. Övergaard et al. (2007) ~~showed~~observed that the mean mast year interval was about 5 years from the end of the seventeenth century up to the 1960s, but decreased to 2.5 years between 1974 and 2006 in southern Sweden. Paar et al. (2011) calculated that a mean interval of 4.7 years for full- and half-masts between 1839 and 1987 decreased to 2.6 years. This was obtained from the results of litter fall observations at ten ICP Forests Level

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II plots between 1988 and 2010 in Lower Saxony and Hesse, Germany. Thus, ~~compared to historic data~~ a doubling of mast frequency ~~seems to be very likely~~in recent times occurred at least in Germany and southern Sweden.

~~In~~ The annual amount of leaf litterfall ranged from 2.76 to 3.88 Mg ha^{-1} (Table 3) and was in the same order of magnitude (2.95 to 3.33 Mg ha^{-1}) as in 36 old-growth forest stands of Fagus sylvatica across a broad gradient of soil fertility covering nine mesozoic and kaenozoic parent material types (three limestones, two sandstones, two clay stones, one sand and one loess substrate) (Meier et al., 2005). Leaf litterfall in mast ~~year~~years did not differ from that in non-mast years (Tab. 3), as was also observed by Müller-Haubold et al. (2015). However, a significant correlation between total and leaf litter fall was observed in this study (Tab. 6, Fig. 5). Similar correlations were reported by Meentemeyer et al. (1982). In mast years an additional 1.4 to 2.9 Mg ha^{-1} dry mass was returned to the soil ~~when compared to the non-mast years (Table 3).~~surface. By assuming that under similar biomass production and litterfall conditions mast ~~frequency has been~~frequencies had doubled when compared to the historic ~~values,~~mast frequency, the mean annual total litterfall ~~may~~might have increased by 0.5 Mg ha^{-1} to 5.11 Mg ha^{-1} and mean NPP by about 4 %. A fertilizing effect of N deposition on forest growth in Europe has been identified for many regions, most pronounced for the sites ~~having~~with high C/N ratios in ~~the soil~~soils (Solberg et al., 2009, Etzold et al., 2020~~). The results suggest~~), suggesting that an increase in ~~NPP based on a higher frequency of fructification and a higher~~ tree growth would not have been achieved under ~~conditions of~~ low N availability. The additional ~~annual~~ N demand for the production of total litter ~~production in~~during mast years ~~compared to non-mast years~~ amounted to 32.4 kg N ha^{-1} ~~and increased the N uptake for total litter production by~~which translated into an annual increase of 8.7 kg N to 58.6 kg N ha^{-1} as compared to historic conditions. The additional N uptake for total litter production ~~may be~~was even higher if the lower availability of N in historic times ~~is~~was considered. Leaf litterfall as an indicator increased the biomass and N increment of trees at nutrient~~-~~rich sites (Table ~~7~~6, Fig. 5).

4.2 Recovery of leaf litter N under high fructification frequency

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The ^{15}N leaf litter exchange experiment on the beech forest sites indicated that about half of N added with the leaf litter, 17 kg N ha^{-1}, was recovered in the upper 40 cm of the soil during the 5.5 years ~~on the beech forest sites~~ (Table ~~6~~5). A higher recovery of N was observed in a similar litter exchange experiment with labelled beech litter in three European beech stands (Zeller et al., 2001). In their study about 88 % of the labelled N remained in the upper 30 cm of the soil, whereas only 2 to 4 % was incorporated in the tree biomass during three years. The higher recovery in th~~is~~e study of Zeller et al. (2001) may be attributed to a shorter duration of the experiment as immobilization of ~~nitrogen~~N exceeded the release of leaf litter N by mineralization during the first two years of the litter exchange ~~(Zeller et al., 2001).~~

~~Primarily, the chemical composition of soils determined the partitioning of leaf litter N between the organic layer and mineral soil. Soils exhibiting a delayed decomposition developed a thicker organic layer thus retaining more leaf litter N in that layer (BBR, NHB, SOB) (Fig. 2a, 2b). Under more favourable conditions of decomposition, leaf litter N was predominantly transferred into the mineral soil (FRE, EBR, GW, HOM). One example of high retention of leaf litter N in the mineral soil was the base-rich GW site where a high abundance of saprophagous organisms (Lumbricidea and Diplopoda) was observed~~ ~~.(Schäfer et al., 2009; Schäfer and Schauermann, 2009). These organisms play a dominant role in the incorporation of leaf litter N into the mineral soil. The peak~~ ~~^{15}N$_{excess}$ retention at GW was observed at 7 – 10 cm depth, indicating the deepest incorporation among the seven study sites (Table 5).~~

The recovery of leaf litter N was closely related to total litterfall (Fig. 3a), but showed no relation to leaf litterfall (Fig. 3b), suggesting that fruit components as a part of total litterfall were primarily involved in the retention of leaf litter N (Table ~~7~~6). Fruit production increased the dry mass of total litterfall by ~~49~~50 % compared to non-mast years (Table 4). Seeds are rich in N and P representing lower C/N and C/P ratios ~~whereas seed~~. Seed cupules~~, which~~ contributed 51 % to the dry mass of the fruit components~~,~~, and showed the highest C/N and C/P ratios of all litter fractions and may cause a high N demand during its decomposition. Seed cupules are woody phyllomes composed of highly recalcitrant lignocellulose tissue (Fukasawa et al., 2012). In a study on fungal succession and decomposition of Japanese beech cupule litter (*Fagus crenata* Blume), 77 % of the original cupule weight remained at the end of a 30-month study period (Fukasawa et al., 2012). An even more delayed weight loss was recorded in England where only 6 % of the cupules of European beech decomposed over a 2-year~~s~~ period (Carré, 1964). Most of the weight loss of seed cupules was related to the selective decomposition of holocellulose, and very little to the loss of acid-non-hydrolyzable residues (Fukasawa et al., 2012). Seeds usually decompose ~~at higher rates~~faster than e.g. needle litter (Zackrisson et al., 1999), ~~but we are not aware of any comparative study on the decomposition of leaves, seeds~~ and most likely much faster than seed cupules~~. However, the decomposition processes of the different litter fractions might be spatially and temporarily decoupled. A high~~ causing an N demand during ~~the~~its decomposition ~~of seed cupules~~which may be fulfilled to some extent by ~~N deposition or~~ the release of N from the decomposition of leaf litter. Even if the fruit compounds decompose simultaneously, a similar C/N ratio of fruits (44) compared to leaf litter ~~and seeds~~(43) would cause a higher N demand during the decomposition of fruits in mast years.

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Acid soils with moder type humus (BBR, NHB, SOB) and less acid soils with mull type humus (FRE, EBR, GW, HOM) retained almost the same amount of leaf litter N (16 – 17 kg N ha^{-1}). While the majority of leaf litter N was retained in the organic layer of moder type humus soils, under more favourable conditions for decomposition most of the leaf litter N was transferred into the mineral soil of mull type humus soils (Fig. 2). A high retention of leaf litter N in the mineral soil was observed at the base-rich GW site, because of the high abundance of saprophagous organisms (Lumbricidae and Diplopoda) (Schäfer et al., 2009; Schäfer and Schauermann, 2009). These organisms play a dominant role in the incorporation of leaf litter N into the mineral soil. The highest enrichment of ^{15}N labelled N at the GW site was observed at 7 – 10 cm depth, indicating the deepest incorporation among the seven study sites. An explanation for the similar recovery of ^{15}N labelled leaf litter in moder and mull type humus soils may be the short duration of the study, providing an intermediate stage of ^{15}N incorporation into microbes and microbial products after few years of turnover, but was probably not transformed into physically and chemically protected fractions (Parton et al., 1988) after of 5.5 years of litter exchange. Input and output flux measurements indicated that the soil at the GW site was in a quasi-steady state of formation and decomposition of humus (see 4.3).

4.3 N fluxes and N budgets

Positive soil N pool changes (Δ~~S~~N_S, Eq. 1) indicated ~~the~~a retention of N in the soil at all sites except the BBR site where a ~~small~~slightly negative budget may point to humus degradation (Ulrich, 1992) (Table ~~6). The acid soil at the SOB site with moder type humus retained almost all N deposited during the high N emission period between 1981 and 1989 which was not used for tree N increment or gaseous N losses, thus indicating a high potential for soil N retention of 30 kg ha-1 yr-1 (Brumme and Khanna, 2009). In contrast, at the less acid GW site with mull type humus very little amount of N was retained in the soil during high N deposition period and most of that was used for tree N increment or leached.~~5). Soil ~~acidity seems to be an important factor in the retention of deposited N in forest ecosystems.~~

~~Soil~~ N change was ~~unrelated~~not related to the total litterfall (Table ~~7) despite the retention of leaf litter N exerted by fruit compounds in the litterfall fraction,~~6), indicating that mast ~~event~~ was not the ~~primary~~prevailing factor controlling ~~N~~the retention of deposited N in soils. ~~This~~Our study ~~showed~~suggest that soil P was involved in processes regulating N retention in soils. Soil N retention rate was associated with high N/P ratios in the organic layer and high C/P ratios in the mineral soil (Fig. 4, Fig. 5). High N depositions, may have induced an imbalance of P and N nutrition. Several studies indicated that N deposition ~~until the 1990s~~ increased the N retention rate in soils until the 1990s (Hyvönen et al., 2008; ~~de~~De Vries et al., 2006; Brumme and Khanna, 2008; Meiwes et al., 2009). Talkner et al. (2015) observed that foliar P content in 79 ICP Forests Level II European beech plots in Europe decreased during 1991 to 2010 indicating a reduced P availability ~~in acid forest soils. N deposition probably changed the balance of P and N nutrition through higher N availability, and reduced the~~

~~mineralization of organic P due to increasing soil N/P ratios.~~with increasing N enrichment and increasing soil acidification. Critical N/P ratios for litter decomposition are often suggested in the literature (Aerts, 1997; Smith, 2002; Güsewell and Freeman, 2005) implying that the decomposition of litter with high N/P ratios is limited by ~~low~~insufficient P~~.~~ availability. Moreover, the bioavailability of inorganic P can be severely limited in acid soils by Al ~~because mobilized Al forms stable complexes with inorganic P and functionally~~which may be restrict the functionality of the microbial community~~ due to P limitation~~ (Goldberg et al., 1997; DeForest and Scott, 2010).

~~On average trees retained twice as much N via tree N increment as compared to soils via positive N pool change (Table 6), especially at the sites with low C/N ratios in the mineral soil (Fig. 5).~~The seven sites studied here are a part of 53 Level II plots in Germany of which half of them (n = 27) retained N in the soil calculated by input-output balances (Brumme and Khanna, 2008). N retention increased with the level of total N and sulphur deposition and the thickness of the organic layer at sites with moder type humus (n = 21) indicating the role of organic layers for the retention of N input in acid soils under high atmospheric load. In several studies simulated acid rain and ammonium additions affected soil microbial activity and thus the C and N cycling in ecosystems in the short-term (Persson and Wiren, 1993; Berg and Matzner, 1997; Janssens et al., 2010). In the long-term, atmospheric deposition may lead to the formation of a decomposer refuge by soil acidification (Ulrich, 1992) and high-N leaf litter, which decompose at lower rate than litter with low N in the later stages of decomposition, increased the accumulation of C and N in the organic layer (Berg et al., 1995). Field measurements confirmed the high potential for soil N retention in an acid soil with moder type humus at the SOB site but not in the less acid soil with mull type humus at the GW site (Meiwes et al., 2009; Brumme and Khanna, 2009). Almost all of the deposited N in excess for plant increment or gaseous outputs was retained in the organic layer of the SOB site as indicated by the soil inventories for the period of 1966 to 2001 (Meiwes et al., 2009). The annual increase in the organic layer equalled 21 kg N ha^{-1} and 347 kg C ha^{-1} and was confirmed by input and output measurements between 1981 and 2002 (Brumme and Khanna, 2009). In contrast, at the less acid GW site with mull type humus most of the N was either used for tree N increment or leached with seepage water with little retention in the soil. Hence, the SOB site was classified to be in the state of humus accumulation (accumulation type) and the GW site in a (quasi)-steady state of formation and decomposition of humus (Brumme and Khanna, 2008). Recent observations at two forest sites proved the direct effect of S deposition as the main driver for N retention in forest soils. After emission control at the end of the 1990s and reduced atmospheric deposition the C and N pools in the organic layer declined at SOB site from 1.86 Mg N ha^{-1} in 1993 to 0.99 Mg N ha^{-1} in 2010 (Förster et al., 2017) as well as at a spruce stand in the Czech Republic (Oulehle et al., 2011) indicating a predominant effect of atmospheric deposition on microbial activity and N retention.

Studies with ^{15}N labelled N deposition provide a useful insight into the initial retention processes of N deposition in the forest ecosystems. Irrigation studies with ^{15}N labelled ammonium on undisturbed soil cores (30 cm length) from the SOB site in the field indicated a N retention of 20 % in the organic layer and 26 % in the mineral soil over a period of 12 months (Brumme et al., 2009a). Irrigation studies of undisturbed cores from different soil depths of the SOB soil showed a N retention of 54 % in the organic layer and of 34 % in each of the mineral soil layers (0 – 10 cm, 10 – 20 cm depth) after a two-month irrigation with $^{15}NH_4$ at 8°C in the laboratory. Low nitrification rates (heterotrophic) at the SOB site (Bauhus et al., 1996; Brumme et al., 2009b) result in the adsorption of ^{15}N labelled ammonium and contributed 3 % to the N retention of 54 % in the organic layer, 24 % of 34 % in 0 – 10 cm, and 30 % of 34 % in 10 – 20 cm soil depth. A high adsorption capacity for ammonium extended the residence time and the potential for transformation processes due to microbial immobilization and plant uptake in acidic soils and may have increased the transformation of deposited ammonium in organic compounds. Nitrate was only marginally retained in the soil layers of the SOB site (< 3 %) as shown by a comparable study with ^{15}N labelled nitrate (Brumme et al., 2009a). The less acid GW site had a similar retention of 45 % of ^{15}N labelled ammonium in 30 cm long soil cores as compared to the acid SOB site (46 % recovery). However, the adsorption of ammonium at the GW site was negligible due to high autotrophic nitrification. Most of the ^{15}N retained in the GW cores was transformed to organic compounds in the mineral soil. The high N retention in the mineral soil of the less acid GW site was evident from the high microbial biomass which was two times higher at the GW compared to the SOB site, especially in the mineral soil, where it was five times higher (Brumme et al., 2009c). Ammonium retention was closely related to the microbial biomass at the SOB and GW soils indicating its dominant control on ammonium retention in forest soils in the short-term. Within the NITREX project, where the fate of doubled ^{15}N labelled $^{15}NH_4{}^{15}NO_3$ in throughfall was studied over a 12-month period, N retention was twice as high in the organic layer as in the mineral soil of a podzolic soil in Denmark (26 % versus 12 % recovery, Tietema et al., 1998). The uptake of ^{15}N by ground vegetation and trees amounted to 45 % of the applied ^{15}N showing that a large part of the deposited N was introduced into the internal N cycle. Most of the N usually returns back to the soil with litterfall in the following year and may be retained in the soil by mast products, as was observed in the ^{15}N labelled leaf litter exchange experiment. Thus, the initial microbial retention of N is one pathway into labile organic N compounds while the repeated plant uptake and litterfall of N is probably the common transformation processes producing more stable N compounds in soils.

Tree N increment increased with decreasing C/N ratio in the mineral soil (Fig. 5) and retained an average twice as much N as compared to changes in the N pool of soils (Table 5). Sites with a low C/N ratio in the mineral soil are often characterized by high soil biological activity increasing N content in relation to C (Swift et al~~.~~., 1979). The base~~-~~-rich GW site for example contained an almost two times higher microbial biomass and a high abundance of earthworms ~~in contrast to~~than the acid SOB site (Brumme et al., 2009a; Schäfer et al., 2009) and retained +60 % N by tree increment and -71 % N by soil N change as compared to the SOB site. N budgets of 53 ICP Level II plots in Germany confirmed the dominant role of the soil chemical status for the retention of N in soils and trees (Brumme and Khanna, 2008). It was found that N retention by trees decreased and that of soils increased with a decrease in the availability of base cations. N retention processes by trees and ~~in the soil~~soils in conjunction with total N deposition determined the seepage output of N at our study sites, whereas gaseous N losses were of minor importance~~ (Table 6).~~. A positive relationship between seepage N losses and contents of N, C, P and clay in the mineral soil (Fig. 5) suggests that sites with a high N pool in the mineral soil retained less N in soil and plants than sites with a low N pool. High mineral soil N pools are found typically at sites ~~which~~that are close to an (quasi-) steady state with high elasticity ~~where~~against environmental changes like deposited acidity, which is buffered by silicates or carbonates~~ and have~~. These sites usually exhibit a high biological activity in the mineral soils forming a mull type humus (Ulrich, 1992; Brumme and Khanna, 2008). At such sites most of the N is retained through tree uptake~~ for tree increment~~ and any additional N from deposition is leached from the soil with the seepage water flux.

5 Conclusions

The role of mast in the nutrient cycling processes in beech forests has so far ~~has ~~received little attention because of the irregular nature of the mast production. When comparing historic data with results from litterfall observations across Europe since the 1990s, an increase in fructification frequency ~~seems likely. Elevated fluxes of biomass to the organic layer due to a high mast frequency most probably affect the carbon and nutrient cycling in forest ecosystems. Higher~~is obvious. The higher mast frequency has increased the amount of ~~carbon~~C and ~~nutrients~~N additions to the soil ~~and~~which increased the internal cycling between plants and soil~~. High total litterfall~~ including decomposition. Litterfall fluxes were accompanied by a change in the litter quality involving high amounts of easily decomposable seeds on the one hand and less decomposable (recalcitrant) seed cupules ~~on the other hand. The dynamics of litter decomposition changed mainly due to seeds with low, and seed cupules ~~with very high C/N and C/P ratios on the other. The application of ^{15}N labelled leaf litter indicated that these changes may be responsible for increased ~~N ~~sequestration of leaf litter N during decomposition of seed cupules ~~at~~in stands with a high mast frequency. ~~Mast~~Thus, mast affected the retention of N after plant uptake and leaf litterfall, but did not affect ~~soil N~~the retention of deposited N calculated by input and output fluxes~~ because confounding factors such as soil~~

~~acidification and N saturation processes exerted an important control on N retention. Soil N~~. The retention ~~occurred mainly in acid soils. At these sites, soil N retention is still continuing despite a reduction in~~ of N in the soil is controlled by atmospheric ~~N~~ depositions~~.~~ and soil acidity as indicated by input and output flux measurements. Atmospheric depositions affected N retention by reducing decomposition processes but also by changing the environment of decomposers through soil acidity and nutrient imbalances. The N/P ratio and soil acidity ~~may~~ have increased, reducing the P availability and litter decomposition processes. In our study N retention ~~by trees dominates~~ in acid soils increased with the thickness of the organic layer and the N and S deposition, while in less acid soils with higher nutrient turnover and low C/N ratios in the mineral soil layers~~.~~, elevated plant uptake dominates the N retention. Such sites are characterized by a low ~~N retention in the soil. As long as~~soil N retention ~~is maintained at the current level the risk of enhanced leaching losses of N from less acid soils seems to be low.~~ .

Data availability

The majority of data used for regression and correlation analysis is being presented here in the tables. The raw and not yet aggregated data and other datasets are available from the authors upon request.

Author contributions

RB, BA, and HM designed and conceptualized the study. All authors contributed to preparation, pre-processing and aggregation of measurement data (deposition, litterfall, seepage flux, uptake, tree growth, etc.) of the different federal states included. RB: experimental setup, sampling and interpretation of the ^{15}N data. All authors contributed to writing with reviewing, editing and commenting of the manuscript.

Declaration

The field studies did not involve endangered or protected species and no specific permission was required for these locations/activities.

Competing interests

The authors declare that they have no conflict of interest.

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Table 1. Site and stand characteristics of seven European beech (*Fagus sylvatica* L.) forest ecosystems (reference year 2010). Site abbreviations are explained in the text.

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	BBR	FRE	EBR	NHB	GW	SOB	HOM
Latitude (N)	50°02',	48°24',	49°51',	50°24',	51°32',	51°46',	50°56',
longitude (E)	9°56'	11°39'	10°32'	7°43'	10°03'	09°35'	09°20'
Elevation (m a.s.l.)	850	550	450	390	420	504	375
Slope (°)	1.0	4.8	6.8	3.0	0.3	1.9	7.4
Mean temperature (°C)	6.0	8.3	7.7	8.3	7.4	6.9	7.3
Mean annual precipitation (mm)	1048	845	783	971	712	1209	712
Stand age (years in 2010)	134	157	94	117	142	163	141
Stand density (N, stems ha^{-1})	389	452	175	160	235	140	148
Mean diameter Dg (cm)	36.1	32.6	49.4	50.6	47.9	48.5	51.9
Stand height Hg (m)	26.5	29.4	32.5	37.8	35.5	30.1	39.8
Beech fraction of total basal area (%)	100	66[a]	91[b]	100	91[c]	100	94[d]
Clay/silt/sand (%) (0-10 cm)	40/50/10	16/60/24	19/55/26	23/38/39	36/61/3	20/49/31	12/68/20
Humus type	moder	mull	mull	moder	mull	moder	mull
Parent material	basalt	loess over upper marine molasses	sandstone	pumice stone	limestone	loess over sandstone	basalt

a-: 34 % *Quercus robur*; b-: 9 % Quercus petraea,; c: *Fraxinus*, *Acer*, *Quercus*, *Ulmus*,; d: *Picea abies.*

Table 2. Chemical characteristics of foliage, soil organic layer, and the upper mineral soil (0-–10 cm) of seven European beech (*Fagus sylvatica* L.) ecosystems.

	BBR	FRE	EBR	NHB	GW	SOB	HOM
Foliage							
N (mg g^{-1})	24.9	24.0	23.5	23.9	24.5	24.6	22.5
P (mg g^{-1})	1.41	1.35	1.11	1.07	1.06	1.26	1.36
N/P	17.7	17.8	21.3	22.3	23.2	19.4	16.5
Organic layer							
Mg C ha^{-1}	27	4	6	25	10	34	13
C/N	19	26	26	24	23	19	25
C/P	262	372	503	418	397	378	356
N/P	14	14	19	17	17	20	14
Mineral soil (0-10 cm)							
pH(H_2O)	4.3	4.4	3.9	4.5	6.1	3.6	4.2
BS (%)	42	24	26	14	98	7	58
~~C/N~~	~~14~~	~~12~~	~~19~~	~~15~~	~~13~~	~~20~~	~~17~~
~~C/P~~	~~65~~	~~41~~	~~172~~	~~71~~	~~136~~	~~120~~	~~136~~
~~N/P~~	~~4.7~~	~~3.0~~	~~11.0~~	~~4.7~~	~~11.0~~	~~6.6~~	~~7.8~~
C (%)	12.4	1.1	4.2	8.0	7.4	6.5	5.4
N (%)	0.89	0.09	0.22	0.52	0.55	0.33	0.31
P (%)	0.19	0.03	0.02	0.11	0.05	0.05	0.04
C/N	14	12	19	15	13	20	17
C/P	65	41	172	71	136	120	136
N/P	4.7	3.0	11.0	4.7	11.0	6.6	7.8

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Table 3.~~-~~ Above ground annual net primary production (NPP) and annual tree increment (INCR) (Mg dry mass ha^{-1}) at the study sites during the period 1995~~-~~ – 2008. Annual means of dry weight (Mg ha^{-1}) and nitrogen (kg ha^{-1}) of total litterfall (TLF) and leaf litterfall (LLF) for all years (overall mean), for years with mast (full- and half-mast) (MY), for non-mast years (NMY), and as difference between years with mast and non-mast years ~~(%)~~(change %) for seven beech forests. Years with mast (full-mast years in bold) and the number of mast and non-mast years~~, the number of total years of measurements,~~ and years per mast events are given for the study sites.

	mean		BBR		FRE		EBR		NHB		GW		SOB		HOM	
	TLF	LLF	TLF	LLF	TLF	LLF	TLF	LLF	TLF	LLF	TLF	LLF	TLF	LLF	TLF	LLF
								Dry mass								
NPP	11.80		10.49		14.59		7.58		14.86		10.67		9.65		14.75	
INCR	6.69		6.19		8.94		2.80		9.75		5.74		4.61		8.80	
Overall mean	5.11	3.12	4.30	2.86	5.65	3.88	4.78	2.76	5.11	3.44	4.93	2.95	5.04	2.89	5.95	3.09
MY	6.10	3.15	5.07	2.86	6.05	3.90	5.27	2.79	6.28	3.67	6.12	2.97	5.96	2.85	7.94	3.03
NMY	4.09	3.11	3.86	2.86	4.60	3.80	3.64	2.70	4.44	3.41	4.03	2.94	4.11	2.94	3.95	3.14
MY – NMY	2.01	0.04	1.21	0	1.45	0.10	1.63	0.09	1.84	0.26	2.09	0.03	1.85	-0.09	3.99	-0.11
Change (%)	+49	+1.3	+31	±0	+32	2.6	+45	+3.3	+41	+7.6	+52	+1.0	+45	-3.1	+101	-3.5
								Nitrogen								
Overall mean	58.6	34.6	52.5	35.0	62.6	39.1	53.5	29.3	56.9	38.0	56.8	33.7	63.8	34.8	64.3	32.3
MY	74.2	36.3	65.5	34.4	70.7	41.0	61.9	31.4	72.3	42.3	75.5	35.6	82.8	36.1	90.6	33.2
NMY	41.8	32.5	45.1	35.4	41.1	34.1	32.9	23.9	48.1	36.8	42.8	32.4	44.8	33.5	37.9	31.3
MY – NMY	32.4	3.8	20.4	-1.0	29.6	6.9	29.0	7.5	24.2	5.5	32.7	3.2	38.0	2.6	52.7	1.90
Change (%)	+77	+11.7	+45	-2.8	+72	20	+88	+31	+50	+15	+76	+10	+85	+7.8	+139	+6.1
Mast years			**2002**, **2004**, **2006**, 2007		1998, **1999**, **2001**, 2002, **2003**, 2004, **2006**, 2007		1998, 2000, 2001, **2002**, **2003**, **2004**, **2006**, 2007		1995, **2000**, **2002**, **2004**		**1995**, **2000**, 2002, **2004**, **2006**, 2007		**1995**, 1998, **2000**, **2002**, **2004**, **2006**, **2007**		**1998**, **2000**, **2002**, **2004**, **2006**, **2007**	
~~Mast yrs / yrs / yrs per mast~~	~~43 / 85 /2.0~~		~~4 / 11 / 2.8~~		~~8 / 11 / 1.4~~		~~8 / 11 / 1.4~~		~~4 / 12 / 3.0~~		~~6 / 14 / 2.3~~		~~7 / 14 / 2.0~~		~~6 / 12 /2.0~~	
number MY's	43		4		8		8		4		6		7		6	
number NMY's	42		7		3		3		8		8		7		6	
(MY+NMY)/MY	2.0		2.8		1.4		1.4		3.0		2.3		2.0		2.0	

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Table 4. Annual means of dry weight (Mg ha^{-1}), nitrogen (N), phosphorous (P) and sulfur (S) (kg ha^{-1}) of litter fractions (leaf litter, seeds, seed cupules, twigs, total litterfall, and a fraction of small pieces which were not separated (residual)), ~~total litterfall,~~ and the ratios of the elements at three European beech (*Fagus sylvatica* L.) stands in Rhineland-Palatinate from 1995- – 2005 (Neuhäusel Bims NHB, Kirchheimbolanden KHB, Neuhäusel Quarz NHQ). For the dry mass and nitrogen additional means are listed for years with mast (MY) (full- and half-mast), non-mast years (NMY), and the difference between mast and non-mast years. The changes of dry mass and N of litter fractions and total litterfall in mast years compared to non-mast years are given in %.

	Leaf litter	Seeds	Cupules	Twigs	Residual	Total litterfall
			Dry mass			
Overall mean (n = 33)	3.24	0.29	0.59	0.29	0.47	4.87
MY (n = 11)	3.32	0.78	1.30	0.31	0.56	6.27
NMY (n = 22)	3.21	0.04	0.23	0.28	0.43	4.18
MY – NMY	0.11	0.75	1.07	0.03	0.14	2.09
Change (%)	+3.3	+2059	+457	+11	+32	+50
			Nitrogen			
Overall mean	37.0	8.0	2.0	2,5	6.6	56.1
MY	39.7	22.2	4.0	2.8	8.7	77.0
NMY	35.9	0.9	0.9	2.4	5.8	45.9
MY – NMY	3.8	21.3	3.1	0.3	2.9	31.1
Change (%)	+11	+2412	+331	+14	+49	+68
P	2.1	0.73	0.21	0,14	0.41	3.48
S	3.4	0.46	0.19	0,19	0.48	4.69
C/N	43	19	144	58	34	43
C/P	747	209	1358	1067	550	663
C/S	472	332	1475	765	470	511
N/P	17	11	9	18	16	16
N/S	11	17	10	13	14	12

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Table 5. ~~Recovery of $^{15}N_{excess}$ (% $^{15}N_{excess}$ recovery per plot) within the soil after 5.5 years of litter exchange with ^{15}N labelled beech leaf litter at seven European beech (Fagus sylvatica L.) sites. The organic layer (>15 % C) is indicated by underlines.~~

(cm)	BBR	FRE	EBR	NHB	GW	SOB	HOM
L	0.0	0.0	0.0	0.0	0.0	0.0	0.1
0-1	0.3	0.3	0.6	0.2	0.2	0.0	0.4
1-2	0.9	1.5	2.5	2.3	0.0	2.9	2.7
2-3	4.4	3.5	6.5	10.4	4.3	16.9	12.4
3-4	9.0	8.0	10.6	9.9	8.5	19.7	16.5
4-5	4.9	9.0	9.0	6.6	6.8	8.3	13.5
5-7	4.1	9.5	7.1	7.7	9.0	9.5	14.7
7-10	3.2	5.1	3.3	4.8	9.3	1.6	5.4
10-20	2.3	2.7	2.3	2.1	5.3	2.1	6.5
20-30	2.2	1.9	0.4	0.6	1.7	0.7	0.0
30-40	0.3	0.8	0.3	0.2	0.3	0.0	0.0
sum	32	42	43	45	45	62	72

~~**Table 6.**~~ Average total N deposition (N_D), tree N increment (N_U), net gaseous N ~~exchange~~emission (N_E-N_F), seepage N outputs (N_L) and soil N pool change (Δ~~S~~N_S, calculated from Eq. 1) for the period 1994 to 2008, and ^{15}N recovery of applied labelled ~~N~~^{15}N with leaf litter of seven European beech (*Fagus sylvatica* L.) forest ecosystems. The ^{15}N recovery 5.5 years after litter exchange is given in % of applied $^{15}N_{excess}$~~;~~ and in kg N of mean annual leaf litterfall N~~, and in % of total recovery found in the organic layer~~.

Site	Total N deposition	Tree N increment	Net gaseous N ~~exchange~~	Seepage N output	Soil N pool change	Recovery of $^{15}N_{excess}$ ~~total~~ %	~~organic~~% ~~kg N ha^{-1}~~	~~kg~~ ~~%~~
	------ kg N ha^{-1} yr^{-1} ------							
BBR	20.5	9.4	0	12.0	-0.9	32	11	~~81~~
FRE	17.9	14.2	0	0.8	2.9	43	17	~~5~~
EBR	19.4	4.4	0	2.3	12.7	43	13	~~8~~
NHB	21.7	11.8	0	6.5	3.4	45	17	~~84~~
GW	21.1	11.2	0	6.6	3.3	45	15	~~10~~
SOB	23.8	7.0	1.4	4.3	11.2	59	21	~~94~~
HOM	20.8	12.9	0	0.9	7.0	72	23	~~22~~
mean	20.7	10.1		4.8	5.7		17	~~43~~

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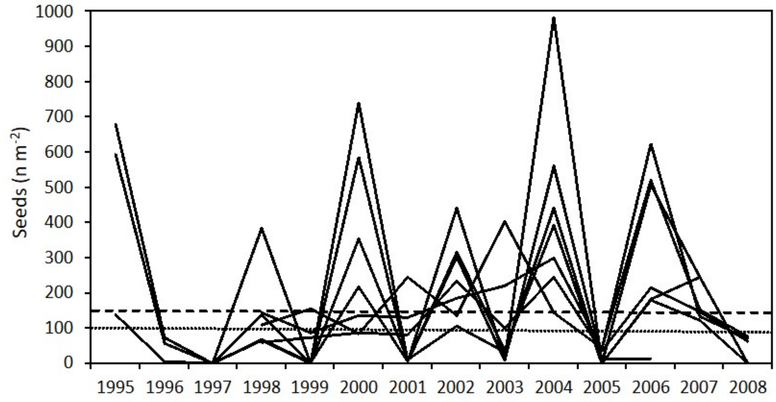
Table ~~7~~6. Correlation analyses (Spearman correlation coefficients, r_{Spear}, p) between leaf N recovery, total litterfall, leaf litterfall, and the input and output fluxes of nitrogen (N) and biomass (DM, dry mass). Significant correlations ($p < 0.05$) are indicated by bold numbers.

	Leaf N recovery kg N ha^{-1}		Total litterfall Mg ha^{-1} yr^{-1}		Leaf litterfall Mg ha^{-1} yr^{-1}	
	r_{Spear}	p	r_{Spear}	p	r_{Spear}	p
Total litterfall DM	**0.86**	0.014			**0.82**	0.023
Total litterfall N	**0.96**	<0.001	**0.89**	0.007	0.57	0.180
Leaf litterfall DM	0.54	0.215	**0.82**	0.023		
Leaf litterfall N	0.00	1.000	0.21	0.645	0.64	0.119
Total N deposition	0.50	0.253	0.07	0.879	0.00	1.000
Tree increment DM	0.32	0.482	0.61	0.148	**0.86**	0.014
Tree increment N	0.43	0.337	**0.79**	0.036	**0.~~9 3~~93**	0.003
Seepage N output	-0.50	0.253	-0.71	0.071	-0.43	0.337
Soil N pool change	0.39	0.383	0.11	0.819	-0.36	0.432



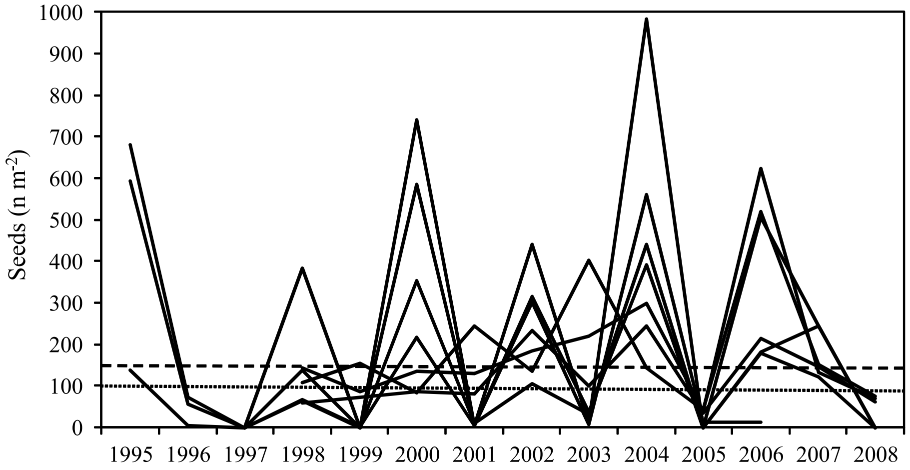
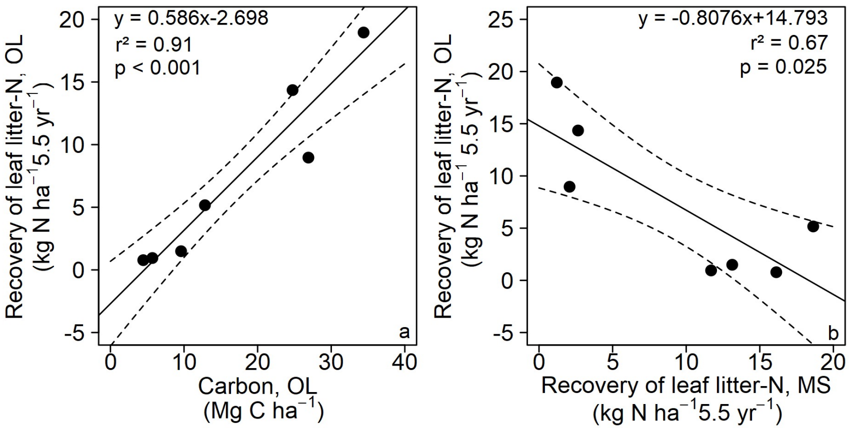
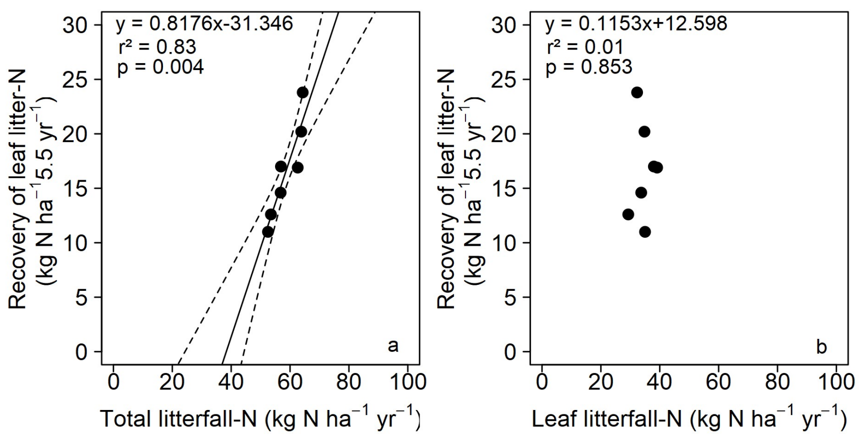


Figure 1. Production of seeds (seeds m^{-2}) at the study sites. Horizontal lines indicate years with half-mast (100 - 149 seeds m^{-2} – dotted line) and full-mast (>150 seeds m^{-2} –dashed line).



(cm)	BBR	FRE	EBR	NHB	GW	SOB	HOM
L	0	0	0	0	0	0	0.1
0-1	0.3	0.3	0.6	0.2	0.2	0	0.4
1-2	0.9	1.5	2.5	2.3	0	2.9	2.7
2-3	4.4	3.5	6.5	10.4	4.3	16.9	12.4
3-4	9	8	10.6	9.9	8.5	19.7	16.5
4-5	4.9	9	9	6.6	6.8	8.3	13.5
5-7	4.1	9.5	7.1	7.7	9	9.5	14.7
7-10	3.2	5.1	3.3	4.8	9.3	1.6	5.4
10-20	2.3	2.7	2.3	2.1	5.3	2.1	6.5
20-30	2.2	1.9	0.4	0.6	1.7	0.7	0
30-40	0.3	0.8	0.3	0.2	0.3	0	0
sum	32	42	43	45	45	62	72

Figure 2. ~~Recovery of leaf litter N (kg N ha^{-1}) calculated from~~Recovered ^{15}N labelled ~~beech litter~~ leaf litter (% $^{15}N_{excess}$ recovery per plot) within the soils after 5.5 years ~~after~~of leaf litter exchange at ~~the study~~seven European beech (*Fagus sylvatica* L.) sites ~~(a) in the~~. The organic layer ~~(OL) versus carbon stock in organic layer~~(>15 % C) is indicated by dark grey filled area and ~~(b) in the organic layer versus the recovery in the~~ mineral soil ~~(MS). Solid line = regression line, dotted lines = confidence bands of regression, with p = 0.90. Spearman's rank correlation revealed for a) r_{Spear} = 0.96***, p < 0.001 and for b) r_{Spear} = -0.71, p = 0.071~~by light grey filled area. L = loose leaf litter.



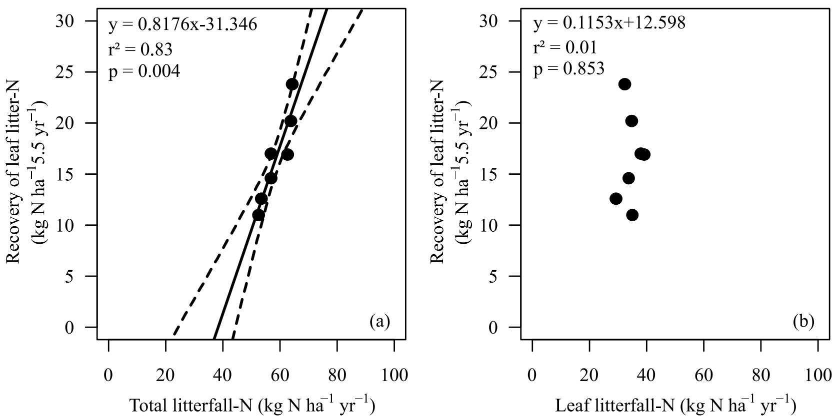


Figure 3. Recovery of leaf litter N (kg ha^{-1} yr^{-1}) calculated from ^{15}N labelled beech litter 5.5 years after litter exchange versus N flux with (a) total litterfall N and (b) with leaf litterfall N (kg N ha^{-1} yr^{-1}) at the study sites~~.~~ (n = 7). Solid line = regression line. Dotted lines = confidence bands of regression with p = 0.90. Spearman's rank correlation (a) $r_{Spear} = 0.96$, $p < 0.001$; (b) $r_{Spear} = 0.00$, $p = 1.0$.

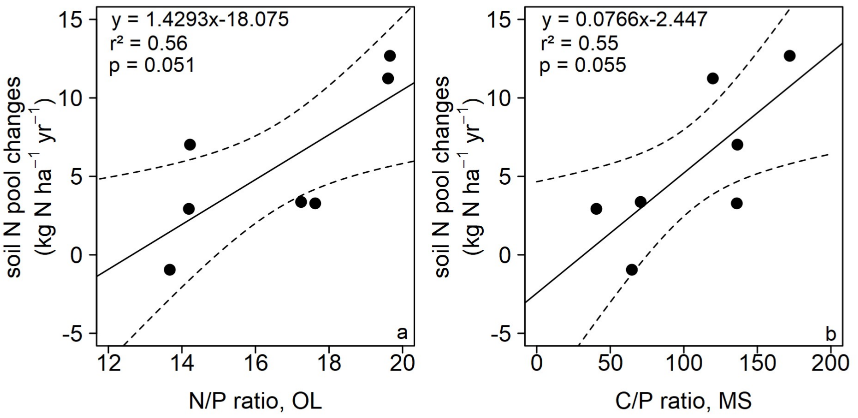


Figure 4. Soil N pool changes (Δ~~S~~N_S, kg N ha^{-1} yr^{-1}) ~~a~~ versus N/P ratio in the organic layer (OL) (a) and versus the C/P ratio in the upper mineral soil (0 – 10 cm) (MS) (b). Solid line = regression line. Dotted lines = confidence bands of regression with p = 0.90. Spearman's rank correlation (a) $r_{Spear} = 0.86$, $p < 0.05$; (b) $r_{Spear} = 0.79$, p = < 0.05.

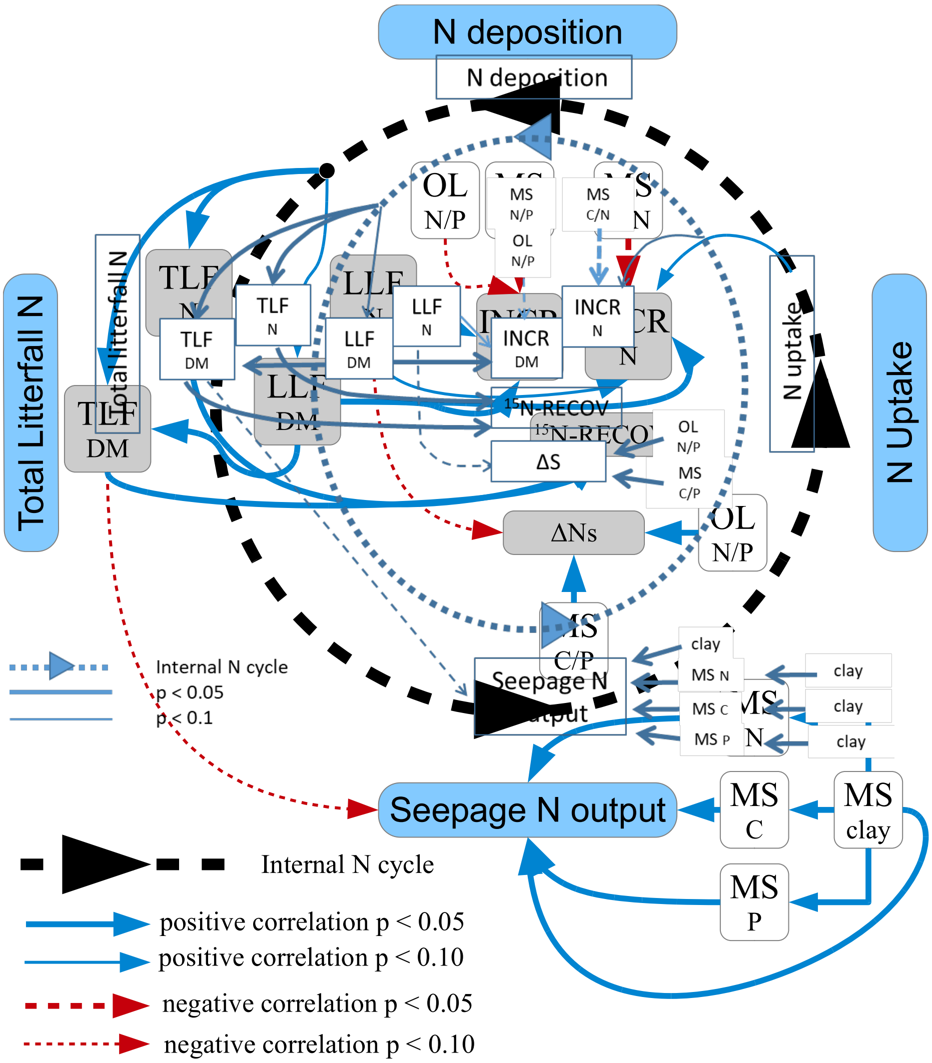


Figure 5. Schematic view of the ~~internal~~detected effects of N ~~cycling (N~~ uptake ~~by trees for leaf, fruit, and tree increment production; N release by,~~ total litterfall, TLF, ~~including~~ leaf litterfall, LLF~~)~~, and soil properties of the organic layer, OL and the ~~external N cycling (deposition, seepage output,~~mineral soil, MS, on the N retention by tree increment, INCR, the soil N pool change, Δ~~S, tree increment, INCR) and~~ N_S, the leaf ^{15}N recovery ~~(,~~ ^{15}N RECOV~~)~~, and on the seepage N output. Significant positive correlations (Spearman correlation coefficients) are indicated by continuous arrows, negative correlations by dashed arrows, other significant correlations with site and stand characteristics or the chemical characteristics were not found. Width of the line is proportional to the significance. Significant correlations ($p < 0.05$), ~~high but insignificant~~tendency of correlations ($p < 0.1$). ~~Mineral soil (MS), organic layer (OL), dry mass (DM).~~