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A multi-nutrient budget helps to understand masting regulation in beech forests along a fertility gradient

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Abstract. Forest ecosystem fertility and tree nutrition strongly depend on efficient biogeochemical nutrient cycles. Mast events require large amounts of carbon and nutrients and may therefore affect cycling efficiency. This study aimed to quantify the impact of episodic mast events on multiple nutrient fluxes under contrasting fertility conditions.

We conducted a multi-nutrient study (K, Mg, P, S and N) over an 12-year period (2012–2023) in three mature European beech (Fagus sylvatica L.) forests along a fertility gradient (S1>S2>S3). Nutrient fluxes associated with aboveground biomass production (wood, leaves and reproductive organs), canopy leaching, and leaf nutrient resorption were quantified. Mast effects were assessed by comparing mast years (MY) and non-mast years (NMY).

Across ecosystems, total aboveground biomass production increased by 19% on average during MY due to reproductive organ formation, while wood and leaf production remained unchanged. MY significantly enhanced nutrient fluxes via litterfall but also via canopy leaching particularly for K (+46%, +9 kg ha^{-1} yr^{-1}), with impacts on seasonal dynamics. In contrast, leaf nutrient resorption was globally not affected by MY. The total nutrient content in aboveground biomass production (NCB ; sum of all the measured fluxes) increased for all nutrients during MY compared to NMY, with the strongest responses observed for Mg (+53%), K (+44%) and P (+43%), and more moderate effects for S (+24%) and N (+9%). Overall, our results highlight that canopy leaching and resorption, which remain understudied, are essential for accurately estimating nutrient budgets in aboveground biomass production.

A clear fertility effect was observed, with higher fruit production and increasing K, Mg and P requirements from S3 to S1. Despite elevated nutrient demands, MY did not induce nutrient limitation or reduce vegetative growth, indicating that current soil and tree nutrient reserves accross the 3 ecosystems are sufficient to buffer reproductive costs under present climatic conditions. This study highlights the importance of a multi-nutrient perspective and proposes a novel indicator comparing MY nutrient budgets with available nutrient reserves to better assess nutritional constraints associated with masting.

Key words. Masting, Beech forest, Nutrient cycling, Canopy leaching, Biomass production, Fertility gradient

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1 Introduction

In forests, tree nutrition is tightly linked to ecosystem fertility, which is mainly driven by nutrient cycle efficiency (Legout et al., 2020). Because most forests develop on nutrient-poor, unfertilized soils, biological cycling is widely recognized as the primary driver of forest ecosystem fertility (Ponette et al., 2001; Ranger et al., 2002)~~,~~ . This cycle corresponds to the recycling of nutrients between trees and soils and relies on above- and belowground litter production, canopy leaching, soil organic matter decomposition, and root uptake. As an example, the biological cycle at the Hubbard Brook site (New Hampshire, U.S.) represents 69% of N needs to support stand growth (Likens, 2013; Yanai, 1992). In addition, the biochemical cycle, corresponding to nutrient translocation and internal recycling between tree organs, is another recycling strategy to support tree nutrition. For temperate deciduous trees, the resorption process during leaf senescence is especially efficient as it can resorb 60% of the N from the leaves to the branches prior to leaf abscission, (Vergutz et al., 2012). This nutrient reserve can be directly remobilized for leaf formation thus reducing tree dependence on soil nutrient availability. Finally, nutrient inputs can also occur in forest ecosystems, through the geochemical cycle with mineral weathering or atmospheric deposition.

Thus, the nutrient content in aboveground biomass production each year (hereafter called NCB) is either derived from tree nutrient reserves (R_T) through internal recycling, either derived from soil nutrient reserves (corresponding to nutrient available pool; R_s) which are mainly supported by biological recycling (blue arrows in **Fig. 1**). In return, the NCB highly contributes to supply nutrients to these two reserves thanks to leaf resorption, canopy leaching and litter production (red arrows in **Fig. 1**). In addition, a part of the NCB is stored in perennial biomass through annual growth increment (black arrow in **Fig. 1**). At a larger timescale, this stock will return to the forest floor with dead wood (thin red arrow in **Fig. 1**) that will undergo degradation to contribute to the soil reserves just like litterfall.

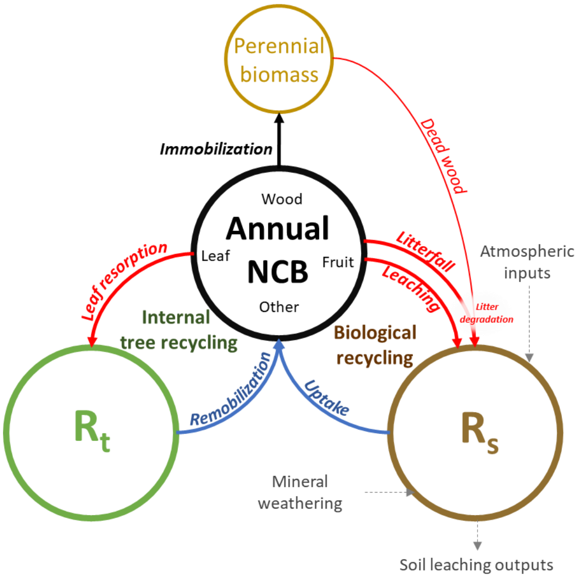

Figure 1: Conceptual diagram of the different fluxes and pools involved in tree nutritive cycles. NCB = nutrient content in total aboveground biomass production ; Rt = Tree nutrient reserves ; Rs = Soil nutrient reserves.

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This system, based on multiple exchanges and relationships, allows an efficient tree nutrition under normal conditions; however, various stressors can disrupt this balance. These stressors includ abiotic drivers such as droughts and heatwaves, as well as biotic pressures such as pests and pathogens, all of which are usually external to the ecosystem. In addition, some recent ecophysiological studies suggest that phenomena such as masting may also act as biotic stress factor (Nussbaumer et al., 2021). Mast events correspond to the synchronized production of fruits and seeds between individuals of the same species and the same stand. This reproductive strategy, frequent among perennial plants, seems to provide evolutionary advantages and economies of scale, notably through enhance pollination efficiency and predator satiation (Han and Kabeya, 2017; Koenig, 2021). However, these benefits come at a substantial cost in terms of carbon and nutrient investment as mast events require a major mobilization of resources. Therefore, the occurrence of two consecutive mast years is highly unlikely. As a consequence, resource demand for reproductive organs differs markedly between mast years and non-mast years (hereafter referred to as MY and NMY, respectively). Current literature on mast events in forest ecosystems has mainly looked on the ultimate (evolutionary pressures ; Han and Kabeya, 2017; Koenig, 2021) and the proximate drivers like climatic cues (Allen et al., 2014; Fernández-Martínez et al., 2017; Hacket-Pain et al., 2025; Lebourgeois et al., 2018; Meng et al., 2022; Müller-Haubold et al., 2015; Nussbaumer et al., 2018) or ressources accumulation (Abe et al., 2016; Han et al., 2014; Han and Kabeya, 2017) leading to the occurrence of MY. As an example, the general increase of temperature with climatic changes may partly explain the increase frequency of MY for some deciduous species in Europe, during the past decades (Allen et al., 2014; Bogdziewicz et al., 2020; Nussbaumer et al., 2016). The current research also focuses on the impacts of MY on stand functioning through biomass production and carbon cycle. For example, the observed increase in frequency of MY in beech forests in Germany has led to an 4% increase of their average NPP (Brumme et al., 2021). It has been demonstrated multiple times that leaf production and stem growth can be reduced during MY, probably due to resources limitations (Bajocco et al., 2021; Hacket-Pain et al., 2025; Müller-Haubold et al., 2015; Nussbaumer et al., 2021). Although the notion of nutrient resource is often mentioned, a more limited number of studies have explicitly looked at the impacts of MY on nutrients. These studies are generally limited to N (with P and K to a lower extent). It has been demonstrated that the high fruit production during MY is sometimes related to a decrease of N concentration or content in leaves (Han et al., 2011, 2014; Müller-Haubold et al., 2015; Nussbaumer et al., 2021), but also in other tree organs (Han et al., 2014). However, despite the existence of general patterns, substantial heterogeneity in results and conclusions across study sites suggests that ecosystem-specific properties, particularly ecosystem fertility, may modulate the magnitude of the impacts associated with mast years.

When considering the concept previously presented in **Fig. 1**, we notice a lack of real quantification of the impact of MY on important nutrient pathways such as canopy leaching, nutrient resorption (Yasumura et al., 2006) or even the total nutrient content in aboveground biomass production (NCB ; **Fig. 1**). However, literature results tend to indicate that MY may modify the nutrient recycling dynamics, that are the key to an efficient tree nutrition. In the current context of climate changes, MY may act as additional stress factor increasing the risks of nutrient resource depletion (Hacket-Pain et al., 2025). Thus, it is important to quantify their impacts on the biogeochemical cycles of the different macronutrients.

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The objectives of our study are to quantify, during MY and NMY, (i) the aboveground biomass production and the NCB of N, K, P, S and Mg, (ii) the different nutrient fluxes through the two main recycling pathways, i.e., the internal recycling (leaf resorption) and the biological recycling (canopy leaching and litterfall production) and (iii) to assess whether differences in fertility may modulate the impact of MY on the biogeochemical cycles and ecosystems responses. Considering literature, we expected an increase of total biomass production and NCB during MY compared to NMY. Moreover, the massive fruit biomass production was expected to impact canopy composition and thus the canopy leaching and resorption, leading to modification of recycling dynamics. Depending on the ecosystem fertility and potential nutrient limitation the impact of MY on recycling strategy and nutrient needs may vary, with less fertile ecosystems being relatively more impacted.

To answer our objectives, a medium-term monitoring of the biogeochemical cycles of several forest ecosystems – including MY and NMY – is needed. Thus, we chose to conduct our study on the Montiers site (Meuse, France) where 3 mature beech forests developed on 3 different soils corresponding to gradient of fertility/production (Calvaruso et al. 2017). These 3 ecosystems are highly instrumented for the monitoring of the different fluxes and stocks of N, K, P, S and Mg within aboveground biomass production and solutions. This study was conducted from 2012 to 2023, and includes 4 MY and 8 NMY.

2 Material and methods

2.1. Study site and experimental set up

The present study was conducted at the Montiers experimental site, located in the Montiers-sur-Saulx forest in northeastern France (Meuse department; 48°31’05’’ N, 5°16’00’’ E; 365 m above sea level). The site covers an area of 73 ha and was build in 2012 in the framework of the Perennial Observatory of the Environment (https://ope.andra.fr/) of the French National Radioactive Waste Management Agency (Andra). The infrastructure of the Montiers site is part of the AnaEE research network (https://www.a naee.com/) and is jointly managed by Andra and INRAE-BEF (Biogeochemical Cycles in Forest Ecosystems Research Unit of the French National Institute for Agricultural Research).

The region is characterized by a semi-continental climate. Over the 2004-2023 period, the mean annual precipitation and temperature were 1035 mm and 9.9 °C (Météo-France data). These conditions are in the middle of the ecological range of the main species of this site, the European beech (*F. sylvatica ;* 88% of the stand), which naturally occurs in areas receiving ~500 to 2,000 mm of rainfall annually (Peters, 1997). The other deciduous species found are sycamore maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*), pedunculate oak (*Quercus robur L.*), European hornbeam (*Carpinus betulus L.*), and wild cherry (*Prunus avium*) (Calvaruso et al., 2017).The forest stand is even-aged and was 51 ± 3 years old at the onset of the experiment in 2012 (Calvaruso et al., 2017). Forest management is homogeneous across the site and consists of harvesting approximately 30 t ha^{-1} of dry biomass (stems and branches >7 cm diameter) every 7–8 years to sustain stand growth. The last harvesting campaign took place before the growing season of 2018. In 2011, the stem density averaged around 800 stems ha^{-1}, and dominant beech height reached 26.8 ± 2.2 m (Kirchen et al., 2017). Between 2012 and 2015, annual stand productivity ranged from 5.8 ± 0.8 to 10.0 ± 0.5 t ha^{-1} yr^{-1} (Turpault et al., 2019), corresponding to the highest beech yield classes in north-eastern France (Seynave et al., 2008).

Geologically, the Montiers site corresponds to Valanginian detrital formations (silt, clay, coarse sand, and iron oxides), with Portlandian limestone outcrops (calcium carbonate and ~ 3% clay minerals) occurring on the lower slope (Calvaruso et al., 2017). The experimental Montiers site, consisting in three main ecosystems, was set up accordingly to the typical pedology developped from these parent materials: one on a Dystric Cambisol (S1 ; acidic deep soil >2m), one on a Eutric Cambisol (S2 ; calcareous soil ≈60cm), and one on a Rendzic Leptosol (S3 ; shallow calcareous soil <30cm). Four plots of 2500m² were distinguished in each ecosystem. Soil water-holding capacity (SWHC) measured of the fine earth fraction decreases markedly along the soil gradient, ranging from 204 mm in the Dystric Cambisol (S1) to 58 mm in the Rendzic Leptosol (S3) (Kirchen et al., 2017). Their main physico-chemical characteristics, up to 60cm depth, are provided in **Table 1** (Calvaruso et al., 2017; Kirchen et al., 2017). According to Calvaruso et al., 2017 who studied the relationships between soil water and nutritive resources and stand growth, S3 can be considered as the less fertile ecosystem of the site with low nutrient and water reserves, while S1 (with the highest water reserve capacity) and S2 (with the highest soil nutrient reserves) are equivalents.

Table 1: Physico-chemical properties of the three soils in the Montiers site ; plot S1 – Dystric Cambisol; plot S2 – Eutric Cambisol; plot S3 – Rendzic Leptosol (Table adapted from Kirchen et al. 2017). Mean values are presented for soil water holding capacity (SWHC), soil pH (pH) measured with water addition, textural distribution (g.kg^{-1} ; clay: <2 µm, silt: 2-50 µm, sand: 50µm-2 mm), total rock volume (RV), organic matter content (OM), cation exchange capacity (CEC ; cmol^{+}kg^{-1}) and base-cation saturation ratio (S/CEC, with S being the sum of base cations). Standard deviation of values among the three replicates are given in brackets

	Depth	SWHC	pH$_{water}$	Clay	Silt	Sand	RV	OM	CEC	S/CEC
	cm	mm			g.kg^{-1}		%	g.kg^{-1}	cmol+.kg^{-1}	%
S1 Dystric Cambisol (Acidic mull)	0–5	8.2	4.9	255 *(25)*	441 *(21)*	306 *(28)*	1.4	68 *(22)*	6.7 *(3)*	64 *(23)*
	5–15	16.5	4.8	245 *(26)*	438 *(23)*	315 *(32)*	1.4	*43 (16)*	*4.2 (2.2)*	35 *(21)*
	15–30	22.7	4.8	268 *(28)*	441 *(26)*	285 *(38)*	1.8	*26 (9)*	*3.5 (0.9)*	26 *(14)*
	30–45	22.6	4.9	306 *(65)*	412 *(36)*	280 *(40)*	2.3	*15 (5)*	*4.3 (1.6)*	36 *(16)*
	45–60	18.1	5.1	355 *(100)*	355 *(38)*	307 *(44)*	3.6	10 *(2)*	5.7 *(2.6)*	55 *(22)*
S2 Eutric Cambisol (Eutrophic mull)	0–5	9.2	5.4	242 *(52)*	385 *(15)*	373 *(30)*	2.3	73 *(26)*	10.1 *(5.4)*	83 *(14)*
	5–15	18.2	5	241 *(65)*	391 *(15)*	369 *(35)*	3.1	45 *(29)*	7.8 *(7.3)*	59 *(24)*
	15–30	19.1	5.3	294 *(83)*	370 *(20)*	337 *(33)*	7.6	27 *(13)*	7.7 *(3.9)*	61 *(23)*
	30–45	14.7	5.3	420 *(141)*	295 *(37)*	285 *(42)*	29	17 *(8)*	13.2 *(6.9)*	68 *(27)*
	45–60	10.3	5.4	523 *(136)*	239 *(37)*	239 *(44)*	40.3	11 *(4)*	17.8 *(8.8)*	76 *(17)*
S3 Rendzic Leptosol (Eutrophic mull)	0–5	9.8	5.7	449 *(80)*	350 *(40)*	160 *(27)*	2.3	109 *(27)*	24.9 *(8.3)*	98 *(5)*
	5–15	19.2	5.7	430 *(82)*	338 *(46)*	182 *(29)*	5	71 *(23)*	20 *(7.9)*	94 *(7)*
	15–30	12.5	6	516 *(81)*	246 *(44)*	165 *(33)*	36	42 *(10)*	23.2 *(6.4)*	99 *(5)*

2.2. Samplings and measurements

In each of the 3 monitored forest ecosystems – S1, S2 and S3 – 3 out of the 4 plots were identically equipped for water below canopy and biomass samplings. Concurrently, the 4 plots of each ecosystem were integrated into the stem growth monitoring.

2.2.1. Water samplings

Precipitations volumes above canopy were from Biencourt-sur-Orge Météo France weather station (4.3 km from the Montiers site). In addition, atmospheric bulk depositions were sampled, for chemical analysis, on the flux tower – located near S1 – thanks to three collectors (0.24 m² opening) connected to storage containers (50 L).

Throughfall samples were collected – for chemistry and volumes – thanks to four polyethylene gutters (0.39 m² opening) per replicates, connected to storage containers (120 L). Six trees that cover the range of trunk circumferences of S1, S2 and S3 were chosen in each replicate to collect stemflow – for chemistry and volumes – thanks to polyethylene collars installed horizontally to the stem at 1.5 m and connected to storage containers (120, 150 and 310 L). Note that we took care to store the containers of throughfall and stemflow in underground cellars that were thermally insulated in order to limit microbial processing between 2 sampling campaigns.

Water samples were collected every 28 days from January 2012 to December 2023. Before chemical analysis, all water samples were filtered at 0.45 µm.

2.2.2. Biomass samplings

Green leaves were sampled by rifle shooting every year in August, on 5 beech trees per plot.

Six litter traps (0.34m² each) on each replicate were used to collect litterfall in March, May, August and five times from October to December each year. The litterfall was sorted in three compartments: senesced leaves, senesced fruits (seeds + cupules) and others (mainly bud scales and male flowers). Dead wood was not considered in this study as it comes from the perennial part of the trees and does not correspond to an annual biomass production.

Before chemical analysis, all biomass samples were stocked in a stream air-drier at 65°C during 72h and then grounded. Note that to allow stocks and fluxes quantification, litterfall samples were also weighed before the grounding process.

2.2.3. Stem measurements

Stem growth was monitored by measuring the trunk circumference at 1.30m (C130) for every trees on each replicate. This monitoring was assessed every November at the end of the growing season – from 2011 to 2023 – with a measuring tape and by two independent operators consecutively.

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2.3. Chemical analyses

Water samples were analysed for K, P, Mg and S concentrations with inductively coupled plasma-atomic emission spectrometry (700 Series ICP-OES, agilent Technologies). N concentration was quantified with a TOC analyser (TOC-L, Shimadzu).

Biomass samples were analysed for K, P, Mg and S concentrations with an X fluorescence sequential spectrometer S8 TIGER 1 kW (Bruker, Marne la Vallee, France). N concentrations was quantified with a CHN analyser (EA/NA 1110, Thermo Quest). The samples were always tested against certified standards. The measurement uncertainty is at most 10%.

2.4. Calculation and model

2.4.1. Water fluxes

Water (mm.period^{-1}) for each sampling period (i.e. number of days between two consecutive sampling dates) and each replicate were obtained by multiplying the volume (L) with the collecting surface (m²). The procedure used to convert individual-tree stemflow volumes into water fluxes (mm) follows the method detailed in Turpault et al. (2021). For a given species, stem circumference measured at 1.30 m is assumed to be the primary determinant of the variability in stemflow volume among trees. Based on this principle, the total stemflow volume for each replicate and sampling period was estimated from the number of trees, their circumferences, and the circumference–stemflow relationship established for the instrumented trees. The corresponding water flux (mm) for each replicate was then calculated by dividing this total volume by the replicate area (2500 m²).

The K, Mg, N, P and S fluxes (kg.ha^{-1}.period^{-1}) were obtained by multiplying the measured concentrations by the water periodic fluxes (mm.period^{-1}), followed by a conversion to a per-hectare basis. Annual water and nutrient fluxes (mm.yr^{-1} and kg.ha^{-1}.yr^{-1}) were obtained by summing the periodic fluxes within the same year.

2.4.2. Litterfall production

The biomass fluxes (t.ha^{-1}.yr^{-1}) of senesced leaves (Leaf$_S$), senesced fruits (Fruit$_S$) and Others, for each sampling period and replicate were obtained by multiplying the dry mass (g) with the collecting surface (m²), followed by a conversion to a per-hectare basis. The K, Mg, N, P and S fluxes (kg.ha^{-1}.period^{-1}) were obtained by multiplying the measured concentrations by the biomass periodic fluxes. Annual Leaf$_S$ and Others fluxes (kg.ha^{-1}.yr^{-1}) correspond to the sum of periodic fluxes within the same year. Annual fluxes of senesced fruits correspond to the sum of seeds and cupules collected from August to December of the current year and in March of the subsequent year. Finally, the total litterfall production is the sum of Leaf$_S$, Fruit$_S$ and Others annual fluxes.

2.4.3. Green leaf pools

As green leaf biomass could not be measured, the annual nutrient pool in green leaves were derived from the **Eq. (1)**:

$$Leaf_g = \frac{Biomass\ Leaf_S}{0.784} \times [Leaf_g] \quad (1)$$

Where $Leaf_g$ is nutrient pool in green leaves (kg.ha^{-1}), Biomass $Leaf_S$ is the annual senesced leaf biomass flux (kg.ha^{-1}.yr^{-1}), [$Leaf_g$] the nutrient concentration in green leaves in August (g.kg^{-1}), and 0.784 the correcting factor determined by Vergutz et al., 2012 (a meta-analysis for deciduous woody angiosperms in different climate conditions) to account for the leaf mass loss (21.6%) during the senescence process.

2.4.4. Canopy exchanges

According to Turpault et al., 2021, the relationship leading to soil deposition (SD) can be described by the Eq. (2) :

$$SD = TF + SF = BD + CE + DD \quad (2)$$

Where, each nutrient, TF is the flux in throughfall, SF the flux in stemflow, BD the atmospheric bulk deposition, CE the canopy exchange and DD the dry deposition <0.45µm captured by the canopy. The latter is determined by using the canopy budget model developed by Ulrich, 1983 and extended by Draaijers et al., 1997. Na is used as a tracer ion of dry deposition (DD) as its CE flux is assumed to be negligible, thus dry deposition of Na is calculated as followed :

$$DD_{Na} = SD_{Na} - BD_{Na} \quad (3)$$

Then, the dry deposition were estimated thanks to the Na DD factor :

$$DD = \frac{DD_{Na}}{BD_{Na}} \times BD \quad (4)$$

Thus the nutrient flux within the canopy exchanges CE were calculated as followed :

$$CE = SD - BD - DD \quad (5)$$

Note that DD fluxes are only calculated for K and Mg. Canopy exchange corresponds either to absorption (when <0) or leaching (when >0). These calculations are done for periodic fluxes that were then sumed to obtained annual canopy exchanges.

2.4.5. Tree internal recycling fluxes

The quantification of the leaf resorption needs to be done during the senescence period, from September to November included. For NMY (2012, 2013, 2015, 2017, 2018, 2019, 2021 and 2022), we admit that the majority of the canopy exchanges during senescence corresponds to foliar leaching and foliar absorption. Thus, the leaf resorption during the senescence period R_S (in kg.ha^{-1}.yr^{-1}) is obtain with the following Eq. (6) from Turpault et al., 2021:

$$R_S = Leaf_g - (Leaf_S + CE_s) \quad (6)$$

With R_S corresponding to the leaf resorption (kg.ha^{-1}.yr^{-1}) during the senescence period, $Leaf_g$ the nutrient stock in green leaves (kg.ha^{-1}), $Leaf_S$ the nutrient flux with senescent leaves (kg.ha^{-1}.yr^{-1}) and CE_s the canopy exchange during the senescence period (i.e., sum of the canopy exchanges from September to November). The $Leaf_S$ and CE_s fluxes corresponds to the biological recycling.

During MY, a large part of the canopy is composed of fruits during the senescence period. Thus, it is necessary to estimate the part of the canopy exchange, especially the leaching, related to this compartment before quantification of resorption fluxes between leaves and branches. For each nutrient we created two models using R (v4.5.2), with the package glmmTMB (Gamma family distribution with a log link function or gaussian family distribution in presence of negative values) to modelize the canopy exchanges during senescence. To account for non-linear relationships, each fixed effects was modelled using natural cubic splines with 3 degrees of freedom (function ns() of the splines package). All continuous predictors were centred and scaled prior to analysis. The first model – CE_{sV1} ; **Eq. (7)** – was calibrated from NMY data and we considered the nutrient stock in green leaves ($Leaf_g$) and the cumulated water fluxes in soil deposition (SD_S) and mean temperatures (T_S ; data from Meteo France) during senescence as fixed effects and the replicates (1|Replicate) as random effect :

$$CE_{sV1} = \beta_0 + ns(Leaf_g) + ns(SD_S) + ns(T_S) + (1|Replicate) \tag{7}$$

The second model – CE_{sV2} ; **Eq. (8)** – was calibrated using all the data from 2012 to 2023, and we included the nutrient fluxes with senescent fruits ($Fruit_S$) in the fixed effect :

$$CE_{sV2} = \beta_0 + f_1(Leaf_g) + f_2(Fruit_S) + f_3(Rainfall_S) + f_4(T_S) + (1|Replicate) \tag{8}$$

We evaluated the models CE_{sV1} and CE_{sV2} for each nutrient via diagnostic checks (using the DHARMa package) and marginal and conditional R² (Nakagawa and Schielzeth, 2013). We modelled the canopy exchanges for each replicate during the senescence period of the MY using the two models. Thus, the part of leaching related to the fruits is expressed as a factor (f_{CE}) and was calculated as followed, for each replicate, during each MY:

$$f_{CE} = (CE_{sV2} - CE_{sV1})/CE_{sV2} \tag{9}$$

The f_{CE} for each nutrient during each MY in the three ecosystems are available in Table S1. Using these factors, the leaf resorption fluxes during the senescence period of MY was calculated for each nutrient on each replicate as followed:

$$R_S = Leaf_g - (Leaf_S + (CE_s - (CE_s * f_{CE}))) \tag{10}$$

The R_s can be either positive indicating flux from leaves to branches during senescence, or negative, indicating flux from branches to leaves during senescence. The latter is called negative resorption or accretion.

2.4.6. Wood production and nutrient immobilization

Stem and branches are defined as the aboveground perennial compartment, also referred as ‘wood’ in this paper. Each year, the total wood biomass was estimated for each tree according to allometric equations considering the measured dbh (see Calvaruso et al., 2017). Thus, annual wood production for each tree corresponds to the difference of wood biomass between 2 consecutive years. The wood production of each replicate ($t.ha^{-1}.yr^{-1}$) was calculated by summing individual wood productions and dividing it by the replicate area (2,500 m²) to obtain a per-hectare basis.

The nutrient immobilization through wood production was calculated by multiplying nutrient concentrations from Calvaruso et al., 2017 to the annual wood production in each replicates. Briefly, in 2009, stem, bark and branches of different diameters (<4, 4-7 and >7cm) were collected from nine trees on S2 to determine K, Mg, N, P and S concentrations.

2.4.7. Nutrient Content in Biomass production (NCB)

The NCB is defined as the total amount of nutrient ($kg.ha^{-1}$) required for the biomass production in a year (aboveground parts only). Thus, it has to include the nutrient amount ($kg.ha^{-1}.yr^{-1}$) in the different tree compartments : immobilization in Wood ($Wood_i$), green leaves ($Leaf_g$), green Fruits ($Fruit_g$) and other annual parts (buds scales, flowers ; $Other_g$). For some nutrients it has also to includes the foliar absorption (when CE< 0, mainly concerns N), and foliar accretion (when $R_S < 0$). As nutrient stocks in green parts (Leaves, Fruits and Others) cannot be directly measured, the NCB is quantify in this study thanks to **Eq. (11)**, by summing the nutrient amount in $Wood_i$, in litterfall (sum of senesced parts returning to the forest floor), in Foliar resorption (when $R_S > 0$) and in canopy leaching (when CE > 0):

$$NCB \ = Wood_i + Litterfall + R_{S+} + CE_+ \tag{11}$$

Finally, the NCB partitioning between the different compartments (Leaching, Wood, Other, Fruit, Leaf, and Leaf Resorption) was determined for each replicate and for each nutrient by calculating the percentage of NCB in each compartment.

2.5. Statistical analysis

Statistical analyses were carried out on R (version 4.5.2.). First to highlight effect of masting on biomass production, NCB, the different nutrient fluxes or the % of NCB in the different compartments we determined the significant differences between the two year types (i.e., MY and NMY) using the Wilcoxon test. In addition, we performed linear mixed effect model (from package glmmTMB, version 1.1.10) to highlight various specific differences. The tested variables and the fixed effects of the different models are listed in **Table 2**. In each case, the replicates were always defined as random effect (1|Replicate). When the mixed model identified significant impact of the fixed effect on the tested variable, a post-hoc test was performed using 'emmeans' function (package emmeans, version: 1.10.6) followed by 'pair' function with Tukey correction.

Table 2: Synthesis of the different tested variables, fixed effects and random effects in the performed linear mixed models

Tested variables	Fixed effects	Random effect
• Total biomass prod. • Biomass prod. In each compartment • NCB of each nutrient • Nutrient fluxes through Canopy exchanges/Litterfall/Resorption	Interaction : Year type*Ecosystem	1|Replicate
Total biomass prod. for S1, S2 & S3 individually	Year	
• Wood prod. • Leaves prod. • Other prod.	Fruit prod.	
Fruit prod.	Interaction : Wood production*Ecosystem	
• Green leaf concentrations • Cost of reproduction (NCB_{MY} - NCB_{NMY})	Ecosystem	

The significance levels of 0.05 (* or distinct letters for post-hoc test) was applied for all statistical tests. In addition, significance levels 0.01 (**) and 0.001 (***) were also applied when relevant. The Gamma family distribution with a log link was preferentially used for all linear mixed model, and was replaced by the gaussian family distribution only in presence of negative value (i.e. resorption fluxes). Residuals were checked using the DHARMa package (version 0.4.7)

3. Results

It is important to distinguish two types of MY on S1 and S2 ecosystems, i.e., 3 full MY (2016, 2020, and 2023) and 1 half MY (2014) with a lower fruit production. For this reason, year 2014 is systematically distinguished in the Figures presented below. The statistical results always include both half and full MY, and, when necessary, additional letters are mentioned in grey to specify statistical results without the half MY 2014.

3.1. Aboveground biomass production and partioning

As shown in **Fig. 2**, total aboveground biomass production during MY reaches 17.3 ± 0.8, 14.6 ± 0.9, and 11.9 ± 1.1 $t\ ha^{-1}\ yr^{-1}$ on S1, S2, and S3, respectively. Relative to NMY, with values of 14.0 ± 1.1 $t\ ha^{-1}\ yr^{-1}$ on S1, 12.4 ± 1.3 on S2, and 10.4 ± 1.0 on S3, the total aboveground biomass production increases significantly during MY by 23%, 18%, and 14% at S1, S2, and S3 respectively. A significant soil effect was observed in both MY and NMY, with consistently higher biomass production at S1 than at S2 and S3 (S1 > S2 > S3). Regardless of soil type, the total aboveground biomass production increases on average by 19% during mast years.

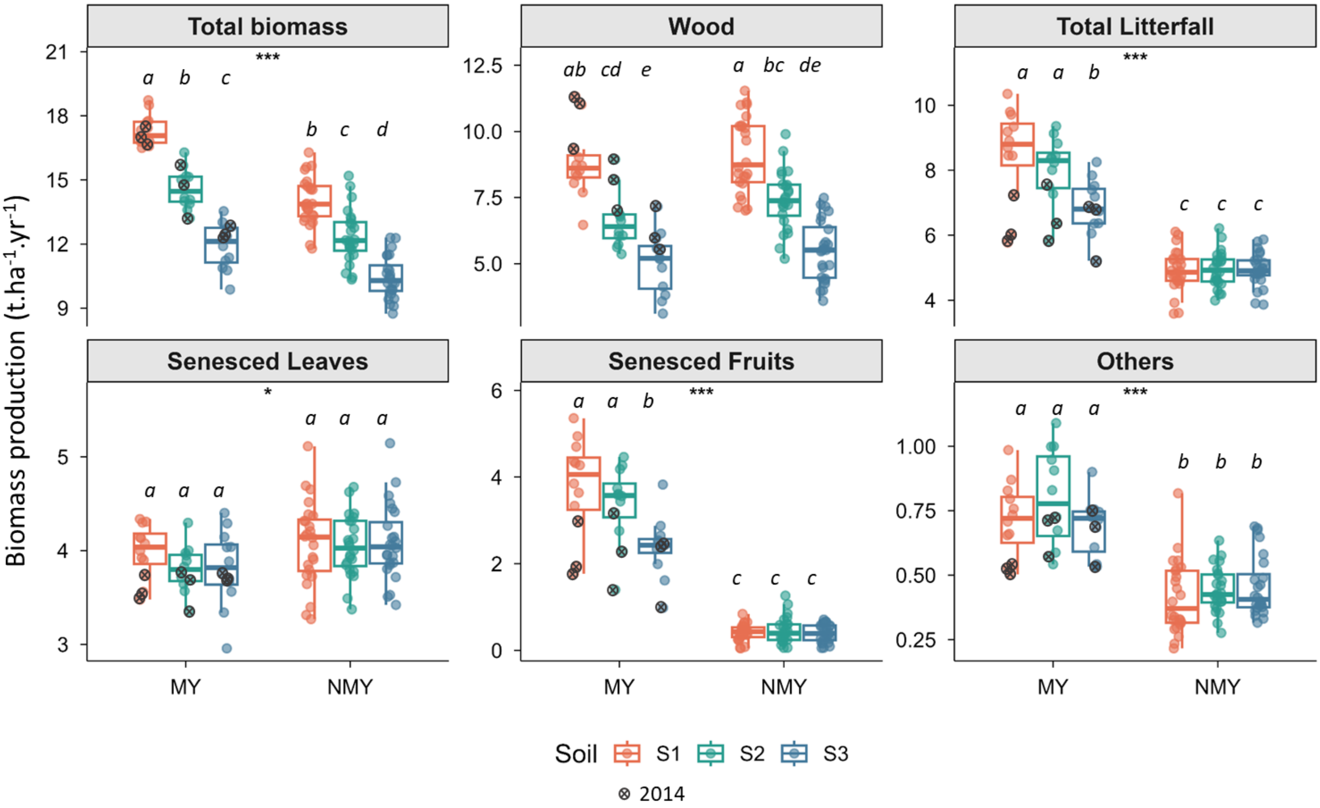

Figure 2: Annual production (t.ha^{-1}.yr^{-1}) of total biomass, wood, total litterfall, senesced leaves, senesced fruits and other non perennial parts, during MY vs. NMY and in the three studied ecosystems (S1, S2, S3). Asterix indicate significant differences between MY and NMY without ecosystem distinction (*<0,05 ; ** < 0,01 ; * < 0,001). Different letters indicate significant differences among groups (i.e. ecosystem*year type), with a threshold p value of 0,05. The half MY of 2014 is differenciate from the other MY with crossed cycles, but is not excluded from the statistical tests.**

No significant difference is observed between MY and NMY for wood production (**Fig. 2**) and the same soil effect (S1>S2>S3) as for total biomass is detected. Thus, the average annual wood production for the 2012-2023 period is of 9.0±1.4 t.ha^{-1}.yr^{-1} on S1, 7.1±1.1 t.ha^{-1}.yr^{-1} on S2 and 5.3±1.2 t.ha^{-1}.yr^{-1} on S3.

Total litterfall production during MY reaches on average 8.5 ± 1.5, 8.0 ± 1.1 and 6.9 ± 0.8 t·ha^{-1}·yr^{-1} for S1, S2 and S3, respectively, which represents a significant increase of 73%, 61% and 39% compared to NMY during which litterfall represents on average 4.9 ± 0.6 t·ha^{-1}·yr^{-1}. This corresponds to an average increase of 58%. A significant soil effect is also detected during MY, with higher litterfall production on S1 and S2 compared to S3, while no significant soil effect is detected during NMY.

For senesced leaves, no soil effect is detected during both MY and NMY (**Fig. 2**). The leaf production is on average of 3.8±0.3 t.ha^{-1}.yr^{-1} during MY and of 4.1±0.4 t.ha^{-1}.yr^{-1} during NMY. A significant decrease of 5% is detected during MY compared to

NMY, when the three soils are combined (wilcoxon test). However, as it is not detected through pair comparisons, this difference is considered weak.

In contrast, senesced fruits show a strong difference between MY and NMY (**Fig. 2**), as it reaches mean values of 3.8 ± 1.1, 3.4 ± 0.9 and 2.4 ± 0.7 t·ha⁻¹·yr⁻¹ on S1, S2 and S3 respectively, while it remains in average around 0.4±0.2 t.ha^{-1}.yr^{-1} during NMY. A significant soil effect is observed during MY (S1 & S2 > S3), whereas no soil-related differences are detected during NMY.

Finally, for the Others litter compartment, no soil effect is detected during both MY and NMY (**Fig. 2**). This compartment exhibits a significant difference between MY and NMY, as their contribution is on average of 0.7±0.2 t·ha^{-1}·yr^{-1} during MY which is 67% higher than during NMY (0.4±0.1 2 t·ha^{-1}·yr^{-1}).

The part of the total aboveground biomass production allocated to fruits during MY is at least of 13% and at most of 27% while it ranges from 0.4 to 5.8% during NMY (**Fig. S1)**.

3.2. Tree nutrient status

Figure 3 presents the average tree nutritive status (i.e. concentrations in green leaves) of K, Mg, N, P and S in the three ecosystems (S1, S2 and S3) over the study period (2012-2023).

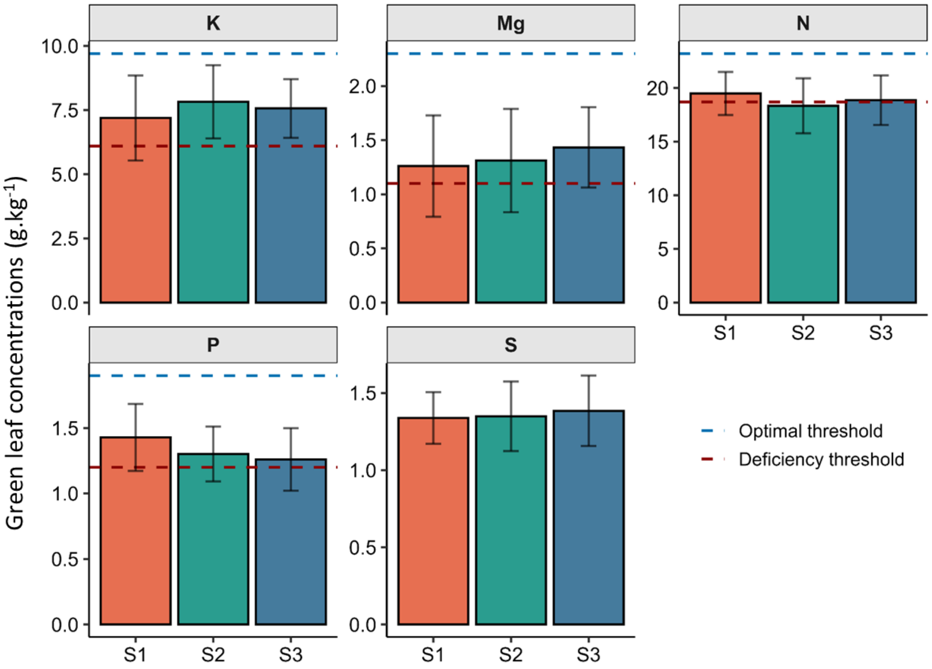

Figure 3: Average green leaf concentrations (g.kg^{-1}) for K, Mg, N, P and S, for the periode 2012-2023, and in the three studied ecosystems (S1, S2, S3). For each element no statistical differences were detected between ecosystems. Bars represent standard error. The optimal (blue) and deficiency (red) thresholds defined by Meller & Göttlein (2012) are mentionned for K, Mg, N and P by dashed lines.

For all nutrients, green leaf concentrations do not exhibit significant differences between ecosystems. Mg, N and P status range between 1.3–1.4 g.kg^{-1}, 18–19 g.kg^{-1} and 1.3–1.4 g.kg^{-1}, respectively, and are generally close to the deficiency thresholds (1.1 for Mg, 18.7 for N and 1.2 for P) defined for adult beech by Mellert and Göttlein, 2012. K concentrations range between 7.2-7.8 g.kg^{-1}, being closer to its deficiency threshold (6.1g.kg^{-1}) than its optimal threshold (9.7 g.kg^{-1}). S concentrations are of 1.3-1.4 g.kg^{-1} and no optimal or deficiency thresholds is defined for this nutrient. Note that the year type (MY or NMY) do not impact the concentrations in green leaves of any nutrients according to wilcoxon tests and linear mixed models.

3.3. Nutrient Content in total aboveground Biomass production (NCB)

As shown in **Fig. 4**, the NCB of all nutrients (K, Mg, N, P and S) is significantly higher during MY compared to NMY, when the three soils are combined (wilcoxon tests) but also for each soil separately (pair comparisons). Unlike the total aboveground biomass production, the soil effect is generally not significant. The only exceptions are observed during MY during which K is lower on S3 compared to S2 and P is lower on S3 compared to S1. The K, Mg, N, P and S contents in total aboveground biomass production during MY are respectively 44%, 53%, 9%, 43% and 24% higher than during NMY. Mean nutrient NCB during MY vs. NMY were 86 ± 17 vs. 60 ± 7 kg ha^{-1} yr^{-1} for K, 14 ± 3 vs. 9 ± 1 for Mg, 134 ± 21 vs. 123 ± 13 for N, 14 ± 3 vs. 10 ± 1 for P, and 11 ± 1 vs. 9 ± 1 for S.

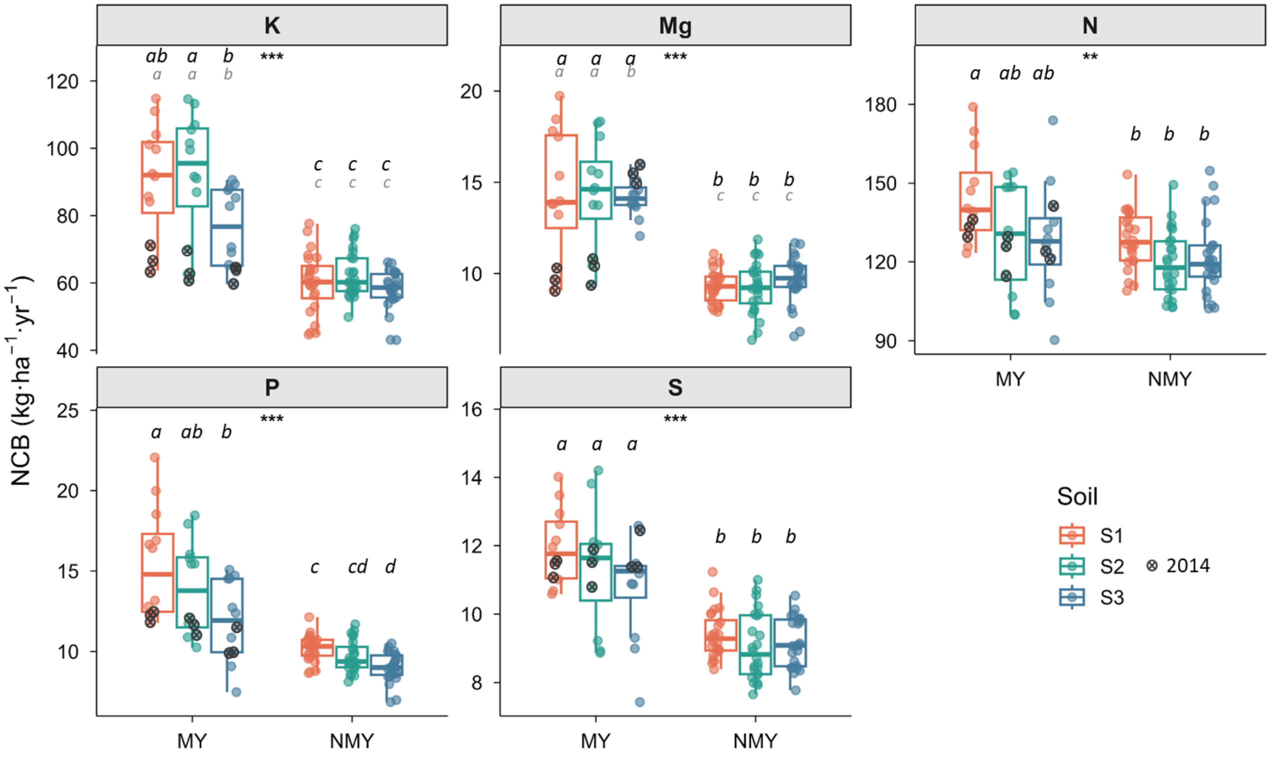

Figure 4: Annual NCB (kg.ha^{-1}.yr^{-1}) for K, Mg, N, P and S, during MY vs. NMY and in the three studied ecosystems (S1, S2, S3). Asterix indicate significant differences between MY and NMY without ecosystem distinction (*<0,05 ; ** < 0,01 ; * < 0,001). Different letters indicate significant differences among groups (i.e. ecosystem*year type), with a threshold p value of 0,05. The half MY of 2014 is differenciate from the other MY with crossed cycles, but is not excluded from the statistical tests. When necessary grey letters indicate statistical results without the half MY 2014**

3.4. Biological recycling fluxes

3.4.1. Canopy Exchanges

As shown in **Fig. 5**, K, Mg and P canopy exchange are strictly positive, indicating that leaching is the dominant process for these nutrients. Canopy exchanges of N and S are positive during MY and vary between positive and negative values during NMY, indicating that canopy absorption may also occurs. The canopy exchanges of all nutrients (K, Mg, N, P and S) are significantly higher during MY compared to NMY when the three soils are combined (wilcoxon tests). The soil effect is generally not significant both during MY or NMY, with one exception for the P leaching during NMY being lower in S3 compared to S2. Thus, regardless of soil types, canopy nutrient exchanges during MY were significantly higher than during NMY for all the nutrients, with increases of 46% for K and Mg, 182% for N, 40% for P, and 145% for S. Mean fluxes during MY reached 27.9 ± 6.4 kg ha^{-1} yr^{-1} for K, 1.2 ± 0.3 for Mg, 2.5 ± 1.7 for N, 2.8 ± 2.0 for P, and 0.9 ± 0.4 for S, compared with 19.1± 4.9, 0.8 ± 0.3, 0.9 ± 2.9, 2.0 ± 0.9, and 0.3 ± 0.6 kg ha^{-1} yr^{-1} during NMY, respectively.

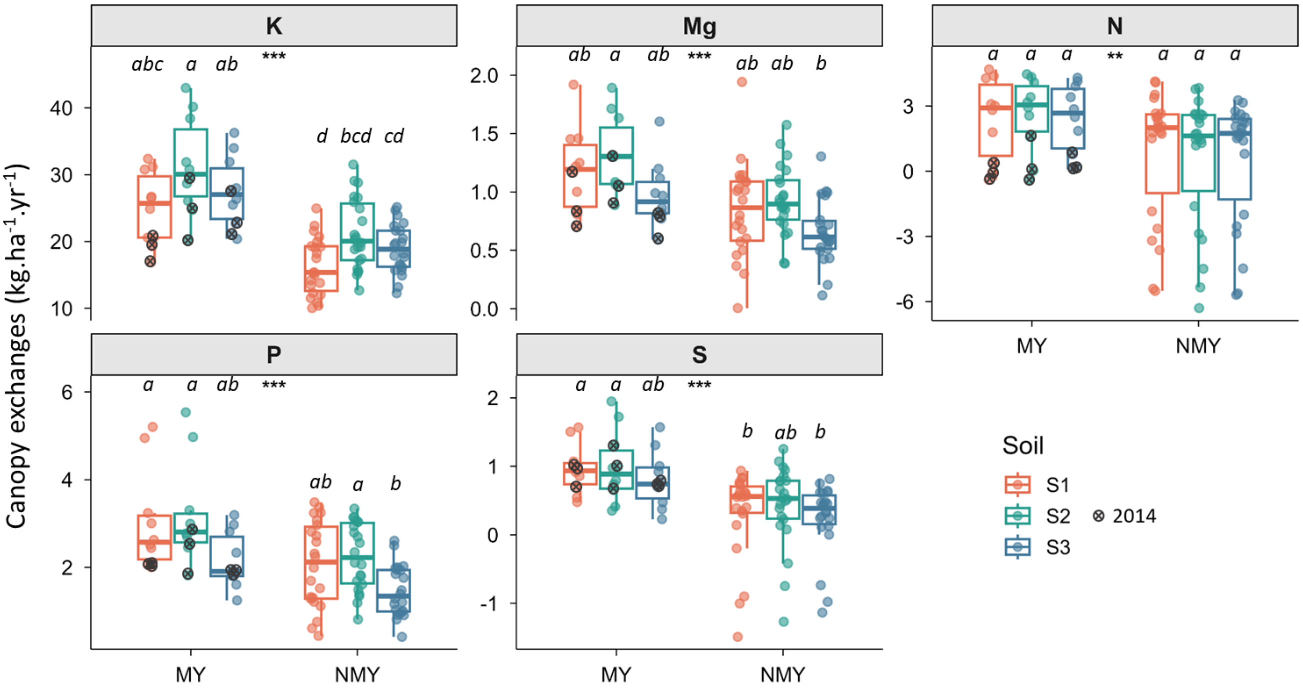

Figure 5: Annual canopy exchanges fluxes (kg.ha^{-1}.yr^{-1} ; 0< foliar leaching ; 0> foliar absorption) for K, Mg,N, P and S, during MY vs. NMY and in the three studied ecosystems (S1, S2, S3). Asterix indicate significant differences between MY and NMY without ecosystem distinction (*<0,05 ; ** < 0,01 ; * < 0,001). Different letters indicate significant differences among groups (i.e.**

ecosystem*year type), with a threshold p value of 0,05. The half MY of 2014 is differenciate from the other MY with crossed cycles, but is not excluded from the statistical tests.

However, a high variability is observed, especially for N and S and it is important to note that pair comparisons (letters on **Fig. 5**) do not indicate significant difference between MY and NMY within each soil, except for K leaching.

Figure 6 shows the intra-annual variability (i.e., among the 13 sampling periods) of the canopy exchanges during MY and NMY. Except for N (weak fluxes, variability and MY vs. NMY differences), the canopy exchanges exhibit 2 main leaching peaks : (i) around period 6 (spring) and (ii) around period 11 (autumn). During MY these peaks are generally more important than during NMY.

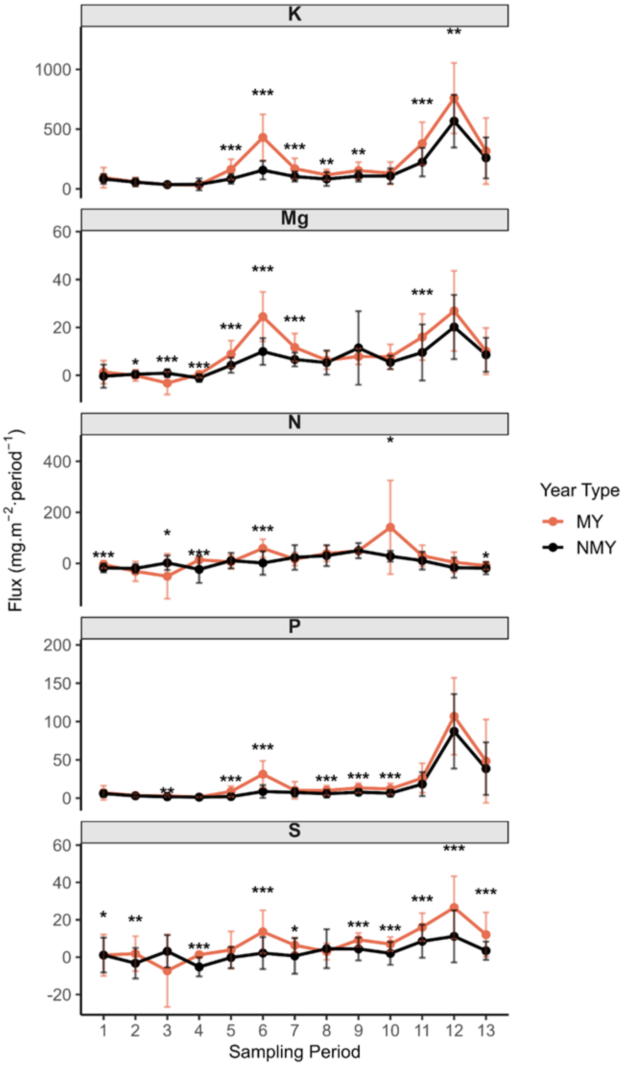

Figure 6: periodic canopy exchanges fluxes (mg.m^{-2}.period^{-1} ; 13 sampling period of 28 days in a year; 0< foliar leaching ; 0> foliar absorption) for K, Mg,N, P and S, during MY (red line) vs. NMY (black line). Asterix indicate significant differences between MY and NMY without ecosystem distinction (*<0,05 ; ** < 0,01 ; * < 0,001).**

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3.4.2. Litterfall

As shown in **Fig. 7**, the nutrient litterfall fluxes are all significantly higher during MY compared to NMY, when the three soils are combined (wilcoxon tests) but also for each soil separately (pair comparisons). The soil effect is generally not significant except during NMY with a lower P and higher S fluxes on S3 compared to S1.

Thus, during MY, all nutrient contents in litterfall fluxes were significantly higher during MY than during NMY, with increases of 95% for K, 54% for Mg, 39% for N, 59% for P and 34% for S, regardless of soil types. The mean nutrient fluxes through litter fall during MY vs. NMY in $kg\ ha^{-1}\ yr^{-1}$ were 40±11 vs. 20±7 for K, 10±6 vs. 6±1 for Mg, 65±12 vs. 47±8 for N, 8±2 vs. 5±1 for P, and 7±1 vs. 5±1 for S.

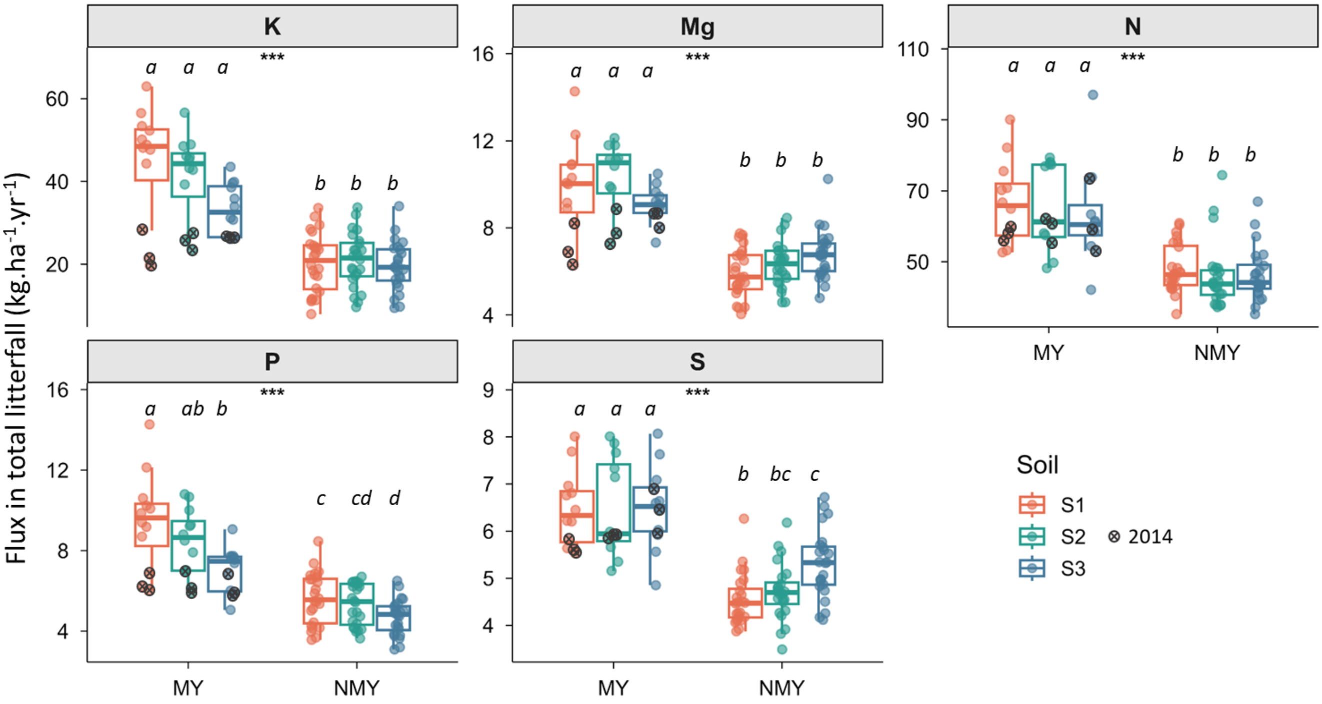

Figure 7: Annual fluxes with total litterfall ($kg.ha^{-1}.yr^{-1}$) for K, Mg,N, P and S, during MY vs. NMY and in the three studied ecosystems (S1, S2, S3). Asterix indicate significant differences between MY and NMY without ecosystem distinction (*<0,05 ; ** < 0,01 ; * < 0,001). Different letters indicate significant differences among groups (i.e. ecosystem*year type), with a threshold p value of 0,05. The half MY of 2014 is differenciate from the other MY with crossed cycles, but is not excluded from the statistical tests.**

3.5. Tree internal recycling fluxes: leaf resorption

Figure 8 illustrates that no significant difference is generally observed for resorption fluxes between MY and NMY. Exceptions concern Mg and N that are respectively slightly higher and lower during MY, only when the three soils are combined (wilcoxon tests). No significant soil effect is detected both during MY or NMY. A high variability is reported for all nutrients, as K resorption fluxes range from 0.2 to 21.7 kg.ha^{-1}.yr^{-1}, Mg from -2.8 to 4.7 kg.ha^{-1}.yr^{-1}, N from 37.5 to 88.0 kg.ha^{-1}.yr^{-1}, P from -1.6 to 3.5 kg.ha^{-1}.yr^{-1} and S from 1.0 to 4.6 kg.ha^{-1}.yr^{-1}.

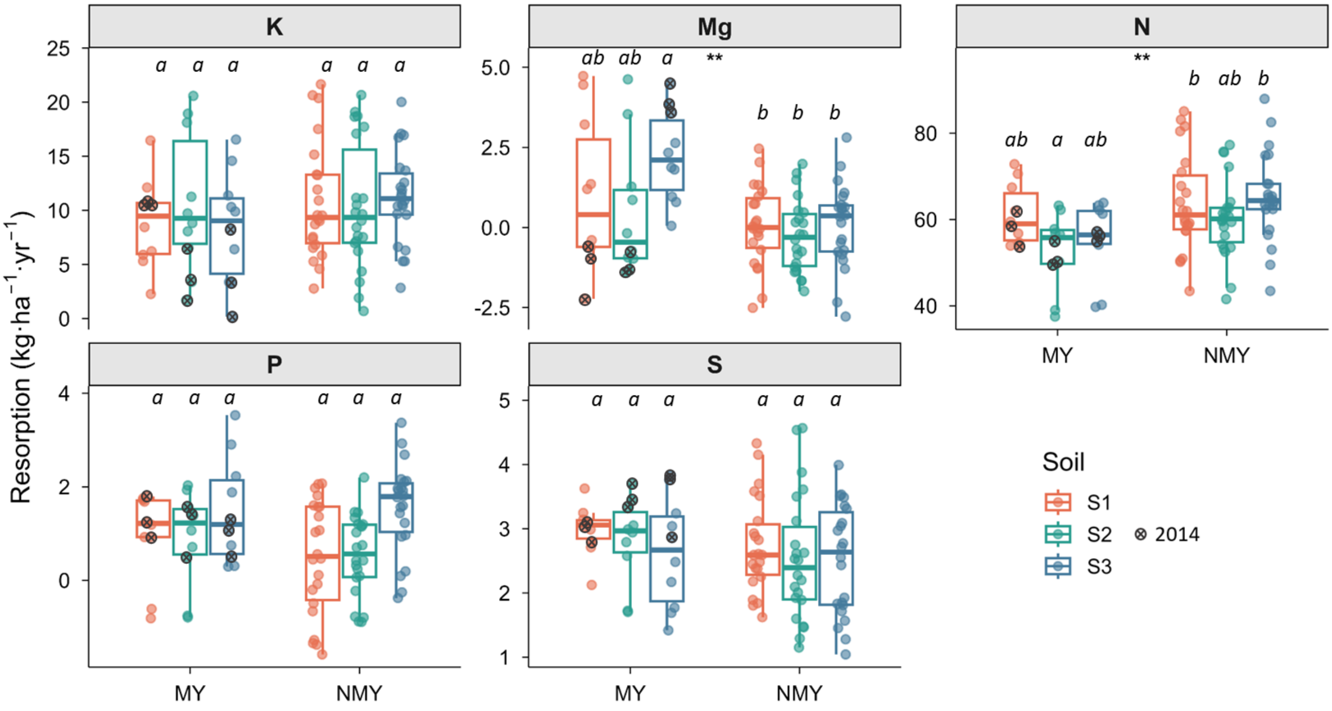

Figure 8: Resorption flux during the senescence period (kg.ha^{-1}.yr^{-1}) for K, Mg, N, P and S, during MY vs. NMY and in the three studied ecosystems (S1, S2, S3). Asterix indicate significant differences between MY and NMY without ecosystem distinction (*<0,05 ; ** < 0,01 ; * < 0,001). Different letters indicate significant differences among groups (i.e. ecosystem*year type), with a threshold p value of 0,05. The half MY of 2014 is differenciate from the other MY with crossed cycles, but is not excluded from the statistical tests.**

4. Discussion

4.1. Masting effect on biomass production (4 MY)

Mast frequency on the Montiers site from 2012 to 2023 is on average every 3 years which is in the range of recent studies looking at *F. sylvatica* mast behaviour in Europe (Brumme et al., 2021; Lebourgeois et al., 2018; Nussbaumer et al., 2016). The S3, S2, S1 average litterfall production during the 4 MY increased respectively of 1.9, 3.0 and 3.5 t.ha.yr^{-1} corresponding to +39, +61 and +73% compared to NMY. The same order of increase were reported on seven beech forests in Germany (+1.4 to +2.9 t.ha^{-1}.yr^{-1} corresponding to 31 to 101% ; Brumme et al., 2021). The litterfall increase is mainly due to fruits production (**Fig. 2**), as well as the « others » compartment, as it includes males flowers, numerous during masting years for beech (Geburek et al., 2012). This mast effect is reflected on the total aboveground biomass by increasing its production by 23%, 18% and 14% during MY, on S1, S2 and S3 respectively.

In contrast, mast events at the Montiers site do not influence significantly wood or leaf biomass production (**Fig. 2**, and **Fig. S2**). The literature reports contrasting results regarding the effects of mast years on vegetative growth. While multisite studies conducted at national and international scales generally report a reduction in wood and leaf production during mast years (Hacket-Pain et al., 2025; Müller-Haubold et al., 2015; Nussbaumer et al., 2021) , substantial site-dependent variability has been documented. Accordingly, this general pattern is not observed at Montiers forest, similarly to the seven German beech forests studied by Brumme et al., 2021. Likewise, Yasumura et al., 2006, in a Fagus crenata forest in northeastern Japan, reported no effect of mast years on leaf production, while wood production was reduced only during full mast years. In contrast, reductions in wood growth and leaf production during mast years have been reported respectively in a beech forest in England (Hacket-Pain et al., 2017) and in a beech forest in Switzerland (Han et al., 2011). These discrepancies may likely reflect differences in site conditions, particularly in terms of water and nutrient availability or climate conditions, which may modulate carbon allocation trade-offs between reproduction and vegetative growth.

4.2. Masting effect on canopy exchanges and recycling fluxes

We show for the first time that annual canopy leaching of nutrients is significantly higher during MY than during NMY (**Fig. 4**) due to significant increased fluxes during spring and senescence (**Fig. 6**), especially for K, which is the most soluble element (Dincher et al., 2020; Gosz et al., 1973; Schreeg et al., 2013). The observed enhancement of canopy leaching during MY likely results from several combined explanations: (i) the modification of the surface available for interactions between rainfall and canopy, which is a key driver of solution enrichment (Berg et al., 2025; Grundmann et al., 2024; Ponette-González et al., 2016; Van Stan, Ii et al., 2020) coupled with a (ii) high leaching potential of the various canopy organs particularly during their senescence (André et al., 2008; Helmisaari, 1992; Ulrich, 1983). Accordingly, during MY, in addition to leaves (3.8 $t.ha^{-1}.yr^{-1}$ in litterfall), large amounts of flowers are present in the canopy at the beginning of the growing season, followed by fruit development until their senescence (3.2 $t.ha^{-1}.yr^{-1}$ in litterfall), thereby explaining the higher leaching fluxes observed during these two periods.

The important increases of nutrient fluxes within litterfall during MY (**Fig. 7**) are consistent with previous studies (Aoyagi et al., 2018; Brumme et al., 2021; Han et al., 2014; Yasumura et al., 2006). As an example, Han et al., 2014 showed that a full MY on mature *F. crenata* trees doubled their N fluxes through litterfall production, due to additional fruit biomass. Moreover, similarly to canopy leaching, litterfall nutrient-fluxes during NMY occur mainly during senescence, whereas during MY substantial nutrient fluxes are also produced in spring by the “others” compartment, largely composed of male flowers.

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During MY, the total K, Mg, N, P and S fluxes within biological recycling (litterfall + leaching) are respectively 72%, 42%, 53%, 56% and 43% higher than during NMY. This represents additional fluxes of 28.4 kg.ha^{-1} for K, 3.8 kg.ha^{-1} for Mg, 20.0 kg.ha^{-1} for N, 4.0 kg.ha^{-1} for P and 2.3 kg.ha^{-1} for S.

However, because nutrient returns to forest floor occur through different pathways (solid or dissolved) and at different periods (spring or autumn), their potential availability for tree nutrition is highly variable. Nutrient fluxes released in spring during MY are directly available for tree growth of the current year, particularly in a dissolved form, whereas those released during senescence are only beneficial for the subsequent growing season. In addition, nutrient inputs via litterfall benefit trees only if efficient decomposition of organic matter occurs ~~in the soil~~, a process that may be negatively affected by the fruit biomass during MY (Brumme et al., 2021; Michaud et al., 2024).

Despite the increase in aboveground biomass production and associated nutrient fluxes during mast years, leaf resorption fluxes remain broadly stable across nutrients. Moreover, the strong interannual variability suggests that this process is mainly driven by factors other than masting. Our results are in line with literature which generally reported no masting effect on resorption fluxes (Han and Kabeya, 2017). However, studies investigating the effects of masting on nutrient resorption are few and mostly focused on N,. Thus, to our knowledge, our study is the first to simultaneously quantify the resorption of multiple nutrients while explicitly accounting for masting and its effects on resorption calculation. In addition the slight decrease in N resorption observed here is consistent with the hypothesis that the translocation of N from leaves to developing fruits (Han et al., 2011; McDowell et al., 2008; Miyazaki et al., 2002) may reduce the amount of N resorbed from leaves during senescence (Han et al., 2014).

4.3. Masting effect on NCB and NCB partitioning

By increasing total aboveground biomass production, MY induced substantial rises in NCB, with average increases of 53% for Mg, 44% for K and 43% for P compared to NMY (**Fig. 4**). Smaller increases were observed for S (+24%) and N (+9%). Although N is the most frequently studied element in the literature, our results indicate that it is the less impacted nutrient in the three ecosystems during MY.

Fig. 9 highlights the patterns of nutrient partitioning within the NCB during MY and NMY and further emphasizes the importance of accounting for canopy leaching and resorption fluxes, which remain largely understudied in the current literature. Our results show that neglecting canopy leaching leads to a significant underestimation of nutrient requirements during MY, particularly for K and P, for which the leaching pool accounts for 33% and 21% of the NCB, respectively. Similarly, resorption pool represents a substantial fraction of the NCB for N (42% during MY vs. 51% during NMY) and S (24% during MY vs. 28% during NMY). **Figure 9** shows that the variable impact of MY on NCB among nutrients can thus be explained by differences in their internal partitioning among the measured pools (canopy leaching, resorption, senesced organs and wood). It is worth noting that nutrients allocated to the leaching and resorption pools ultimately originate from the non-perennial canopy organs (leaves, fruits and others). For K, P, and Mg, NCB is largely driven by increases in fluxes within reproductive organs (fruits and others) and within the pool of canopy leaching, which together account for 62%, 49%, and 32% of the total NCB, respectively. In contrast, N shows a distinct pattern, as most of its NCB is found in the resorption pool during MY, which offsets the reproductive cost linked to fruit production and limits the increase of the NCB. Finally, S has an intermediate behaviour: although nearly one quarter of its NCB is resorbed during MY, this only partially compensates for the increased contribution of reproductive organs and canopy leaching pools, which together represent 28% of the NCB. Despite the increase in NCB during MY, the tree nutritive status, characterized by green leaf concentration (**Fig. 3**), appears to be unaffected by mast events.

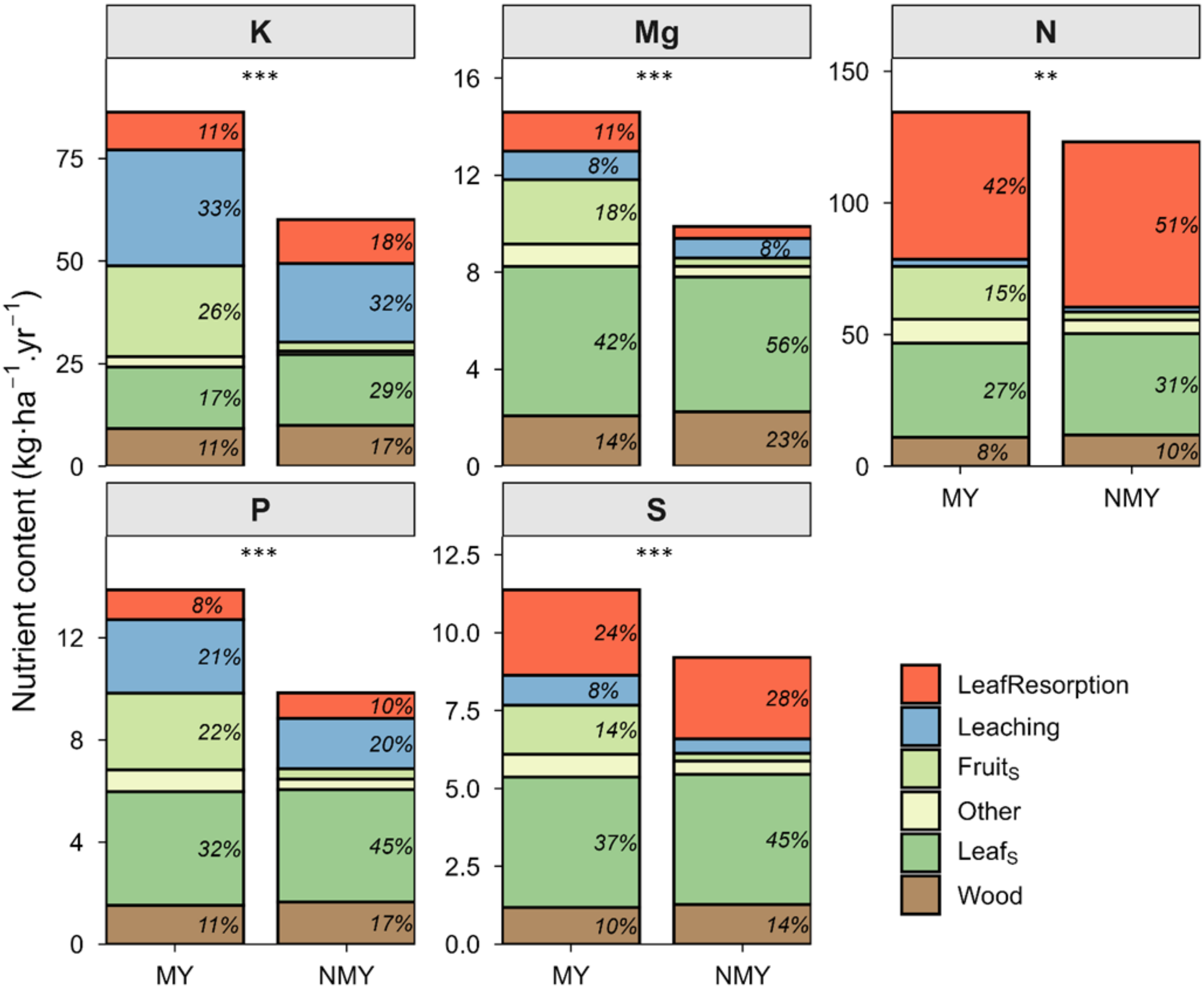

Figure 9: Average NCB and the partitioning between the different compartments (Leaf resorption, canopy leaching, senescened fruits, others, senesced leaves and wood) in total aboveground biomass production(kg.ha^{-1}.yr^{-1}) for K, Mg,N, P and S, during MY vs. NMY. Asterix indicate significant differences between MY and NMY without ecosystem distinction (*<0,05 ; ** < 0,01 ; * < 0,001). The percentage of NCB included in each compartment is mentionned.**

4.4. Relationship between ecosystem fertility and masting

At the Montiers site, the three studied ecosystems share the same characteristics in terms of tree species composition, stand age, density, silvicultural practice and climatic conditions. The main factor differentiating these ecosystems is the soil type, which generates a clear fertility gradient (S3 < S2 < S1), as previously identified based on wood production (Calvaruso et al., 2017). As illustrated in **Fig. 10**, fruit production during full MY (2016, 2020 and 2023) increases consistently along the fertility gradient, with the highest production observed in the most fertile soil (S1) and the lowest in the least fertile one (S3). These results indicate that reproductive investment during MY increase with the ecosystem fertility. This positive relationship is consistent with the previous findings of Fernández-Martínez et al., 2017 who showed that European forests with higher gross primary productivities produce larger fruit biomass. However, this relationship is not observed for the 2014 MY in our study, as fruit production is similar across the three soil types (i.e. half MY on S1 and S2). This pattern may find its origin in specific climatic conditions and/or resource availability that constrained fruit production in 2014 at S1 and S2 (Abe et al., 2016).

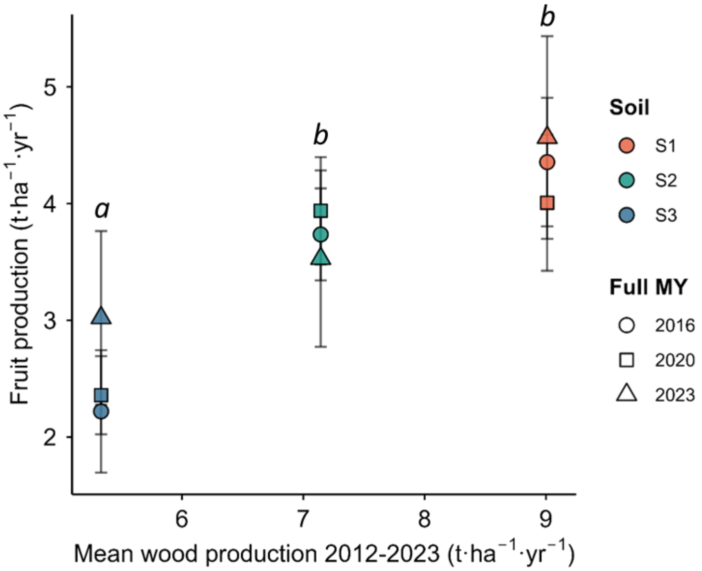

Figure 10: Fruit biomass production ($t.ha^{-1}.yr^{-1}$) during the full MY 2016, 2020 and 2023 in relation with the average (2012-2023) wood production on the three studied ecosystems (S1, S2, S3). Bars represent standard errors. Different letters indicate significant differences among ecosystems with a threshold p value of 0,05.

The increase in reproductive biomass along the ecosystem fertility gradient is associated with a corresponding increase in the nutrient additional cost of masting, for all nutrients (in $kg.ha^{-1}.yr^{-1}$, during full MY ; **Table 3**). This pattern of fertility gradient is also apparent for K, Mg and P when considering the contents in total aboveground biomass production (NCB ; **Fig. 2**, full MY only).

Table 3: Additionnal cost of reproduction (kg.ha^{-1}·yr^{-1}) during full MY, compared to NMY (difference of average NCB during full MY and NMY, for each replicate), for N, K, P, Mg and S. Different letters indicate significant differences among ecosystems with a threshold p value of 0.05.

	N	K	P	Mg	S
			kg.ha^{-1}.yr^{-1}		
S1	20.4 (3.0)*a*	38.2 (2.2)*a*	6.3 (0.4)*a*	6.7 (0.6)*a*	2.8 (0.2)*a*
S2	13.0 (4.7)*ab*	39.0 (2.9)*a*	5.0 (0.2)*b*	6.6 (0.2)*a*	2.3 (0.4)*a*
S3	6.5 (8.1)*b*	22.8 (2.5)*b*	3.4 (0.7)*c*	4.1 (0.6)*b*	1.3 (0.6)*b*

However, despite relatively low nutritional status, sometimes close to deficiency thresholds for several key nutrients (**Fig. 3**), MY did not induce any decrease in green leaf nutrient concentrations in the three studied ecosystems even on the less fertile one, in consistency with unaffected leaf and wood biomass production. This contrasts with the general hypothesis that MY generates nutrient demands exceeding the annual assimilative capacity of trees (Isagi et al., 1997). In fact, the consequences generally observed are reduce nutritive status (Jonard et al., 2009; Müller-Haubold et al., 2015), and/or biomass production due to nutrient trade-off from vegetative to reproductive organs.

Such contrasting responses among ecosystems may be explained by the balance between nutrient demand during MY and the size and renewal capacity of nutrient reserves (see **Fig. 1**) in both trees (R_t) and soils (R_s). This balance likely defines nutrient-specific and ecosystem-dependent "trade-off thresholds" that condition tree responses to MY. In ecosystems where masting induces a decline in leaf nutrient concentrations and/or in leaf and wood biomass, this would imply that nutrient demand of at least one nutrient during MY exceeds the readily available reserves. Conversely, when combined nutrient reserves (R_t+R_s) exceed the nutrient content in total biomass production (NCB) across all elements, indicators such as leaf and wood production or leaf nutrient status are not affected by MY. This multi-element regulation can be illustrated by comparing previous studies conducted in beech forests with high average N concentrations in green leaves (around 24 g.kg^{-1}, close to the optimal threshold reported by Mellert and Göttlein, 2012) and that have reported contrasting responses to masting. Brumme et al. (2021) do not detect any effect of MY on either wood growth or leaf production, just like on our three ecosystems (despite a N status around 18 g.kg^{-1}), whereas Han et al. (2011) observed a significant reduction in leaf production associated with masting. Together, these contrasting outcomes indicate that N alone cannot account for the variable ecosystem responses to mast events. Our results suggest that other nutrients, particularly P, Mg and K, deserve greater attention, as their demands increase strongly during MY and are proportional to the apparent fertility of the ecosystem. In this context, Fernández-Martínez et al., 2017 already highlighted the key role of P availability in regulating fruit production, which appeared more limiting than N availability. Ecosystem sensitive to masting are likely characterised by (i) a high proportional allocation of biomass and a high nutrient cost to reproduction relative to vegetative growth, (ii) limited soil and/or tree nutrient reserves, for instance in highly weathered soils or N-deficient ecosystems, and (iii) low rates of reserve replenishment (reduced organic matter mineralization for example). Such conditions are typically associated with low-productivity sites developed on nutrient-poor soils, where investment in masting may therefore represent a stronger constraint on tree nutrition and growth.

Although direct quantification of tree and soil nutrient reserves coupled with NCB remains scarce in the literature, preventing a direct test of this hypothesis at a broader scale, our results provide insight into this balance for our three studied ecosystems S1, S2 and S3. In fact, as demonstrated in **Table 4**, nutrient reserves stored in the soil (R_s) alone (H1), or in combination with tree internal reserves (i.e. R_t = resorption fluxes ; H2), are sufficient to compensate the average NCB (NCB_a) smoothed over a multi-year period (assuming one mast event every three years). Specifically, these reserves could sustain nutrient NCB for approximately 4 to 10 years for K and N, and for 25 to 105 years for Mg and P. Importantly, this buffering capacity appears largely independent of the fertility gradient among the three ecosystems.

Table 4 : Soil nutrient available stock (60 first cm ; Calvaruso et al 2017), in relation with average annual nutrient content in the biomass NCB_a (when considering one mast event every 3 years ; $NCB_a = (NCB_{fullMY} + NCB_{NMY} \times 2)/3$), for K, Mg, N and P, on the 3 studied ecosystems (S1, S2 and S3) and the reserve duration (in year) with two hypotheses. For hypothesis 1 (H1), the reserve duration = soil reserve/NCB_a. For hypothesis 2 (H2) reserve duration= soil reserve + resorption/NCB_a considering that element resorsbed in branch are remobilized.

	K				Mg				N				P			
	Rs	NCB_a	**Reserves duration**		Rs	NCB_a	**Reserves duration**		Rs	NCB_a	**Reserves duration**		Rs	NCB_a	**Reserves duration**	
			H1	**H2**			**H1**	**H2**			**H1**	**H2**			**H1**	**H2**
	kg.ha⁻¹	*kg.ha⁻¹.yr⁻¹*	*years*	*years*	*kg.ha⁻¹*	*kg.ha⁻¹.yr⁻¹*	*years*	*years*	*kg.ha⁻¹*	*kg.ha⁻¹.yr⁻¹*	*years*	*years*	*kg.ha⁻¹*	*kg.ha⁻¹.yr⁻¹*	*years*	*years*
S1	293	74	**4**	**4**	360	12	**31**	**34**	652	135	**5**	**9**	1196	12	**97**	**105**
S2	566	85	**7**	**8**	479	11	**42**	**44**	653	124	**5**	**9**	785	11	**69**	**75**
S3	304	66	**5**	**5**	274	11	**25**	**31**	702	124	**6**	**10**	271	10	**27**	**31**

Thus, in the absence of nutrient limitation, masting (and NCB during MY) across the three ecosystems is not directly regulated by the available nutrient reserves (R_s and R_t). Instead, it is driven by the ecosystem productivity regulated by the observed “fertility” effect, controlled by water availability (Kirchen et al., 2017). This, in turn, depends on both soil water-holding capacity (S1 > S2 > S3) and pluviometry during the growing season. Furthermore, previous studies at the Montiers site have shown that severe water stress strongly affects both tree productivity and nutritional status, leading to the emergence of K deficiency (Touche et al., 2022). In the context of climate change, MY may exacerbate the impacts of droughts and heatwaves, as previously discussed by Hacket-Pain et al., 2025.

Given that many worldwide forest ecosystems are happened to be characterized by low P or K availability (Cornut et al., 2023; Gonzales et al., 2023; Sardans and Peñuelas, 2015; Yu et al., 2025), future studies addressing the cost of masting should broaden their scope beyond N and aim to comprehensively quantify NCB across multiple nutrients. Such an approach is essential to adequately capture the nutritional constraints associated with reproductive effort.

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5. Conclusion

This twelve-year study, conducted from 2012 to 2023, investigated the impact of masting on the biogeochemical functioning of three mature beech forests differing in fertility (S1 > S2 > S3). Aboveground biomass production and nutrient fluxes (N, K, P, Mg, S) through canopy leaching, litterfall production and resorption were annually calculated, mast effects were assessed by comparison between MY and NMY.

Overall, the total biomass production increased on average by 19% due to the reproductive organ formation (flowers and fruits) during MY. In contrast, no effect of MY was observed on wood growth or leaf production, challenging the general expectation of C allocation shifts during mast events. This pattern can be attributed to the Montiers site, where even the least fertile ecosystem (S3) can provide sufficient resources (from soil or from remobilization within trees), obviating the need for C allocation trade-off during MY.

Our results also exhibit novel findings by highlighting the impact of MY on nutrient canopy leaching, particularly for K being the most soluble one and which increased by 46% (+9 $kg.ha^{-1}.yr^{-1}$). The timing distribution of these fluxes was also modified as during NMY nutrient leaching primarily occurs during senescence while during MY, a portion of nutrients is also released during spring due to flower production. Coupled with strongly enhanced nutrient fluxes through litterfall during MY, this results in markedly higher biological nutrient recycling fluxes compared with NMY, for all the nutrients studied. Additionally, our study addressed the effects of MY on nutrient resorption, an important tree internal recycling flux that has received little attention to date. No MY impact was identified on nutrient resorption except a slight decrease of N and a slight increase of Mg.

A substantial increase in NCB is observed for all nutrients, although the magnitude of this increase differs among elements according to their respective partitioning. Mg (+53%), K (+44%) and P (+43%) are the most affected, as their NCB is largely driven by fluxes associated with non-perennial canopy organs (litterfall and leaching) whereas S (+24%) and especially N (+9%) are less impacted due to the compensatory role of resorption.

By integrating three ecosystems with contrasting fertility levels (S1>S2>S3), this study demonstrates that ecosystem fertility, primarily controlled by water availability at the Montiers site, modulates the mast events and ecosystems responses. Fruit production and the associated reproductive nutrient costs were higher in the more fertile ecosystems (S1 ≥ S2 > S3), a pattern also observed for the NCB of K, P, and Mg. Despite these additional demands, MY do not currently induce nutrient deficiencies or affect leaf production or wood growth, indicating that internal tree reserves and soil nutrient pools are sufficient to buffer the nutritional costs of reproduction under present conditions.

By combining a multi-nutrient approach with an explicit comparison between NCB and available nutrient reserves in soils and trees, across a gradient of ecosystem fertility close to nutrient limitation, this study provides several key insights. First, it proposes a novel indicator for tree nutrition, based on the comparison between nutrient demands during MY (NCB) and the available nutrient reserves ($R_s + R_t$), allowing a more integrative assessment of the potential nutritional constraints associated with masting. Second, the regulation of masting cannot be understood through a single-nutrient framework, but relies on multiple elements, particularly K, P and Mg in addition to N. Finally, in the absence of strong limitation by at least one nutrient ($NCB_{MY} > R_t + R_s$), masting regulation (i.e., reproductive organs production and NCB) appears to be primarily driven by overall ecosystem fertility ($S1 \geq S2 > S3$), itself largely controlled by water availability on the Montiers site, rather than by soil nutrient pools alone.

Thus, mast events do not necessarily constitute a biotic stress under current climate conditions, depending on the ecosystem considered. In the aim to identify potential nutrient trade off threshold that could explain the regulatory effects of MY in some forest stands, future research should further investigate the NCB of K, P and Mg, together with the quantification of available nutrient resources (Rt + Rs).

Data availability

The datasets generated and analysed in this study (8 datasets describing nutrient concentrations, stocks, fluxes, and biomass production across compartments) will be made publicly available upon acceptance of the manuscript. This repository will includ a description of all datasets and variables. During the review process, the datasets can be accessed via a private link to the reviewers.

Other underlying data can be accessed in the Supplement (Table S1 and Figs. S1 and S2)

Author contributions

J. Touche: Conceptualization, Methodology, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, Visualization; M.P. Turpault: Conceptualization, Methodology, Validation, Resources, Data Curation, Writing - Original Draft, Writing - Review & Editing, Supervision, Project administration, Funding acquisition ; P. Santenoise: Supervision, Formal analysis, Writing - Review & Editing; P.O. Redon : Validation, Supervision, Funding acquisition, Resources, Writing - Review & Editing ; C. Calvaruso: Validation, Data Curation, Writing - Review & Editing

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Disclaimer

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