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 soils and plant compartments, and the N output by seepage water. But the processes involved are not fully understood, especially the role of fructification which has increased in its frequency. A field experiment using ^{15}N labelled leaf litter exchange was carried out over a 5.5 years' period at seven long-term monitoring 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 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 a high nutrient demand during their decomposition due to their very high carbon (C) to N and C to phosphorus (P) ratios. 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 litter

35   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.

1 Introduction

Nitrogen (N) is commonly a limiting nutrient in 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

40   regions of the northern hemisphere. Acid deposition decreased soil pH (Hallbäcken and Tamm, 1986) and affected the N
cycling through reduced litter decomposition (Persson and Wirén, 1993; Janssens et al., 2010). High atmospheric deposition
of N has removed N deficiency in forests ecosystems (LeBauer and Treseder, 2008) and increased foliar N contents but has
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 Vries et al.,

45   2014; Etzold et al., 2020). Carbon (C)/N ratios in the organic layers have been reduced, and C sequestration in forest soils
has been increased (de Vries et al., 2006; Hyvönen et al., 2008; Meiwes et al., 2009).
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).

50   There is 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 forests, which was

55   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 every 4 to 6 years in Sweden. A review by Wachter (1964),
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 that the definition of a mast year was not based on uniform protocols in the past.

60   The classification of fructification in full-, half-, "spreng"-mast (sprinkle amount) and missing mast are based on litter trap
measurements during the most recent three decades and allowed the 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,

65   Germany. A similar mast interval was reported for 1981 to 2004 period by Schmidt (2006) and Khanna et al. (2009) 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).

70 Differences in summer temperature between the two years preceding mast may affect the amount of fruit produced (Kelly et al., 2013; Vacchiano et al. 2017; Lebourgeois et al., 2018; Nussbaumer et al., 2018). Mund et al. (2020) reported a positive effect of summer precipitation two years prior to fruit production at a beech forest in Thuringia, Germany. A detailed analysis of litterfall at three 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). To what extend a higher mast
75 frequency was involved in the observed accumulation of nitrogen in the soil was not studied.

The objective of our study was to determine the influence of high frequency of fructification on the N fluxes in European beech ecosystems (Fagus sylvatica L.). Results of a ^{15}N labelled leaf litter exchange experiment on 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 the soil. In addition, site,
80 stand and soil specific factors were studied, which potentially influenced litterfall, N retention by trees and in the soil, and N output with seepage water.

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
85 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 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 in Rhineland-Palatinate at Neuhäusel (NHB, 704). The plots are located at 375 to 850 m above sea level (Table 1). Mean temperature ranged from 6.0 to 8.3°C and mean annual precipitation from 712 to 1209 mm.
90 Soil pH (H$_2$O) in 0-10 cm depth ranged from 3.6 to 6.1. Forest floor 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 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

95 #### 2.2.1 Measurements and calculations of nitrogen fluxes

Changes of the soil N pools (ΔS) were calculated by input and output fluxes as follows (all values given in kg ha^{-1} yr^{-1}):

$$\Delta S = ND + NF - NL - NE - NU ; \tag{1}$$

where ND is the total N deposition with atmospheric deposition, NF the N input from the atmosphere by biological fixation, NL the seepage N output below the root zone, NE the net gaseous N exchange, and NU the net N uptake for tree increment.

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

Total N deposition (ND) 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 in winter times. Stemflow was sampled by

105   fixing polyurethane spirals around the stems, which were coated with paraffin. At each site 3 to 10 replicates were installed. Seepage N output (NL) 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 at each site) at 90 or 100 cm depth of the mineral soil (Nieminen et al., 2016). At 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,

110   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

115   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). 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

120   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 years during the observation period and involved standardized silvicultural methods (Dobbertin and Neumann 2016). We calculated the net N uptake for

125   aboveground tree increment (NU) by multiplying the actual growth increment for each plant compartment (solid timber over 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

130   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 at three of the seven sites. The SOB site was one of the few sites in Germany where high annual N_2O emissions (1.92 ± 0.63 kg N ha^{-1}, Brumme and Borken, 2009) were observed. GW site had low N_2O

135   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). 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 from deciduous forests with background emissions of 0.58 kg N ha^{-1} ($0.37 + (0.34 + 0.07)/2$) equals biological N fixation (Posch

140   et al., 2015). Thus net gaseous N exchange 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 equals 1.99 kg N ha^{-1} and after correcting for N fixation a value of 1.41 kg N ha^{-1} ($1.99 - 0.58$ kg ha^{-1}) was used.

Litterfall was collected from 1995-2005 at the site 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

145   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 fractions, leaves, fruit components (seeds + cupules), and twigs. A residual fraction was included in the fruit fraction. At the stand NHB in Rhineland-Palatinate and

150   two other forest sites with European beech, Kirchheimbolanden KHB and Neuhäusel Quarz NHQ, a detailed fractionation and analysis 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 sites we calculated the number of seeds by assuming a seed

155   weight of 0.22 g. The seed weight was determined by using a sample of 300 seeds which 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 NHN, KHB, and NHQ sites where the mass of seeds and cupules were separately measured.

160   Foliar analyses were performed annually to characterize tree nutrition. Samples from 6 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).

165 ### 2.2.1 ^{15}N-labelled leaf litter exchange experiment

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 received ^{15}N enriched solution in the irrigation water. PVC rings (diameter of 26.6 cm) were inserted at the soil surface. After removing the loose litter 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 litter layers

170 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 into slices of 1 to 10 cm thickness. All soil samples were sieved to 2 mm, grinded, 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.

175 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

180 0.368 atom% ^{15}N in 30 – 40 cm soil.

2.3 Data analysis

The relationships between two variables were tested 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

185 regression functions were calculated. In order to confirm results from linear regression analyses, which are assumed to be quite uncertain given the small sample sizes, additionally r_{Spear} values were calculated. 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

190 locations/activities.

3 Results

3.1 Biomass production, foliar nutrition, and N cycling

Annual aboveground net primary production (NPP) amounted to 11.8 Mg dry mass ha^{-1} 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

195   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 3.88 Mg ha^{-1} and contributed 61 % to the mean annual total litterfall of 5.11 Mg ha^{-1}. Leaf litterfall was closely related to tree increment (Table 7; 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 half-mast was synchronous in almost each stand (Fig. 1). No mast event occurred in 1996, 1997, 2005 and 2008. Mast frequency was

200   highest at FRE and EBR sites, the highest increase in total litterfall due to mast was at HOM site (+101 %). In mast years mean annual litter production increased by 2.01 Mg ha^{-1} to an average of 6.1 Mg ha^{-1} compared to non-mast years. The difference in amount of total litterfall between years with and without mast is a result of seed and seed cupule production as well as of changes in other fractions induced by fructification. 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

205   Rhineland-Palatinate revealed a change of +3.3 % in the leaf fraction, +11 % in the twig fraction, and a very high change of +32 % in the residual fraction indicates an increase in the production of components like pollen and flowers (Table 4).

The mean annual N flux with total litterfall amounted to 58.6 kg ha^{-1} from which 34.6 kg ha^{-1} 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 total litterfall N by 32.4 kg ha^{-1} when mast years were compared with non-

210   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 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

215   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 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 low foliar P and higher foliar N/P ratios than stands on basaltic rock or loess.

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3.2 ^{15}N labelled leaf litter exchange experiment

The highest enrichment of $^{15}N_{excess}$ 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). In the 0 to 1 cm and 30 to 40 cm layers the enrichment was lower than 1 %. No $^{15}N_{excess}$ was found in the L layers except at the HOM site. The recovery of $^{15}N_{excess}$ ranged from 32 to 72 % in the upper 40 cm depth of the soils (mean value 48 % ± 5%). This equals an average recovery of 17 kg N ha^{-1} after 5.5 years, estimated by using the percentage ^{15}N recovery X annual leaf litter N flux. Recovery in the organic layer increased with increasing carbon stock in the organic layer (Fig. 2a). Sites with a low recovery rate in the organic layer exhibited higher recovery in the mineral soil and vice versa (Fig. 2b). The recovery of 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).

3.3 N fluxes and N budgets

Total N deposition (ND) was quite similar at measured sites, whereas net uptake for aboveground tree N increment (NU) and seepage N output (NL) differed considerably (Table 6). Annual total N deposition ranged from 18 to 24 kg ha^{-1} during 1994 to 2008 and tree N increment between 4.4 and 14.2 kg N ha^{-1}. Annual seepage N output was relatively low with values ranging from 0.8 to 6.6 kg ha^{-1} except at BBR, where 12 kg N ha^{-1} yr^{-1} were lost with seepage water. Mean annual total N deposition of 20.7 kg N 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. 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 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.

4 Discussion

4.1 Frequency of fructification, biomass production and N demand

A frequency of a heavy mast (full- and half-mast) every 1.4 to 3.0 years (mean 2.0) in seven German beech forests during the study period from 1995 to 2008 (Table 3) confirmed the prior reports by Paar at al. (2011) for Germany, by 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 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 the past. 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 such studies using historic data and litterfall measurements indicated a decrease in the frequency of

255 fructification. Övergaard et al. (2007) showed 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 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 at

260 least in Germany and southern Sweden.

In a mast year an additional 2 Mg ha^{-1} dry mass was returned to the soil when compared to the non-mast years (Table 3). By assuming that under similar biomass production and litterfall conditions mast frequency has been doubled compared to the historic values, mean annual total litterfall may have increased by 0.5 Mg ha^{-1} to 5.11 Mg ha^{-1} and mean NPP by about 4 %.

265 A fertilizing effect of N deposition on forest growth in Europe has been identified for many regions, most pronounced for sites having high C/N ratios in the soil (Solberg et al., 2009, Etzold et al., 2020). The results suggest 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 total litter production in 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 8.7 kg N to 58.6 kg N ha^{-1} as compared

270 to historic conditions. The additional N uptake for total litter production may be even higher if the lower availability of N in historic times is considered. Leaf litterfall as an indicator increased the biomass and N increment of trees at nutrient rich sites (Table 7, Fig. 5).

4.2 Recovery of leaf litter N under high fructification

The ^{15}N leaf litter exchange experiment indicated that about half of N added with the leaf litter, 17 kg N ha^{-1}, was recovered

275 in the upper 40 cm of the soil during the 5.5 years on the beech forest sites (Table 6). 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 this study may be attributed to a shorter duration of the experiment as immobilization of nitrogen exceeded the release of leaf litter N by mineralization during the first two years of the litter

280 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

285   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),
290   suggesting that fruit components as a part of total litterfall were primarily involved in the retention of leaf litter N (Table 7). Fruit production increased dry mass of total litterfall by 49 % compared to non-mast years (Table 4). Seeds are rich in N and P representing lower C/N and C/P ratios whereas seed cupules, which contributed 51 % to the dry mass of the fruit components, showed the highest C/N and C/P ratios of all litter fractions. Seed cupules are woody phyllomes composed of highly recalcitrant lignocellulose tissue (Fukasawa et al., 2012). In a study on fungal succession and decomposition of
295   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-years period (Carré, 1964). Most 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 than e.g. needle litter (Zackrisson et al., 1999), but we are not aware of any
300   comparative study on the decomposition of leaves, seeds and seed cupules. However, the decomposition processes of the different litter fractions might be spatially and temporarily decoupled. A high N demand during the decomposition of seed cupules may be fulfilled by N deposition or the release of N from the decomposition of leaf litter and seeds.

4.3 N fluxes and N budgets

Positive soil N pool changes (ΔS, Eq. 1) indicated the retention of N in the soil at all sites except the BBR site where a small
305   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. Soil acidity seems to be an
310   important factor in the retention of deposited N in forest ecosystems.

Soil N change was unrelated to total litterfall (Table 7) despite the retention of leaf litter N exerted by fruit compounds in the litterfall fraction, indicating that mast event was not the primary factor controlling N retention in soils. This study showed 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 deposition until the 1990s increased the N
315   retention rate in soils (Hyvönen et al., 2008; 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. 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 P. 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 restrict 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). Sites with a low C/N ratio in the mineral soil are often characterized by high soil biological activity increasing N 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 the acid SOB site (Brumme et al., 2009; Schäfer et al., 2009) and retained +60 % N by tree increment and -71 % N by soil N change 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 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) suggest 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 are close to an (quasi-) steady state with high elasticity where acidity is buffered by silicates or carbonates and have 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 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 so far has received little attention because of the irregular nature of 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 mast frequency has increased the amount of carbon and nutrients additions to the soil and increased internal cycling between plants and soil. High total 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. 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 stands with a high mast frequency. Mast did not affect soil N retention calculated by input and output

fluxes because confounding factors such as soil acidification and N saturation processes exerted an important control on N

350 retention. Soil N retention occurred mainly in acid soils. At these sites, soil N retention is still continuing despite a reduction in atmospheric N depositions. The N/P ratio and soil acidity may have increased, reducing the P availability and litter decomposition processes. N retention by trees dominates in less acid soils with higher nutrient turnover and low C/N ratios in the mineral soil layers. Such sites are characterized by a low N retention in the soil. As long as N retention is maintained at the current level the risk of enhanced leaching losses of N from less acid soils seems to be low.

355 **Data availability**

The majority of data used for regression and correlation analysis is being presented here in the tables. The raw and not yet aggregate 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
360 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.

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.

	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
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.*

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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$_2$O)	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

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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 (%) for seven beech forests. Years with mast (full-
600 mast years in bold) and the number of 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	

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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

610 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 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

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Table 6. Average total N deposition (ND), tree N increment (NU), net gaseous N exchange (NE), seepage N outputs (NL)

630 and soil N pool change (ΔS, calculated from Eq. 1) for the period 1994 to 2008, and ^{15}N recovery of applied labelled 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$_{excess}$, in kg N of 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 %	total kg N ha^{-1}	organic layer %
	--- 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. 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**	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

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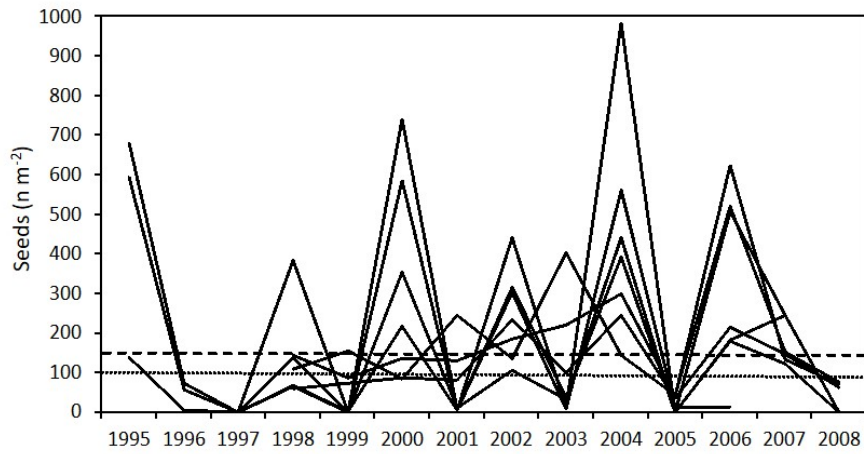
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Figure 1. Production of seeds (seeds m^{-2}) at the study sites. Horizontal lines indicate years with half-mast (100 - 149 seeds m^{-2} – dotted line) and full-mast (>150 seeds m^{-2} –dashed line).

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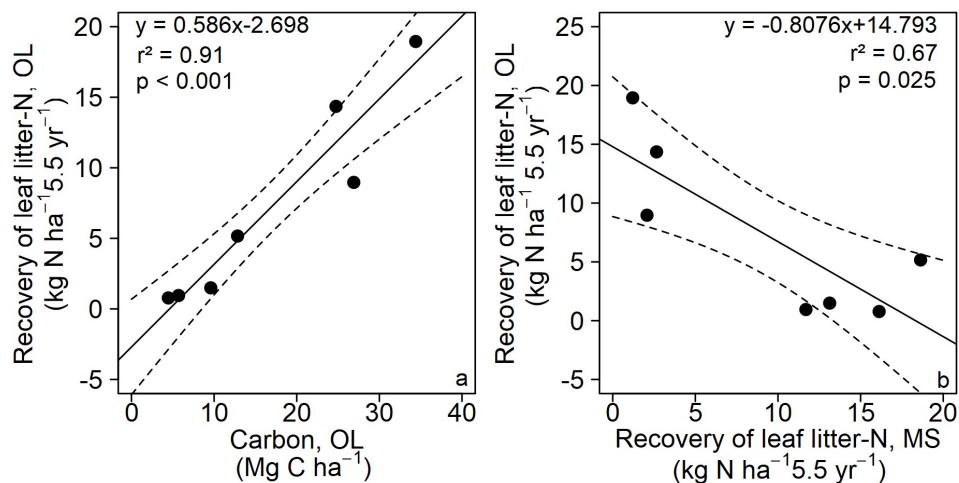
Figure 2. Recovery of leaf litter N (kg N ha⁻¹) calculated from ^{15}N labelled beech litter 5.5 years after litter exchange at the study sites (a) in the organic layer (OL) versus carbon stock in organic layer and (b) in the organic layer versus the recovery in the mineral soil (MS). Solid line = regression 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.
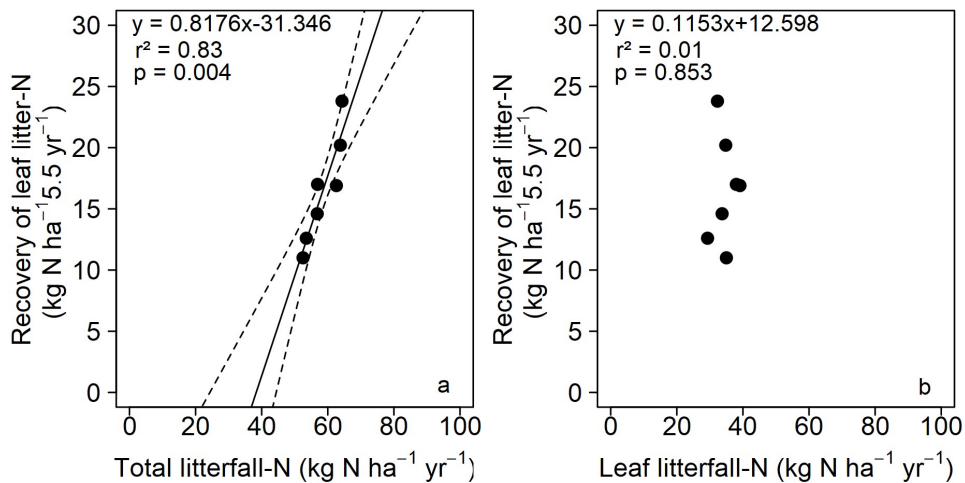
Figure 3. Recovery of leaf litter N (kg ha^{-1} yr^{-1}) calculated from ^{15}N labelled beech litter 5.5 years after litter exchange versus N flux with (a) total litterfall N and (b) with leaf litterfall N (kg N ha^{-1} yr^{-1}) at the study sites. Solid line = regression line. Dotted lines = confidence 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.
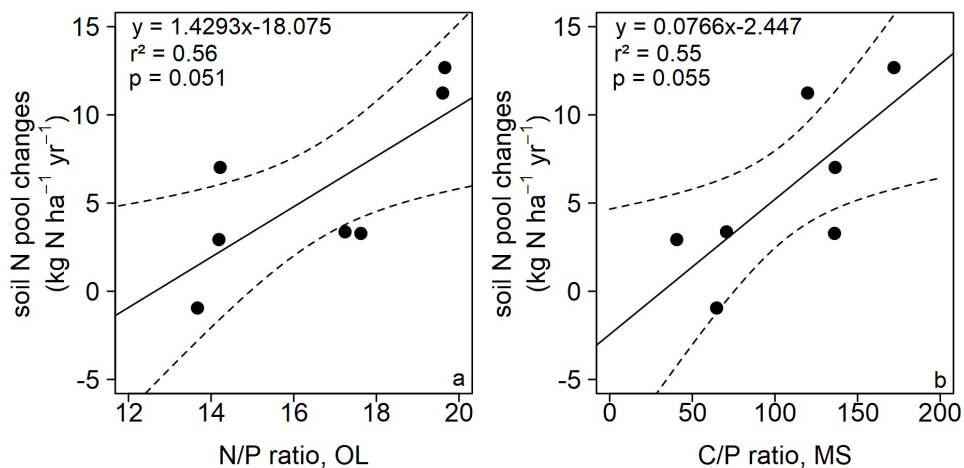
Figure 4. Soil N pool changes (ΔS, kg N ha^{-1} yr^{-1}) a versus N/P ratio in the organic layer (OL) (a) and versus the C/P ratio in the upper mineral soil (0 – 10 cm) (MS) (b). Solid line = regression line. Dotted lines = confidence bands of regression with p = 0.90. Spearman's rank correlation (a) r_{Spear} = 0.86, p < 0.05; (b) r_{Spear} = 0.79, p = < 0.05.
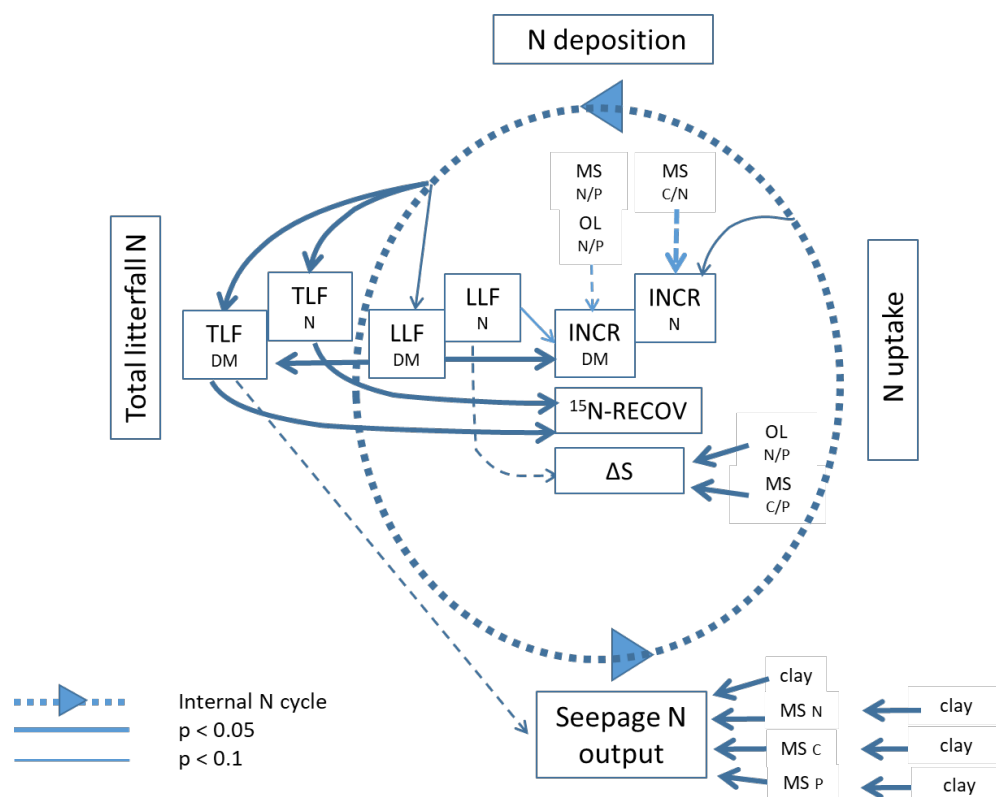
Figure 5. Schematic view of the internal N cycling (N uptake by trees for leaf, fruit, and tree increment production; N release by total litterfall, TLF, including leaf litterfall, LLF) and the external N cycling (deposition, seepage output, soil N pool change, ΔS, tree increment, INCR) and leaf ^{15}N recovery (^{15}N RECOV). 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 correlations ($p < 0.1$). Mineral soil (MS), organic layer (OL), dry mass (DM).