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Artificially induced drought stress affects seasonal foliar litterfall, nutrient contents, and nutrient masses in mature European beech (*Fagus sylvatica* [L.]) and Norway spruce (*Picea abies* [L.] Karst.)

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ABSTRACT

We examined the effects of drought-induced stress on foliar litter production, nutrient contents, and nutrient masses in mature European beech (*Fagus sylvatica* [L.]) and Norway spruce (*Picea abies* [L.] Karst.) over a two-year period (October 2015–September 2017) in southern Bavaria. A rainfall exclusion experiment was conducted with six control plots receiving normal rainfall and six roof plots excluding rainfall. Abscised leaf and needle biomass, as well as the contents and masses of calcium (Ca), potassium (K), magnesium (Mg), nitrogen (N), and phosphorus (P), were monitored across two non-vegetation periods (October–February: NV1, NV2) and two vegetation periods (March–September: V1, V2).

Foliar litter on control plots (set at 100 %) was 4000, 329, 4501, 403 kg/ha for European beech and 3534, 1146, 1352, 607 kg/ha for Norway spruce across the four observation periods (NV1, V1, NV2, V2). Roof plots yielded 2917 (73 %), 364 (111 %), 3710 (82 %), 358 (89 %) kg/ha for European beech and 5841 (165 %), 1040 (91 %), 899 (67 %), 447 (74 %) kg/ha for Norway spruce. Significant differences between control and roof plots were observed only during NV1.

Foliar K contents were significantly lower under drought in both species. For European beech, values were 2.83, 3.83, 2.76, 4.37 g/kg (control plots), compared to 2.38 (84 %), 3.08 (80 %), 2.30 (83 %), 4.01 (92 %) g/kg (roof plots). For Norway spruce, values were 2.64, 2.77, 2.51, 2.13 g/kg (control plots), compared to 2.26 (86 %), 2.33 (84 %), 2.01 (80 %), 1.66 (78 %) g/kg (roof plots). Drought also significantly decreased foliar Ca content in Norway spruce during NV2, from 8.61 to 7.04 g/kg (82 %).

Foliar nutrient masses aligned more closely with biomass abscission patterns than with nutrient translocation patterns. European beech predominantly exhibited significantly reduced abscised nutrient masses under drought during NV1 and NV2, while Norway spruce initially showed significantly increased abscised nutrient masses in NV1, followed by a marked decline in subsequent seasons.

We concluded that European beech responded to drought stress by reducing foliage biomass production, suggesting a potential acclimation strategy, whereas Norway spruce mitigated water loss through transpiration by shedding its needles. However, Norway spruce failed to compensate for the initial high needle losses by regenerating sufficient new needles, indicating its lower resilience to drought.

1. Introduction

Long-lived plants, such as trees, are particularly vulnerable to the impacts of ongoing climate change (Jentsch et al., 2007; Rötzer et al., 2009, 2010; Lindner et al., 2010; Matyssek et al., 2010). The predicted increase in the frequency and duration of drought events is expected to

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significantly affect these trees, gradually weakening their resistance to aridity. Over time, this may lead to higher mortality rates, shifts in species composition (Allen and Breshears, 1998; Bolte et al., 2009; Breshears et al., 2009; Allen et al., 2010; Park Williams et al., 2013), and reduced growth rates (Čermák et al., 1993; Hanson and Weltzin, 2000). Critical physiological processes, such as water and nutrient uptake, as well as photosynthesis, are determined by resource availability, which is influenced by site conditions, precipitation, forest management, and drought occurrences (Pedersen and Bille-Hansen, 1999; Rademacher, 2005; Braun et al., 2017). Although green leaves and needles constitute a small portion of a tree's total biomass, they are essential for photosynthesis and play a crucial role in driving tree growth. In their abscised form, however, they contribute significantly to nutrient cycling, supporting the ecosystem's nutrient supply, productivity, and biodiversity (Binkley, 1986; Vitousek, 2018; Jasińska et al., 2020). European beech (*Fagus sylvatica* [L.]) and Norway spruce (*Picea abies* [L.] Karst.) are currently the dominant tree species in Central European forests, making them particularly important, as their ability to adapt to climate change will determine their presence in future forest communities. Both species exhibit notable differences in their leaf and needle biomass and nutrient contents, with green needle biomass constituting 12 % of the aboveground biomass in mature Norway spruce, compared to only 1 % of green leaf biomass in mature European beech (Göttlein et al., 2012; Ulbricht et al., 2016), and Norway spruce having 3.7 times more dry needle biomass per hectare than the dry leaf biomass of European beech (Jacobsen et al., 2003).

Our study examines the effects of drought-induced stress on leaf and needle abscission in European beech and Norway spruce, focusing on the dynamics of foliar litterfall. Foliar litterfall is a continuous process shaped by seasonal cycles, typically peaking during autumn senescence, but varying annually and seasonally in response to environmental factors (Morffi-Mestre et al., 2020). Precipitation and temperature have been identified as key drivers of litterfall dynamics, as demonstrated in a Chinese temperate mixed forest where the highest litterfall levels occured in September and October. Specifically, mean annual and monthly precipitation, along with May and October temperatures, were strong predictors of annual litterfall production (Wang et al., 2021). Under conditions of sufficient water availability in Denmark, Hansen et al. (2009) documented litterfall biomass ranging from 3200 to 3700 kg ha^{-1} yr^{-1}, with no significant differences in total litter biomass, nutrient contents, or nutrient fluxes among Norway spruce, Sitka spruce (*Picea sitchensis* [Bong.] Carr.), Douglas fir (*Pseudotsuga menziesii*), European beech, and common oak (*Quercus robur* L.). However, the study further emphasized that nutrient-rich sites exhibited significantly higher foliar and total litter biomass over time compared to nutrient-poor sites. Similarly, Pedersen and Bille-Hansen (1999) observed comparable mean annual litterfall among Norway spruce, Sitka spruce, and European beech in Denmark but identified distinct litterfall patterns in response to water scarcity: While European beech maintained consistent annual litterfall, Norway spruce exhibited significant drought-induced fluctuations. Under more arid Mediterranean growth conditions, Gavinet et al. (2019) demonstrated that a 15-year rainfall exclusion experiment in a holm oak (*Quercus ilex* L.) stand reduced aboveground net primary productivity by 10 %, primarily due to declines in leaf and acorn production. Likewise, Liu et al. (2015) noted that experimental drought in a Mediterranean forest dominated by holm oak, green olive (*Phillyrea latifolia*), and strawberry tree (*Arbutus unedo*) significantly decreased aboveground net primary productivity and biomass increment. However, while both studies reported drought-induced suppression of growth-related processes, Liu et al. (2015) further found that drought tended to increase litterfall, suggesting that the effects of drought on litterfall dynamics may vary depending on forest composition and site-specific conditions.

Our research also aims to investigate drought-induced translocation patterns of calcium (Ca), potassium (K), magnesium (Mg), nitrogen (N), and phosphorus (P), and their resulting effects on the nutrient contents of foliar litter in European beech and Norway spruce, with a particular focus on quantifying the abscised nutrient masses. Recognizing seasonal variations in nutrient contents, early studies by Wolff (1871) and Gäumann (1928, 1935) documented the nutrient composition of various tree species. More recently, Carnol and Bazgir (2013) highlighted species-specific nutrient contents in foliage and foliar litter, while Göttlein et al. (2011) provided updated nutrition parameters for Central European tree species. Complementing this work, Flückiger and Braun (2003) underscored the importance of nutrient ratios, rather than absolute concentrations, as a more reliable metric for identifying critical nutrient thresholds. Comparative studies reveal that while European beech foliage generally contains higher nutrient levels than Norway spruce needles (Maňkovská, 1998; Jacobsen et al., 2003; Göttlein et al., 2012), European beech exhibits much lower nutrient contents per unit area of assimilation organs compared to Norway spruce, suggesting greater nutrient-related efficiency in carbon sequestration (Göttlein et al., 2012). Variations in foliar nutrient contents between European beech and Norway spruce depend on growth conditions and tree age (Nihlgård, 1970, 1972; Rademacher, 2002; Rademacher et al., 2002), although species typically exert a stronger influence than soil conditions (Hagen-Thorn et al., 2004). These nutrient dynamics are primarily shaped by the mobility of elements (Bukovac and Wittwer, 1957; Loneragan et al., 1976) and their seasonal translocation patterns (Guha and Mitchell, 1966). Consequently, nutrient contents and their translocation during senescence are closely tied to the chemical properties of individual elements (Chapin, 1980; Staaf, 1982; Helmisaari, 1990, 1992; Marschner, 1995). Environmental factors, particularly drought, can further impact both defoliation and foliar nutrient contents. Reduced soil moisture under drought conditions limits nutrient uptake and transport (Cramer et al., 2009; Waraich et al., 2011; Sardans and Peñuelas, 2012), while drought stress adversely impacts plant morphology and physiology, resulting in decreased photosynthesis (Farooq et al., 2012; Hussain et al., 2019). According to da Silva et al. (2011), water deficiency can severely impair mineral nutrition, negatively affecting plant growth and health. Reduced transpiration rates and imbalances in active transport and membrane permeability restrict nutrient transport from roots to aboveground plant organs, disrupting physiological and biochemical processes and potentially compromising overall plant development.

In contrast, drought-induced leaf and needle senescence contributes to nutrient retranslocation, enabling the remaining plant organs to benefit from the nutrients mobilized from the senescing leaves and needles (Munné-Bosch and Alegre, 2004). However, the impact of aridity on autumnal leaf senescence, a crucial process for deciduous trees and ecosystem functioning, remains unclear (Mariën et al., 2019, 2021). Mariën et al. (2021) further hypothesized that water shortage promotes the onset of leaf senescence, with varying dynamics across different tree species. In contrast, their results showed no impact of drought stress on the onset of autumn leaf senescence in both saplings and mature trees. For deciduous trees in the Northern Hemisphere, Gill et al. (2015) reported that leaf senescence has been progressively delayed in response to rising temperatures, with October temperatures emerging as the strongest predictors of senescence onset. In contrast, elevated carbon dioxide (CO_2) and drought stress have been shown to trigger premature leaf senescence and abscission, although elevated CO_2 can mitigate leaf-level water use under drought conditions. However, severe water scarcity may lead to excessive stomatal closure, potentially negating the benefits of elevated CO_2 (Warren et al., 2011). Among temperate winter-deciduous trees and shrubs in the United States, drought-induced leaf senescence, coupled with the maintenance of higher leaf water potentials, effectively prevented extensive leaf desiccation, thereby minimizing nutrient losses. This adaptive mechanism reduced seasonal nutrient depletion and may confer a competitive advantage during post-drought recovery, potentially shaping species composition within forest ecosystems (Marchin et al., 2010). He and Dijkstra (2014) further found that drought stress influences nitrogen (N) and phosphorus (P) concentrations in plants, indicating distinct nutrient translocation patterns and variations in the amounts of abscised nutrient masses between European beech and Norway spruce under drought conditions. Tree species can therefore play a pivotal role in nutrient return to the soil and nutrient cycling through the quantity and chemical composition of throughfall and litter (Carnol and Bazgir, 2013). In fact, the impact of plant species on nutrient cycling may even surpass that of abiotic factors (Hobbie, 1992). However, generalizing these effects is challenging, as nutrient cycling can vary widely between ecosystems, influenced by factors such as soil type, nutrient buffering capacity in the root zone, microbial communities, plant and animal species, and climate factors that affect nutrient losses through erosion, drainage, and leaching. Moreover, Yanai et al. (2012) documented variability in total foliar litterfall biomass and the associated abscised nutrient masses across years in a northern hardwood forest, influenced by growth conditions. Overall, these findings highlight the importance of conducting species- and site-specific nutrient analyses that account for seasonal and annual variations to accurately estimate foliar litterfall and nutrient fluxes. Despite these insights, limited publications quantify leaf and needle biomass abscission patterns and nutrient translocation patterns for European beech and Norway spruce throughout the year under artificially induced drought conditions.

In summary, our study addresses gaps in understanding these drought-induced patterns by utilizing data from a rainfall exclusion experiment in South Bavaria. It compares control plots, receiving normal rainfall, with experimental plots, where rainfall is excluded, to assess the impacts of water scarcity on foliar biomass production and nutrient cycling. The study focuses on foliar litterfall in European beech and Norway spruce during both the non-vegetation period (October to February) and the vegetation period (March to September). The main objectives are to investigate how drought-induced stress affects (Q1) the biomass of abscised leaves and needles, (Q2) the nutrient contents of abscised leaves and needles, (Q3) the nutrient masses of abscised leaves and needles, and (Q4) whether significant year-to-year variations exist in drought-induced biomass abscission patterns, nutrient translocation patterns, and abscised nutrient masses.

2. Material and methods

2.1. Experimental area

We selected the "Kranzberg Roof Experiment" (KROOF) site, located in the Kranzberg Forest near the Bavarian city of Freising (48° 25′ 12′' N, 11° 39′ 42′' E). This site comprises large groups of European beech surrounded by extensive areas of Norway spruce. The mixed stands in this area were described in detail by Pretzsch et al. (1998) as part of the German Research Foundation (DFG) Collaborative Research Center "Growth or Defense Against Parasites?". As of 2018, the European beech trees had an average age of 87 (± 4) years, while the Norway spruce trees averaged 67 (± 2) years. The site is characterized by a typical temperate humid climate (Enders/BayFORKLIM, 1996), receiving 750–800 mm of annual precipitation (460–500 mm during the vegetation period) and a mean annual air temperature of 7.8 °C (13.8 °C during the vegetation period) (German Weather Service, DWD). According to the Bavarian Geological Survey (Bayerisches Geologisches Landesamt, 1996), the geology surrounding the experimental site primarily consists of tertiary sediments from the Upper Freshwater Molasse, which are erosion products from the Alps deposited in the Molasse Basin by ancient river systems, along with Quaternary deposits from the last Ice Ages. The topsoil and near-surface geology are influenced by gravel, sand, and silt, with variable loess (wind-blown silt) coverage. These factors result in luvisol as the predominant soil group (IUSS Working Group WRB, 2022; Mantel et al., 2023). Digital Soil Mapping data from the Bavarian Environment Agency (LfU) indicate that the soil in this area is of high overall quality, with a high effective cation exchange capacity, consistently moist soil water conditions, and a substantial water-holding capacity of 160 mm. The humus form varies between the two species-dominated areas, with moder humus covering the European beech-dominated areas and mor humus prevalent in the Norway spruce-dominated areas (Zanella et al., 2011). Topographically, the site is located on flat terrain within the natural distribution range of European beech (Peters, 1992; Bohn et al., 2000; Walentowski et al., 2001; Schütt et al., 2002). Phytosociologically, the site is classified within the class Querco-Fagetea, the order Fagetalia sylvaticae, and the alliance Galio odorati-Fagion. The specific forest type is identified as Galio odorati-Fagetum, associated with well-drained, fertile soils under moderate moisture conditions (Fischer, 1995). The site covers 0.5 ha within ecoregion 12 ("Tertiärhügelland") and growth district 12.8 ("Oberbayerisches Tertiärhügelland"), at approximately 450 m above sea level (Arbeitskreis Standortskartierung in der Arbeitsgemeinschaft Forsteinrichtung 2003). The KROOF site was established in 2010 as an artificial rainfall exclusion experiment. It includes 12 experimental plots, each ranging from 110 m^2 to 200 m^2. Six plots (Nos. 2, 4, 6, 8, 10, 12) are treatment plots subjected to roof-induced drought, undergoing controlled wetting and drying cycles, while the remaining six plots (Nos. 1, 3, 5, 7, 9, 11) serve as control plots without rainfall exclusion. The treatment and control plots cover areas of 862 m^2 and 868 m^2, respectively. Each plot includes 4–6 European beeches on one side and 4–6 Norway spruces on the opposite side. In 2010, the 12 experimental plots were trenched to a soil depth of 1 m, where the sandy/silty loam layer severely restricts deeper root growth. Trenching was completed four years before the drought experiment began in 2014 to allow the trees sufficient time to recover, particularly in terms of root surface area (Pretzsch et al., 2016). To regulate precipitation throughfall on the six treatment plots, a novel roof structure was designed and constructed in the summer of 2013. Each roof consisted of rolling shutters, covering approximately 60 % of the roof area, and stationary shutters, which accounted for the remaining 40 % and remained permanently closed. The rolling shutters stayed furled throughout the year but automatically closed at the onset of rainfall during the growing season and reopened one hour after the rainfall ended. On average, this system withheld 69 % (±7 %) of the annual rainfall. The KROOF experiment consisted of two phases. Phase I (drought phase) ran from March 2014 to November 2018, while Phase II (watering and recovery phase) began in early summer 2019 and included three controlled irrigation events (June 25, July 4, and July 10) to restore soil water content in the treatment plots to the same level as the control plots (Grams et al., 2021). A map of the KROOF experimental layout, along with key forest yield data at both stand and tree levels, is provided in the supplementary section (see Fig. S1, Table S1, and Table S2). For simplicity, we refer to the treatment plots as "roof plots". For additional details about the KROOF design, see Häberle et al. (2015), Pretzsch et al. (2014, 2020, 2023), and Grams et al. (2021).

2.2. Experimental design

The "Kranzberg Roof Experiment" (KROOF) aims to assess forest productivity in relation to water availability at both tree and stand levels, with a focus on intra- and interspecific comparisons (Häberle et al., 2015). Another primary objective, as described by Pretzsch et al. (2014), is to elucidate synergies in mixed stands of Norway spruce and European beech and to develop hypotheses about the mechanisms driving these synergies. To collect abscised leaves and needles within the 12 experimental plots, two frames per plot, each equipped with five collecting bags, were installed directly under the tree crowns. One frame was positioned in the Norway spruce section and the other in the European beech section of each plot, yielding a total of 24 frames: 12 in the control plots and 12 in the roof plots. The experiment spanned two years, with collecting bags emptied regularly between August 2015 and September 2017. From August 2015 to July 2016, the bags were emptied monthly at the end of each month. However, due to the labor-intensive and costly nature of foliage and litter collection, emptying intervals were occasionally extended to up to four months. A representative photograph of a control plot and a roof plot, including the frames with collecting bags, is provided in the supplementary section (see Fig. S2).

2.3. *Foliar litter preparation and analysis procedure*

After collection, the litter components were separated into leaves, needles, twigs, bark, and buds. The foliar litter was sorted by tree species (beech, spruce) and treatment (roof, control), then dried in a drying cabinet at 60 °C. To determine periodic foliar litter biomass, the samples were weighed in their entirety. Portions of the sample material were ground into fine powder using an electric rotor mill. A 90.00 mg portion of the dry litter powder was extracted following the method described by Schramel et al. (1980) and subsequently analyzed for calcium (Ca), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), sodium (Na), phosphorus (P), sulfur (S), and zinc (Zn) using inductively coupled plasma optical emission spectrometry (ICP-OES) (Schramel, 1983; Stocker et al., 2005). To determine the nitrogen (N) content, litter powder samples (1.5–1.7 mg) were weighed into tin capsules, and their N content was analyzed using an Elemental Analyzer (Euro EA, Eurovector, Milan, Italy). The arithmetic mean values of characteristic leaf and needle nutrition parameters for the sampled beeches and spruces, grouped by treatment (roof and control), were obtained from nutrient content measurements of samples collected in July 2016. Nutritional boundary values, as defined by Göttlein et al. (2011), are used to evaluate the local nutritional status of various forest tree species. These boundary values classify essential main and minor nutrients into three categories: deficient, normal, and surplus. The nutrient contents of green leaves and needles collected during the specified period (typically July) are categorized within these ranges, enabling an assessment of the trees' nutrient supply (see Tables 2 and 3 in Chapter 3.1). For seasonal comparisons between vegetation and non-vegetation periods, the data were stratified into four periods: October 2015 – February 2016 (first non-vegetation period), March 2016 – September 2016 (first vegetation period), October 2016 – February 2017 (second non-vegetation period), and March 2017 – September 2017 (second vegetation period). Nutrient contents by tree species and treatment were averaged across these four periods. Biomass per hectare and nutrient masses per hectare, by tree species and treatment, were calculated based on the collecting bag data and summed across the four periods. To maintain focus, we prioritized the main nutrients (Ca, K, Mg, N, and P) in the analysis, while results for minor nutrients (Cu, Fe, Mn, Na, S, and Zn) are provided in the supplementary section. A study by Pedersen and Bille-Hansen (1999) revealed that foliar litterfall accounts for approximately 90 % of total litterfall across all examined species. Moreover, the strong correlation between foliar and total litterfall observed by Hansen et al. (2009) suggests that foliar litterfall can be accurately estimated based on total litterfall measurements. In this context, and for simplicity, our study uses the term "litter" to specifically refer to abscised leaves and needles, excluding other components such as twigs, bark, and buds.

2.4. *Statistical analyses of foliar litter biomass, nutrient contents and nutrient masses*

We applied linear mixed models to analyze the dependent variables: foliar litter biomass, and the nutrient contents and masses of Ca, K, Mg, N, and P. These variables were examined as functions of the independent variables: tree species (beech, spruce), treatment (roof, control), and period (non-vegetation periods: October 2015–February 2016 and October 2016–February 2017; vegetation periods: March 2016–September 2016 and March 2017–September 2017). The primary objective was to detect significant differences resulting from drought-induced stress between control plots (no rainfall exclusion) and roof plots (with rainfall exclusion). Random effects were assigned to the experimental plots (control plots: 1, 3, 5, 7, 9, 11; roof plots: 2, 4, 6, 8, 10, 12) and the five collecting bags (1–5) within each frame (two frames per experimental plot). For research questions Q1–Q4, we tested the effects of tree species, treatment, and period, along with their second- and third-order interactions, on foliar litter biomass, nutrient contents, and nutrient masses. We used a basic linear mixed model (see Model 1) as a reference and applied the dredge algorithm from the MuMIn package (Barton, 2023) in R Statistics. The model parameters $a_0,\dots,a_7$ are explained in Model 1. For estimating foliar litter biomass (Q1 and Q4), the dredge algorithm identified Model 2 as the best fit (= basic model). For estimating main nutrient contents of Ca, K, Mg, N, and P (Q2 and Q4), the dredge algorithm selected Models 3–6. Models for minor nutrient contents (Cu, Fe, Mn, Na, S, Zn) are included in the supplementary section (see Models S1–S4). For estimating nutrient masses of Ca, K, Mg, N, and P (Q3 and Q4), the dredge algorithm identified Model 7 as the best fit (= basic model). Models for minor nutrient masses (Cu, Fe, Mn, Na, S, Zn) are also included in the supplementary section (see Models S5–S6).

Model 1 (Basic linear mixed model, Q1 – Q4)

$$\begin{aligned}\textit{Dependent variable}_{ijk} = {} & a_0 + a_1 \times \textit{species}_{ijk} + a_2 \times \textit{treatment}_i + a_3 \times \textit{period}_k \\ & + a_4 \times \textit{species}_{ijk} \times \textit{treatment}_i \\ & + a_5 \times \textit{species}_{ijk} \times \textit{period}_k \\ & + a_6 \times \textit{treatment}_i \times \textit{period}_k \\ & + a_7 \times \textit{species}_{ijk} \times \textit{treatment}_i \times \textit{period}_k \\ & + b_i + b_{ij} + \varepsilon_{ijk}\end{aligned}$$

a_0: Intercept

a_1: Model parameter based on the predictor variable tree species (beech, spruce)

a_2: Model parameter based on the predictor variable treatment (control, roof)

a_3: Model parameter based on the predictor variable period (October 2015 – February 2016, March 2016 – September 2016, October 2016 – February 2017, March 2017 – September 2017)

a_4: Model parameter based on the interaction between predictor variables tree species and treatment

a_5: Model parameter based on the interaction between predictor variables tree species and period

a_6: Model parameter based on the interaction between predictor variables treatment and period

a_7: Model parameter based on the interaction between predictor variables tree species and treatment and period

b: Random effects

i: Experimental plots

j: Litter bag

k: Single observation

ε: i.i.d. errors

Model 2 (Q1 and Q4)

$$\begin{aligned}\textit{Litter biomass}_{ijk} = {} & a_0 + a_1 \times \textit{species}_{ijk} + a_2 \times \textit{treatment}_i + a_3 \times \textit{period}_k \\ & + a_4 \times \textit{species}_{ijk} \times \textit{treatment}_i \\ & + a_5 \times \textit{species}_{ijk} \times \textit{period}_k \\ & + a_6 \times \textit{treatment}_i \times \textit{period}_k \\ & + a_7 \times \textit{species}_{ijk} \times \textit{treatment}_i \times \textit{period}_k \\ & + b_i + b_{ij} + \varepsilon_{ijk}\end{aligned}$$

Model 3 (Q2 and Q4)

$$\begin{aligned}\textit{Nitrogen content}_{ijk} = {} & a_0 + a_1 \times \textit{species}_{ijk} + a_2 \times \textit{treatment}_i + a_3 \times \textit{period}_k \\ & + a_4 \times \textit{species}_{ijk} \times \textit{treatment}_i \\ & + a_5 \times \textit{species}_{ijk} \times \textit{period}_k \\ & + b_i + b_{ij} + \varepsilon_{ijk}\end{aligned}$$

Model 4 (Q2 and Q4)

$$\begin{aligned}\textit{Calcium content}_{ijk} = {} & a_0 + a_1 \times \textit{species}_{ijk} + a_2 \times \textit{treatment}_i + a_3 \times \textit{period}_k \\ & + a_4 \times \textit{species}_{ijk} \times \textit{treatment}_i \\ & + a_5 \times \textit{species}_{ijk} \times \textit{period}_k \\ & + a_6 \times \textit{treatment}_i \times \textit{period}_k \\ & + a_7 \times \textit{species}_{ijk} \times \textit{treatment}_i \times \textit{period}_k \\ & + b_i + b_{ij} + \varepsilon_{ijk}\end{aligned}$$

Model 5 (Q2 and Q4)

(*continued on next page*)

(*continued*)

Magnesium content$_{ijk}$ =	$a_0 + a_1 \times species_{ijk} + a_2 \times period_k$	$+ b_i + b_{ij} + \varepsilon_{ijk}$
Phophorus content$_{ijk}$ =	$+ a_3 \times species_{ijk} \times period_k$	
Model 6 (Q2 and Q4)		
Potassium content$_{ijk}$ =	$a_0 + a_1 \times species_{ijk} + a_2 \times treatment_i + a_3 \times period_k$ $+ a_4 \times species_{ijk} \times period_k$	$+ b_i + b_{ij} + \varepsilon_{ijk}$
Model 7 (Q3 and Q4)		
Calcium mass$_{ijk}$ =	$a_0 + a_1 \times species_{ijk} + a_2 \times treatment_i + a_3 \times period_k$	$+ b_i + b_{ij} + \varepsilon_{ijk}$
Magnesium mass$_{ijk}$ =	$+ a_4 \times species_{ijk} \times treatment_i$	
Nitrogen mass$_{ijk}$ =	$+ a_5 \times species_{ijk} \times period_k$	
Phophorus mass$_{ijk}$ =	$+ a_6 \times treatment_i \times period_k$	
Potassium mass$_{ijk}$ =	$+ a_7 \times species_{ijk} \times treatment_i \times period_k$	

Based on the different linear mixed models (Models 2–7), we applied simultaneous tests for general linear hypotheses following the methodology of Hothorn et al. (2008), using the multcomp package in R Statistics. These tests were performed to identify significant differences in the dependent variables - foliar litter biomass, and the nutrient contents and masses of Ca, K, Mg, N, and P - between various pairwise combinations of the factors tree species, treatment, and period. The contrasts were defined as follows: tree species (beech = 0, spruce = 1), treatment (control = 0, roof = 1), and period (October 2015–February 2016 = 0, March 2016–September 2016 = 0 or 1, October 2016–February 2017 = 0 or 1, March 2017–September 2017 = 0 or 1).

In the linear regression Models 1 - 7, the indexes *i, j*, and *k* refer to the levels of the experimental plot, litter bag, and single observation, respectively. To account for the grouped structure, random effects b_i and b_{ij} were implemented at the levels of the experimental plot and litter bag, in alignment with the standard assumptions of mixed-effects models (e.g., Mehtätalo and Lappi, 2020). These random effects are assumed to be independent across experimental plots and litter bags, and the residual errors ε are assumed to be independent and identically distributed (i.i.d.) across observations, with a mean of 0, constant variance, and no correlation.

In Models 1, 2, 4, and 7, $a_0,\ldots,a_7$ represent the parameters of the fixed effects, including tree species, treatment, period, and their interactions, with a_0 as the intercept. In Model 3, the fixed effects parameters are $a_0,\ldots,a_5$, while in Model 5, they are $a_0,\ldots,a_3$. For Model 6, the fixed effects parameters are $a_0,\ldots,a_4$. For all calculations and graphic illustrations, we used the statistical software R 4.1.0 (R Core Team, 2021), explicitly employing the packages nlme (Pinheiro et al., 2023), ggplot2 (Wickham, 2016), grid (R Core Team, 2023), and plyr (Wickham, 2011).

3. Results

3.1. *Tabular overview of total foliar litter biomass and leaf and needle nutrition parameters*

Table 1 presents the total abscised leaf and needle biomass for October 2015–September 2016 (first non-vegetation and vegetation period) and October 2016–September 2017 (second non-vegetation and vegetation period), as well as the total and mean values for the entire observation period (October 2015–September 2017). The data are categorized by tree species (beech and spruce) and treatment (roof and control).

Table 1
Summed and average abscised leaf and needle biomass per hectare for the periods October 2015 – September 2016, October 2016 – September 2017, and the entire observation period October 2015 – September 2017, categorized by tree species (beech and spruce) and treatment (roof and control).

Period	Beech roof	Beech control	Spruce roof	Spruce control
	[kg/ha]	[kg/ha]	[kg/ha]	[kg/ha]
Sa. Oct. 15-Sep. 16	3281	4329	6882	4680
Sa. Oct. 16-Sep. 17	4068	4904	1346	1959
Sa. Oct. 15 – Sep. 17	7349	9233	8228	6639
Ø Oct. 15 – Sep. 17	3675	4617	4114	3320

Tables 2 and 3 display the characteristic leaf and needle nutrition parameters for the main nutrients Ca, K, Mg, N, and P, along with the corresponding nutritional boundary values defined by Göttlein et al. (2011) for European beech and Norway spruce, respectively. Additional data for the minor nutrients Cu, Fe, Mn, S, and Zn can be found in Tables S3 and S4 in the supplementary section, where they are discussed further (see Discussion S1).

For European beech, the characteristic leaf nutrition parameters indicated that the main nutrient contents of the foliage generally did not differ substantially between the two treatments, except for Ca content. N and Mg levels were sufficient in both treatments, while Ca was sufficient in the control plots but deficient in the roof plots. In contrast, K and P were deficient in both treatments. According to Flückiger and Braun (2003), the recommended median ranges for nutrient ratios are 2.1–3.8 for N/K, 10.4–21.5 for N/Mg, and 10.0–17.1 for N/P. The calculated nutrient ratios in our study were 5.9 for N/K, 12.8 for N/Mg, and 18.5 for N/P in the roof plots, and 4.5 for N/K, 12.6 for N/Mg, and 18.3 for N/P in the control plots.

For Norway spruce, the characteristic leaf nutrition parameters indicated that the main nutrient contents of the foliage were generally within the same range for both treatments, except for N content. Both treatments showed sufficient N supply and very good Ca supply. However, Mg availability was deficient in both treatments, and K and P levels were extremely deficient. According to Flückiger and Braun (2003), the recommended median ranges for nutrient ratios are 1.9–3.6 for N/K, 10.3–20.0 for N/Mg, and 7.0–12.0 for N/P. Our nutrient ratios were 7.3 for N/K, 18.1 for N/Mg, and 16.5 for N/P in the roof plots, and 5.5 for N/K, 17.0 for N/Mg, and 16.9 for N/P in the control plots.

3.2. *Foliar litter biomass (Q1 and Q4)*

The statistical analyses of the abscised leaf and needle biomass revealed that almost all main effect variables and their interactions significantly influenced the estimated litter biomass of Norway spruce and European beech (see Table 4). The key model predictions, along with the results in Fig. 1, indicated that both tree species were affected by periods of drought but exhibited different patterns of leaf and needle fall. Norway spruce was more negatively impacted by water scarcity than the deciduous European beech, exhibiting high needle loss at the start of the observation period after more than a year of rainfall exclusion. However, this needle loss decreased as the drought persisted. In contrast, water scarcity led to lower abscised foliage biomass for European beech initially, but the abscised leaf biomass increased with the duration of the drought. The impact of periodic droughts on the abscised leaf and needle biomass of both species was estimated to decrease over the course of the drought. The effects of aridity were lower during the vegetation periods than during the non-vegetation periods, despite both treatments showing much higher litter biomass in the non-vegetation periods due to natural leaf and needle fall patterns, which overlaid the drought-induced abscission patterns. The standard deviations of the random effects and the residuals were based on Model 2 (see Chapter 2.4). At the experimental plot level, the standard deviation of the random effects was 323.4979 for the intercept; at the litterbag in experimental plot level, the standard deviation of the random effects was 0.0403 for the intercept; and the residual was 824.4916.

Fig. 1 illustrates the pooled abscised leaf and needle biomass data per hectare for the monospecific stands, categorized by tree species (beech and spruce), treatment (roof and control), and period (October 2015 to February 2016, March 2016 to September 2016, October 2016 to February 2017, and March 2017 to September 2017). The corresponding data are provided in Table S5 in the supplementary section.

Table 2
Bold-printed arithmetic mean values of characteristic leaf nutrition parameters for European beech, categorized by treatment. Nutritional boundary values are derived from Göttlein et al. (2011).

European beech (Fagus sylvatica)								
Nutrients	Deficiency			Normal range			Surplus	
	extreme	deficiency	latent	lower	central	upper	luxury	extreme
N (g/kg)	< 17.04	< 18.5	18.5–18.74	18.74–20.04	20.04–22.3	22.3–23.25	23.25–27.46	> 27.46
N roof					**21.644**			
N control					**21.583**			
Ca (g/kg)			< 6.66	6.66–8.15	8.15–11.83	11.83–14.03	> 14.03	
Ca roof			**6.447**					
Ca control				**6.770**				
K (g/kg)	< 4.93	< 3.21	3.21–6.08	6.08–6.95	6.95–8.75	8.75–9.68	9.68–13.0	> 13.0
K roof			**3.682**					
K control			**4.762**					
Mg (g/kg)	< 0.66		< 1.07	1.07–1.31	1.31–1.92	1.92–2.29	> 2.29	
Mg roof					**1.690**			
Mg control					**1.710**			
P (g/kg)		< 1.07	1.07–1.23	1.23–1.38	1.38–1.7	1.7–1.87	1.87–2.0	> 2.0
P roof			**1.168**					
P control			**1.177**					

Table 3
Bold-printed arithmetic mean values of characteristic leaf nutrition parameters for Norway spruce, categorized by treatment. Nutritional boundary values are derived from Göttlein et al. (2011).

Norway spruce (Picea abies)								
Nutrients	Deficiency			Normal range			Surplus	
	extreme	deficiency	latent	lower	central	upper	luxury	extreme
N (g/kg)	< 10.1	< 11.7	11.7–13.2	13.2–13.7	13.7–14.7	14.7–15.3	15.3–18.1	> 18.1
N roof					**13.729**			
N control				**13.280**				
Ca (g/kg)	< 1.2	< 1.5	1.5–2.5	2.5–3.3	3.3–4.8	4.8–5.6	5.6–8.6	> 8.6
Ca roof							**7.030**	
Ca control							**8.032**	
K (g/kg)	< 2.7	< 3.5	3.5–4.6	4.6–5.4	5.4–6.7	6.7–7.3	7.3–9.6	> 9.6
K roof	**1.873**							
K control	**2.395**							
Mg (g/kg)	< 0.4	< 0.5	0.5–0.8	0.8–0.9	0.9–1.1	1.1–1.3	1.3–1.7	> 1.7
Mg roof			**0.758**					
Mg control			**0.779**					
P (g/kg)	< 0.9	< 1.0	1.0–1.3	1.3–1.4	1.4–1.8	1.8–1.9	1.9–2.0	> 2.0
P roof	**0.834**							
P control	**0.788**							

Norway spruce exhibited the highest needle loss during the first non-vegetation period, particularly on the roof plots. The abscised needle biomass in both treatments declined significantly over time, reaching the lowest levels during the second vegetation period. Needle loss on the roof plots exceeded that on the control plots only during the first non-vegetation period, where the difference was highly significant. Comparisons between the first non-vegetation period and the first vegetation period, as well as between both non-vegetation periods, revealed highly significant differences. However, further pairwise comparisons between different periods showed mostly non-significant differences. European beech exhibited high abscised foliage biomass in both treatments during the non-vegetation periods, peaking in the second non-vegetation period, and similarly low biomass during the vegetation periods. Highly significant differences between the non-vegetation and vegetation periods were consistently observed. Comparisons between the two non-vegetation periods and the two vegetation periods mostly showed non-significant differences. Control plots exhibited higher foliar litter biomass than roof plots during non-vegetation periods, with a significant difference observed only during the first non-vegetation period. Overall, the abscised leaf and needle biomass significantly differed between the two tree species during both non-vegetation periods and the first vegetation period, but not during the second vegetation period. Table S6 in the supplementary section provides a detailed overview of the pairwise comparisons of foliar litter biomass, categorized by tree species, treatment, and period.

3.3. Foliar litter nutrient contents (Q2 and Q4)

The statistical analyses of the main nutrient contents in foliar litter revealed that tree species, seasonal periods, and their interactions had mostly significant to highly significant effects on the estimated nutrient contents of Ca, K, Mg, N, and P. In most cases, the nutrient contents in the foliar litter of European beech exceeded those in the foliar litter of Norway spruce. During vegetation periods, both tree species exhibited higher K, N, and P contents, lower Ca contents in Euroepean beech, and nearly equal Mg contents compared to the non-vegetation periods (see Table 5 and the corresponding Table S7 in the supplementary section for additional data on the minor nutrient contents of Cu, Fe, Mn, Na, S, and Zn). The impact of drought on litter nutrient contents varied significantly for Ca, K, Mg, N, and P, depending on the season and tree species. Linear mixed models predicted no significant effects of drought on Mg and P contents or their seasonal translocation patterns for both species. In contrast, drought stress significantly reduced K contents in the foliar litter of both European beech and Norway spruce throughout the year. The N content of foliar litter increased significantly only in drought-stressed Norway spruce. Drought positively influenced the Ca content

Table 4

Statistical analysis of the abscised leaf and needle biomass, categorized by tree species, treatment, and period (calculated according to Model 2). The "x" represents the interaction between two or three predictors (Std. error: Standard error). Significant estimates are marked with asterisks (*: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$).

Predictor variable	Parameter Estimate	Std. error	*p* value	Sig.
Intercept	3999.7600	200.2532	0.0000	***
Species (spruce)	−465.2600	212.8828	0.0294	*
Treatment (roof)	−1057.4780	292.1567	0.0047	**
Period (March 16-Sep. 16)	−3670.8120	212.8828	0.0000	***
Period (March 17-Sep. 17)	−3596.5990	212.8828	0.0000	***
Period (Oct. 16-Feb. 17)	501.4270	212.8828	0.0190	*
Species (spruce) x treatment (roof)	3305.4670	327.5957	0.0000	***
Species (spruce) x period (March 16-Sep. 16)	1281.8400	301.0618	0.0000	***
Species (spruce) x period (March 17-Sep. 17)	669.5150	301.0618	0.0267	*
Species (spruce) x period (Oct. 16-Feb. 17)	−2683.5880	301.0618	0.0000	***
Treatment (roof) x period (March 16-Sep. 16)	1092.5350	309.5012	0.0005	***
Treatment (roof) x period (March 17-Sep. 17)	1012.3710	309.5012	0.0012	**
Treatment (roof) x period (Oct. 16-Feb. 17)	266.2060	309.5012	0.3903	
Species (spruce) x treatment (roof) x period (March 16-Sep. 16)	−3445.6270	444.9238	0.0000	***
Species (spruce) x treatment (roof) x period (March 17-Sep. 17)	−3420.7380	444.9238	0.0000	***
Species (spruce) x treatment (roof) x period (Oct. 16-Feb. 17)	−2967.0400	444.9238	0.0000	***

in the foliar litter of European beech during the second non-vegetation period. In contrast, for Norway spruce, drought had a negative impact on the Ca content in foliar litter, with significant effects observed during the first vegetation period and the second non-vegetation period. The standard deviations of the random effects and residuals, based on Models 3–6 (see Chapter 2.4), are provided in Table S8 in the supplementary section.

Fig. 2 presents the pooled average nutrient contents of Ca, K, Mg, N, and P in foliar litter, categorized by tree species (beech and spruce), treatment (roof and control), and period (October 2015–February 2016, March 2016–September 2016, October 2016–February 2017, and March 2017–September 2017). The corresponding data are provided in Table S9 in the supplementary section, along with additional information on minor nutrient contents (Cu, Fe, Mn, Na, S, and Zn) in Table S10.

The nutrient contents of the foliar litter decreased in the order N > Ca > K > Mg > P for European beech, and in the order N > Ca > K > Mg > P (non-vegetation period) and N > Ca > K > P > Mg (vegetation period) for Norway spruce. These nutrient contents can be roughly divided into three groups: a high-content group (N and Ca), a medium-content group (K), and a low-content group (Mg and P). For European beech, the main nutrient contents of the litter tended to be higher on the control plots compared to the roof plots throughout the entire investigation period, except for N and P contents during the second non-vegetation period. For Norway spruce, the foliar litter showed higher contents of Ca and K on the control plots, but higher contents of N and P on the roof plots over the complete investigation period. Both tree species exhibited similar Mg and P contents between treatments. However, significant differences with lower values on the roof plots were observed for the K content in the foliar litter of both species during both the vegetation and non-vegetation periods, as well as for the Ca content in the foliar litter of Norway spruce during the second non-vegetation period. When comparing the foliar litter nutrient contents of both tree species, nutrient levels were largely similar throughout the investigation period. Exceptions included much higher N contents in the foliar litter of European beech compared to those of Norway spruce during both vegetation periods, higher Ca contents in the foliar litter of European beech during the first non-vegetation period, and higher Mg contents in the foliar litter of European beech throughout the observation period. Despite these similarities, pairwise comparisons, however, revealed mostly significant to highly significant differences between the two tree species. For European beech, seasonal nutrient translocation patterns showed higher contents of N, K, and P, nearly equal Mg contents, and lower Ca contents during both vegetation periods compared to the non-vegetation periods. Norway spruce showed similar patterns for N, Mg, and P, while Ca contents tended to rise and K contents tended to decline over the entire investigation period. Pairwise comparisons of the main nutrient contents in foliar litter predominantly indicated significant to highly significant differences between non-vegetation and vegetation periods. Table S11 in the supplementary section offers a detailed overview of these comparisons, including the minor nutrient contents of Cu, Fe, Mn, Na, S, and Zn, categorized by tree species, treatment, and period.

3.4. *Foliar litter nutrient masses (Q3 and Q4)*

The statistical analyses of the main nutrient masses of the foliar litter revealed that the effect of the variables tree species, treatment, and seasonal periods, and their interactions on the estimated litter nutrient masses of Ca, K, Mg, N, and P was significant in most cases (see Table 6 and the corresponding Table S12 in the supplementary section, which includes additional minor nutrient masses of Cu, Fe, Mn, Na, S, and Zn). Model estimations indicated that drought significantly affected the main nutrient masses in the foliar litter of both European beech and Norway spruce, albeit in contrasting ways. Aridity was predicted to reduce abscised nutrient masses for European beech while increasing them for Norway spruce. These trends varied further between the species: for European beech, abscised nutrient masses increased with the duration of drought during leaf fall periods, whereas for Norway spruce, they decreased with prolonged drought during both vegetation and non-vegetation periods. Similar to the patterns of abscised foliar litter biomass, the effects of aridity on abscised nutrient masses were less pronounced during vegetation periods than in non-vegetation periods for both tree species. The natural seasonal leaf fall cycles in both species overlaid the drought-induced nutrient mass abscission patterns, causing variations depending on the specific nutrients involved. The standard deviations of the random effects and the residuals, based on Model 7 (see Chapter 2.4), are shown in Table S13 in the supplementary section.

Fig. 3 displays the pooled nutrient masses of Ca, K, Mg, N, and P in foliar litter, categorized by tree species (beech and spruce), treatment (roof and control), and period (October 2015 to February 2016, March 2016 to September 2016, October 2016 to February 2017, and March 2017 to September 2017). The corresponding Table S14 can be found in the supplementary section, along with Table S15, which provides additional data on the minor nutrient contents of Cu, Fe, Mn, Na, S, and Zn.

The nutrient masses of Ca, K, Mg, N, and P reflect both the respective biomass and nutrient contents of the foliar litter. Similar to the nutrient contents, the examined nutrient masses can be classified into three groups: a high nutrient mass group (including N and Ca), a medium mass group (including K), and a low mass group (including Mg and P). For European beech, the influence of aridity on the nutrient masses of the litter was significant for Ca, K, Mg, N, and P during the first non-vegetation period, resulting in lower abscised nutrient masses for drought-stressed European beech trees. The impact of drought remained similar for abscised K mass, slightly declined for abscised Mg and Ca masses, and became insignificant for abscised N and P masses during the second non-vegetation period. Generally, aridity did not significantly affect the abscised nutrient masses of the litter during either vegetation period for any of the main nutrients. For Norway spruce, drought showed a strong and highly significant influence on the abscised nutrient masses of Ca, K, Mg, N, and P during the first non-vegetation period, leading to higher abscised nutrient masses for drought-stressed

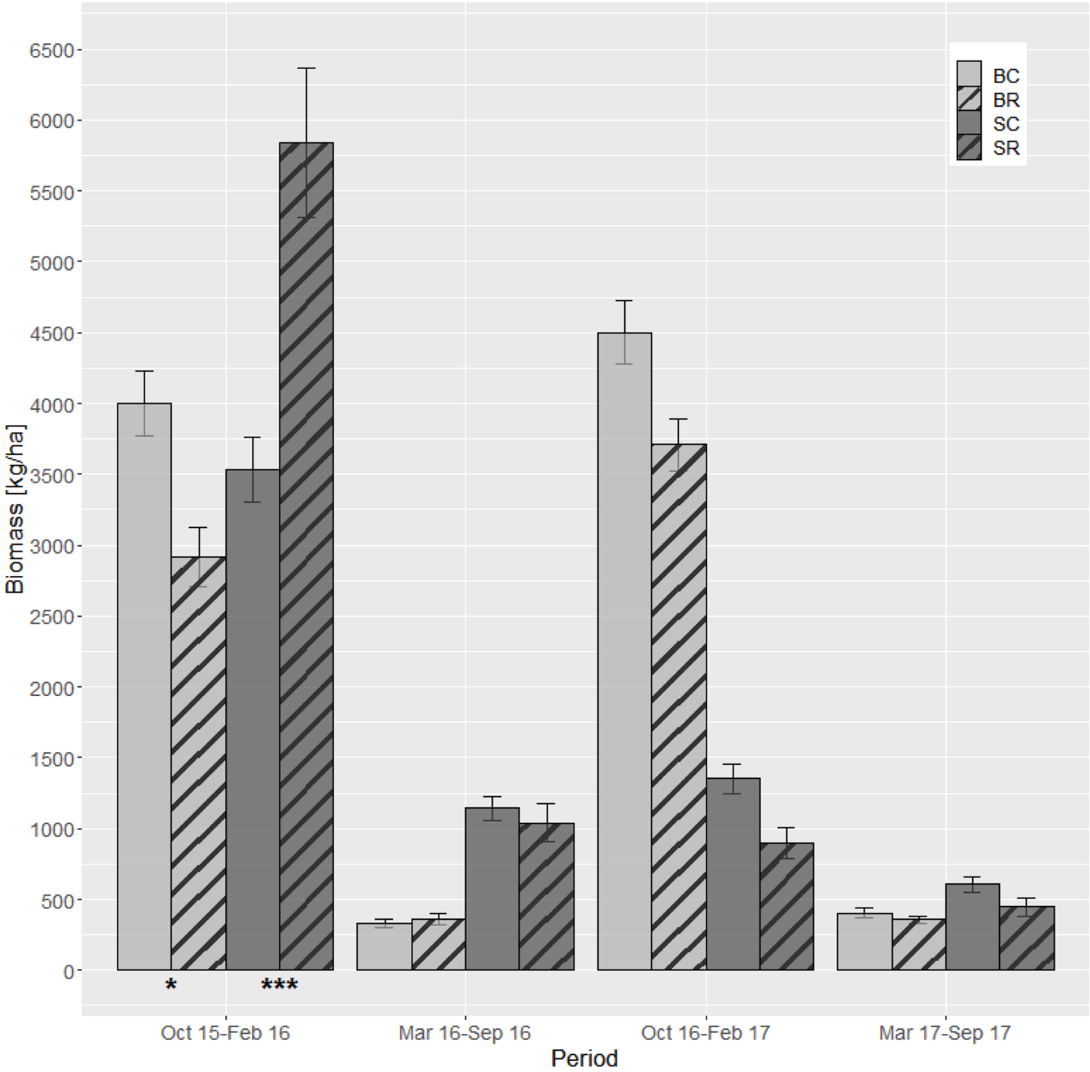

Fig. 1. Abscised leaf and needle biomass per hectare, categorized by tree species, treatment, and period. Thin error bars represent the standard errors of the means. BC: Beech Control, BR: Beech Roof, SC: Spruce Control, SR: Spruce Roof. Significant differences between the roof and control plots are marked with asterisks (*: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$).

Norway spruce trees. However, the impact of aridity diminished with the prolonged drought duration, showing no significant effects during the second non-vegetation period. Similar to European beech, drought did not affect the abscised nutrient masses of the litter during either vegetation period for any of the examined main nutrients. For European beech, the non-vegetation periods showed higher nutrient masses in the litter than the vegetation periods due to autumnal leaf fall. Additionally, the nutrient masses increased during the second non-vegetation period compared to the first, and during the second vegetation period compared to the first. For Norway spruce, nutrient masses were very high during the first non-vegetation period but declined significantly in subsequent periods, with no significant differences between treatments in later periods. As expected, pairwise comparisons of the main nutrient masses between tree species, as well as between non-vegetation and vegetation periods, revealed mostly significant to highly significant differences (see Table S16 in the supplementary section, which includes data on the minor nutrient contents of Cu, Fe, Mn, Na, S, and Zn, categorized by tree species, treatment, and period).

3.5. *Temporal dynamics of foliar litter biomass, nutrient contents and nutrient masses (Q4)*

The development and percentage variance of foliar litter between the roof plots and control plots, categorized by tree species (beech and spruce) and period (October 2015 to February 2016, March 2016 to September 2016, October 2016 to February 2017, and March 2017 to September 2017), are presented in Fig. 4 for abscised biomass, Fig. 5 for nutrient contents, and Fig. 6 for abscised nutrient masses. The percentage values are derived from Fig. 1 for the abscised biomass, Fig. 2 for the nutrient contents, and Fig. 3 for the abscised nutrient masses, respectively.

Distinct percentage abscission patterns of the foliar litter between European beech and Norway spruce on the roof plots were particularly evident during the first non-vegetation period. Compared to the foliar litter biomass on the control plots, which represented 100 %, the abscised leaf biomass of European beech was 72.9 % during the first non-vegetation period, 110.7 % during the first vegetation period, 82.4 % during the second non-vegetation period, and 88.8 % during the second vegetation period. For Norway spruce, the abscised needle biomass was 165.3 % during the first non-vegetation period, 90.8 % during the first vegetation period, 66.5 % during the second non-

Table 5
Statistical analyses of the main nutrient contents in the foliar litter, categorized by tree species, treatment, and period (calculated according to Models 3 - 6). The "x" represents the interaction between two or three predictors. Mep: Main effect parameter estimate, IMep: Interaction estimate between main effect parameters, p: *p*-value, Sig: Level of significance, whereas significant estimates are marked with asterisks (*: $p \leq 0.05$ = significant, **: $p \leq 0.01$ = high significant, ***: $p \leq 0.001$ = highly significant).

Predictor variable		Ca	K	Mg	N	P
Intercept	Mep	9.914	2.863	1.650	11.603	0.558
	p	0.0000	0.0000	0.0000	0.0000	0.0000
	Sig	***	***	***	***	***
Species (spruce)	Mep	−2.846	−0.158	−0.883	−0.483	0.126
	p	0.0000	0.0388	0.0000	0.0400	0.0000
	Sig	***	*	***	*	***
Treatment (roof)	Mep	−0.660	−0.437	—	−0.396	—
	p	0.1669	0.0064		0.3969	
	Sig		**			
Period (March 16-Sep. 16)	Mep	−2.549	0.810	0.016	8.053	0.422
	p	0.0000	0.0000	0.4260	0.0000	0.0000
	Sig	***	***		***	***
Period (March 17-Sep. 17)	Mep	−1.764	1.544	0.016	8.775	0.292
	p	0.0000	0.0000	0.4395	0.0000	0.0000
	Sig	***	***		***	***
Period (Oct. 16-Feb. 17)	Mep	−0.938	−0.115	−0.049	−0.622	0.041
	p	0.0000	0.1731	0.0085	0.0075	0.0342
	Sig	***		**	**	*
Species (spruce) x treatment (roof)	IMep	−0.007	—	—	0.717	—
	p	0.9647			0.0020	
	Sig				**	
Species (spruce) x period (March 16-Sep. 16)	IMep	2.995	−0.750	−0.104	−6.223	−0.273
	p	0.0000	0.0000	0.0000	0.0000	0.0000
	Sig	***	***	***	***	***
Species (spruce) x period (March 17-Sep. 17)	IMep	3.307	−2.135	−0.098	−7.387	0.097
	p	0.0000	0.0000	0.0005	0.0000	0.0010
	Sig	***	***	***	***	***
Species (spruce) x period (Oct. 16-Feb. 17)	IMep	2.483	−0.113	−0.012	0.033	−0.167
	p	0.0000	0.3256	0.6140	0.9167	0.0000
	Sig	***				***
Treatment (roof) x period (March 16-Sep. 16)	IMep	0.189	—	—	—	—
	p	0.3427				
	Sig					
Treatment (roof) x period (March 17-Sep. 17)	IMep	−0.165	—	—	—	—
	p	0.4114				
	Sig					
Treatment (roof) x period (Oct. 16-Feb. 17)	IMep	0.548	—	—	—	—
	p	0.0025				
	Sig	**				
Species (spruce) x Treatment (roof) x period (March 16-Sep. 16)	IMep	−0.803	—	—	—	—
	p	0.0010				
	Sig	***				
Species (spruce) x Treatment (roof) x period (March 17-Sep. 17)	IMep	−0.257	—	—	—	—
	p	0.3503				
	Sig					
Species (spruce) x Treatment (roof) x period (Oct. 16-Feb. 17)	IMep	−1.450	—	—	—	—
	p	0.0000				
	Sig	***				

vegetation period, and 73.6 % during the second vegetation period.

Similar percentage nutrient translocation patterns of Ca, Mg, N, and P were observed on the roof plots for European beech, and for Mg, N, and P in Norway spruce. In contrast, K in European beech and Ca and K in Norway spruce exhibited divergent percentage translocation patterns. Compared to the nutrient contents of the foliar litter on the control plots, which were considered 100 %, the percentage values of the nutrient contents of Ca, K, Mg, N, and P on the roof plots were as follows (in chronological order: first non-vegetation period, first vegetation period, second non-vegetation period, second vegetation period):

For European beech, Ca: 92.3 % → 94.0 % → 99.0 % → 89.9 %; K: 84.1 % → 80.3 % → 83.1 % → 91.6 %; Mg: 97.7 % → 98.0 % → 99.3 % → 93.6 %; N: 98.3 % → 95.9 % → 101.4 % → 94.6 %; P: 93.8 % → 95.3 % → 108.0 % → 101.7 %.

For Norway spruce, Ca: 88.6 % → 82.4 % → 81.8 % → 87.4 %; K: 85.6 % → 83.9 % → 80.2 % → 77.8 %; Mg: 101.5 % → 98.7 % → 101.3 % → 98.7 %; N: 102.4 % → 100.8 % → 106.7 % → 101.8 %; P: 102.3 % → 102.7 % → 107.5 % → 106.2 %.

For both European beech and Norway spruce, similar percentage abscission patterns of the nutrient masses of Ca, K, Mg, N, and P were observed on the roof plots throughout the entire observation period. Compared to the nutrient masses of the foliar litter on the control plots, which were set at 100 %, the percentage values of the nutrient masses of Ca, K, Mg, N, and P on the roof plots were as follows (in chronological order: first non-vegetation period, first vegetation period, second non-vegetation period, second vegetation period):

For European beech: Ca: 67.3 % → 104.0 % → 81.6 % → 79.8 %; K: 61.3 % → 88.9 % → 68.5 % → 81.3 %; Mg: 71.3 % → 108.4 % → 81.8 % → 83.1 %; N: 71.7 % → 106.1 % → 83.5 % → 84.0 %; P: 68.4 % → 105.5 % → 89.0 % → 90.3 %.

For Norway spruce: Ca: 146.4 % → 74.8 % → 54.4 % → 64.3 %; K: 141.5 % → 76.2 % → 53.4 % → 57.3 %; Mg: 167.8 % → 89.6 % → 67.4 % → 72.6 %; N: 169.3 % → 84.6 % → 70.9 % → 74.9 %; P: 169.1 % → 93.3 % → 71.5 % → 78.1 %.

4. Discussion

4.1. *Abscised leaf and needle biomass (Q1 and Q4)*

4.1.1. *Physiological aspects*

Our results demonstrate that foliar litter biomass varies considerably depending on tree species, seasons, and growth conditions, with leaf and needle biomass production known to be size- and age-dependent (e.g., Li et al., 2006; Liu et al., 2020; Turski et al., 2024), and differences in size and age between the sampled European beeches and Norway spruces may also contribute to the identified variation in abscised foliar litter biomass. However, the observed differences in abscised leaf and needle biomass between Norway spruce and European beech under our treatments can largely be attributed to their distinct physiological characteristics and strategies for balancing growth and defense (Häberle et al., 2012; Matyssek et al., 2012). Specifically, drought-induced leaf and needle abscission can be explained by differences in their hydraulic systems and xylem anatomy (Pretzsch et al., 2020). Norway spruce, an evergreen species, typically retains 7–8 needle sets and sheds needles year-round due to senescence and environmental factors, with peak abscission occurring in December. It predominantly employs an isohydric strategy, reducing stomatal conductance early during soil drought to maintain water potential (Lyr et al., 1992). In contrast, European beech, a deciduous species, sheds its entire foliage in autumn, with peak leaf fall occurring in October. Unlike Norway spruce, European beech follows an anisohydric strategy, exhibiting lower stomatal sensitivity to soil drought, which allows for greater carbon dioxide uptake under such conditions (Leuschner, 2009, 2020; Nikolova et al., 2009). The differing drought vulnerability of these species also arises from variations in their root systems. Norway spruce has a shallow root system, limiting access to deeper water resources, while European beech possesses a cordate root system capable of accessing deeper and wetter soil layers (Bolkenius, 2001; Bolte et al., 2010; Sagi et al., 2019). Puhe (2003) further emphasized that aridity presents significant challenges for the shallow-rooting Norway spruce. Additionally, the contrasting canopy structures of these species result in differing water dynamics, with European beech exhibiting higher throughfall, stem flow, and interception rates, which enhance soil water supply (Nihlgård, 1970; Hojjati et al., 2009). Nihlgård (1970) estimated that annual throughfall, stem flow, and interception averaged 70 %, 11 %, and 19 % for European beech, and 58 %, 3 %, and 39 % for Norway spruce, respectively, compared to open-field conditions. In southern Sweden, the soil in a

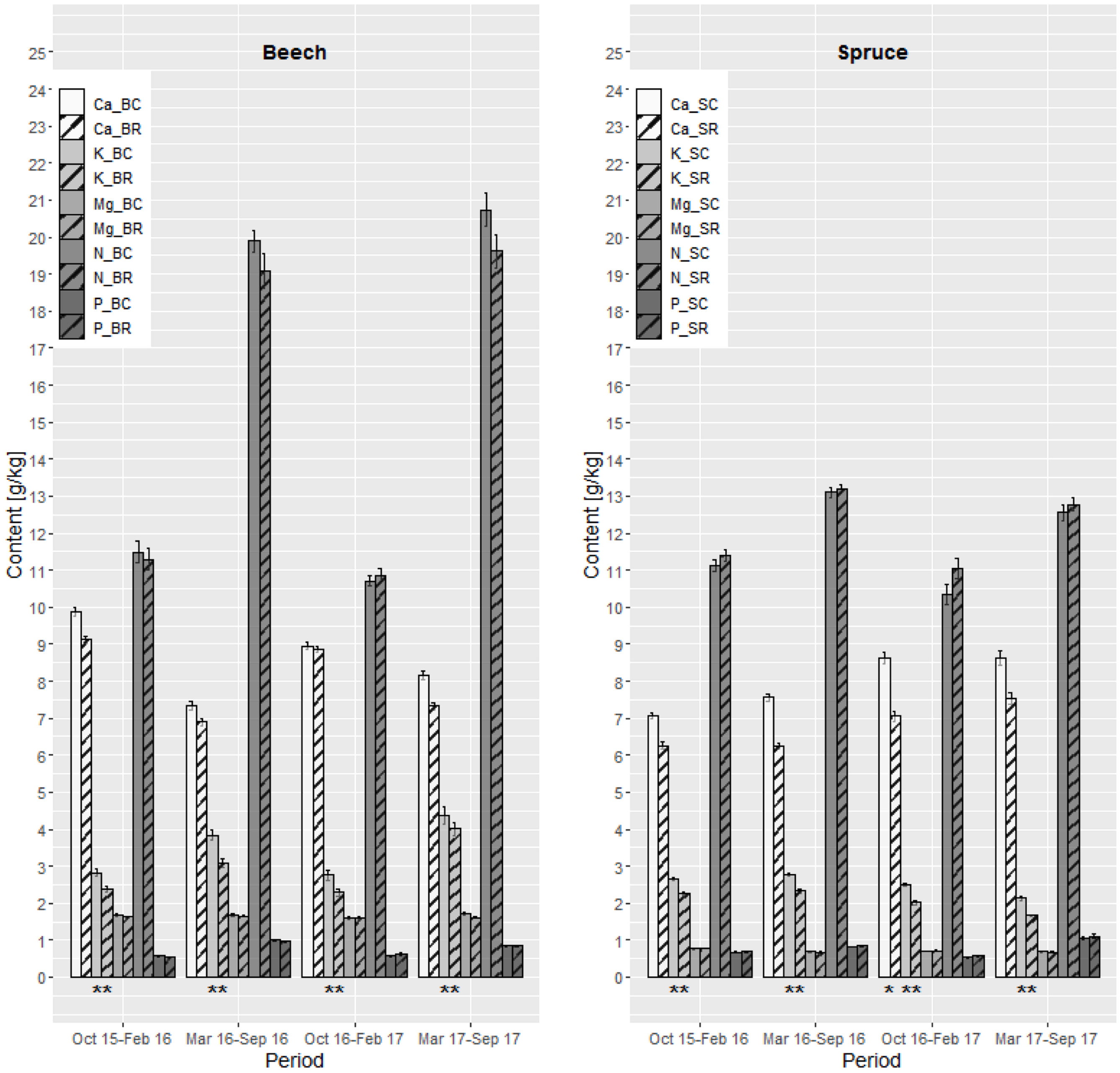

Fig. 2. Average main nutrient contents in the foliar litter, categorized by tree species, treatment, and period. Thin error bars represent the standard errors of the means. BC: Beech Control, BR: Beech Roof, SC: Spruce Control; SR: Spruce Roof. Significant differences between the roof and control plots are marked with asterisks (*: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$).

55-year-old Norway spruce forest was approximately 19 % drier than in a 100-year-old European beech forest due to high interception and prolonged transpiration in the Norway spruce forest. These anatomical and physiological differences influence water availability, with European beech-dominated forests generally exhibiting better water supply. Consequently, European beech can allocate more resources to foliage regrowth, which may explain the contrasting drought resistance and patterns of foliar biomass abscission observed between the two species. However, Munné-Bosch and Alegre (2004) demonstrated that drought-induced senescence, particularly when accompanied by abscission, helps maintain a favorable water balance by reducing transpiration losses. This strategy is particularly evident in the evergreen Norway spruce on our roof plots, where drought conditions prompted the immediate shedding of a substantial portion of green needle biomass.

4.1.2. Evaluation of the abscised foliar litter biomass as modulated by drought

Our findings indicate that European beech experiences significantly higher defoliation during autumn leaf fall, consistent with its natural abscission pattern, while defoliation during spring leaf emergence remains minimal. Jacobsen et al. (2003) estimated an average dry biomass of 3.95 tons ha^{-1} for European beech foliage. In our study, control plots recorded an average of 4.62 tons ha^{-1} throughout the study period - approximately 17 % higher - suggesting more favorable growth conditions with higher water availability. In contrast, roof plots averaged 3.68 tons ha^{-1} during the same period - about 7 % lower - reflecting less favorable conditions due to reduced water availability. Importantly, foliage production increased in both treatments over the observation period, indicating generally improved growth conditions, increased acclimation to water scarcity, and enhanced physiological drought

Table 6
Statistical analyses of the main nutrient masses in the foliar litter, categorized by tree species, treatment, and period (calculated according to Model 7). The "x" represents the interaction between two or three predictors. Mep: Main effect parameter estimate, IMep: Interaction estimate between main effect parameters, p: *p*-value, Sig: Level of significance, whereas significant estimates are marked with asterisks (*: $p \leq 0.05$ = significant, **: $p \leq 0.01$ = high significant, ***: $p \leq 0.001$ = highly significant).

Predictor Variable		Ca	K	Mg	N	P
Intercept	Mep	39.488	11.306	6.690	45.944	2.275
	p	0.0000	0.0000	0.0000	0.0000	0.0000
	Sig	***	***	***	***	***
Species (spruce)	Mep	−14.506	−1.968	−3.974	−6.635	0.099
	p	0.0000	0.0002	0.0000	0.0062	0.4738
	Sig	***	***	***	***	
Treatment (roof)	Mep	−12.637	−4.308	−1.862	−12.729	−0.705
	p	0.0003	0.0002	0.0004	0.0038	0.0049
	Sig	***	***	***	**	**
Period (March 16-Sep. 16)	Mep	−37.078	−10.045	−6.136	−39.402	−1.945
	p	0.0000	0.0000	0.0000	0.0000	0.0000
	Sig	***	***	***	***	***
Period (March 17-Sep. 17)	Mep	−36.202	−9.543	−5.997	−37.583	−1.935
	p	0.0000	0.0000	0.0000	0.0000	0.0000
	Sig	***	***	***	***	***
Period (Oct. 16-Feb. 17)	Mep	0.808	1.120	0.535	2.246	0.312
	p	0.6321	0.0355	0.0371	0.3518	0.0248
	Sig		*	*		*
Species (spruce) x treatment (roof)	IMep	23.887	8.055	3.678	39.165	2.296
	p	0.0000	0.0000	0.0000	0.0000	0.0000
	Sig	***	***	***	***	***
Species (spruce) x period (March 16-Sep. 16)	IMep	20.761	3.882	4.206	15.096	0.512
	p	0.0000	0.0000	0.0000	0.0000	0.0093
	Sig	***	***	***	***	**
Species (spruce) x period (March 17-Sep. 17)	IMep	16.451	1.500	3.699	5.899	0.193
	p	0.0000	0.0466	0.0000	0.0841	0.3239
	Sig	***	*	***		
Species (spruce) x period (Oct. 16-Feb. 17)	IMep	−14.142	−7.069	−2.304	−27.562	−1.960
	p	0.0000	0.0000	0.0000	0.0000	0.0000
	Sig	***	***	***	***	***
Treatment (roof) x period (March 16-Sep. 16)	IMep	12.735	4.169	1.908	13.131	0.723
	p	0.0000	0.0000	0.0000	0.0002	0.0004
	Sig	***	***	***	***	***
Treatment (roof) x period (March 17-Sep. 17)	IMep	11.974	3.980	1.744	11.392	0.672
	p	0.0000	0.0000	0.0000	0.0012	0.0009
	Sig	***	***	***	**	***
Treatment (roof) x period (Oct. 16-Feb. 17)	IMep	5.225	0.398	0.547	4.802	0.422
	p	0.0337	0.6068	0.1423	0.1712	0.0367
	Sig	*				*
Species (spruce) x Treatment (roof) x period (March 16-Sep. 16)	IMep	−26.164	−8.670	−3.807	−41.880	−2.377
	p	0.0000	0.0000	0.0000	0.0000	0.0000
	Sig	***	***	***	***	***
Species (spruce) x Treatment (roof) x period (March 17-Sep. 17)	IMep	−25.092	−8.280	−3.676	−39.741	−2.401
	p	0.0000	0.0000	0.0000	0.0000	0.0000
	Sig	***	***	***	***	***
Species (spruce) x Treatment (roof) x period (Oct. 16-Feb. 17)	IMep	−21.788	−5.725	−2.673	−35.303	−2.220
	p	0.0000	0.0000	0.0000	0.0000	0.0000
	Sig	***	***	***	***	***

resistance. This trend aligns with Liu et al. (2015), who reported drought impact mitigation on litterfall due to demographic compensation, morphological and physiological acclimation, and epigenetic changes. Kozlowski and Pallardy (2002) further noted that environmental stress can benefit woody plants by inducing physiological adjustments that prevent growth inhibition and injury. Short-term exposure to extreme conditions may even enhance growth. The controlled wetting and drying cycles in the KROOF experiment likely promote drought tolerance in woody plants, which may explain the observed foliage abscission patterns in European beech. However, the lower foliar litter biomass on roof plots compared to control plots indicates that water scarcity reduces foliage biomass of European beech, likely through smaller leaves or decreased foliage production, conserving resources and minimizing transpiration losses. Our findings for European beech are consistent with those of Gavinet et al. (2019), who reported reduced aboveground biomass production under drought, primarily due to decreased foliage and acorn production in holm oak. Conversely, Wilson et al. (2022) found that some tree species, including sugar maple (*Acer saccharum*), American linden (*Tilia americana*), red oak (*Quercus rubra*), white oak (*Quercus alba*) and American hop hornbeam (*Ostrya virginiana*), increased foliage production and specific leaf area under drought conditions, contrasting with our results for European beech. Unlike the abscission pattern observed in European beech, Norway spruce exhibited substantial needle loss at the beginning of the investigation period after experiencing more than one year of drought-induced stress, with the loss gradually declining to a minimum over time, likely reflecting the initial shedding of older needle sets, followed by reduced abscission of younger needles. The higher needle loss observed on roof plots can be attributed to increased abscission rates, a strategy aimed at limiting water loss through transpiration. These patterns indicate that Norway spruce is more susceptible to drought and less adaptable than European beech, as it lacks the ability to compensate for needle loss through regrowth. Solberg et al. (2015) demonstrated that dry summers exacerbate brown needlefall in autumn and winter, while high temperatures increase green needlefall in winter. This phenomenon may explain the high needle loss observed during the first non-vegetation period on roof plots, although it does not account for the lower defoliation rates in subsequent seasons. Jacobsen et al. (2003) estimated an average dry biomass of 14.7 tons ha^{-1} for Norway spruce needles. Based on this estimate, Norway spruce lost approximately 40 % of its needles (5.84 tons ha^{-1}) on our roof plots during the first non-vegetation period and 24 % (3.53 tons ha^{-1}) on our control plots. Over the entire examination period, average needle losses were 4.11 tons ha^{-1} (28 %) on roof plots and 3.32 tons ha^{-1} (23 %) on control plots, indicating that needle losses were more effectively mitigated on control plots due to reduced aridity. Similarly, Ozolinčius et al. (2012) observed that artificial drought significantly increased mean defoliation in Norway spruce, resulting in 1.5 to 2 times higher litterfall compared to normal conditions, a trend consistent with our findings. Additionally, Pedersen and Bille-Hansen (1999) reported prolonged elevated needle losses in Norway spruce in response to aridity and disturbances, contrasting with the stable annual litterfall observed in European beech, a pattern that is also reflected in our results. Hansen et al. (2009) found that while total litterfall did not vary significantly among tree species over a shorter research period (3 years), it was higher on sites with better growth conditions over a longer timeframe (6 years). Despite our 2-year monitoring period, our findings for European beech resonate with these long-term observations, showing greater foliar litter biomass on control plots with better growth

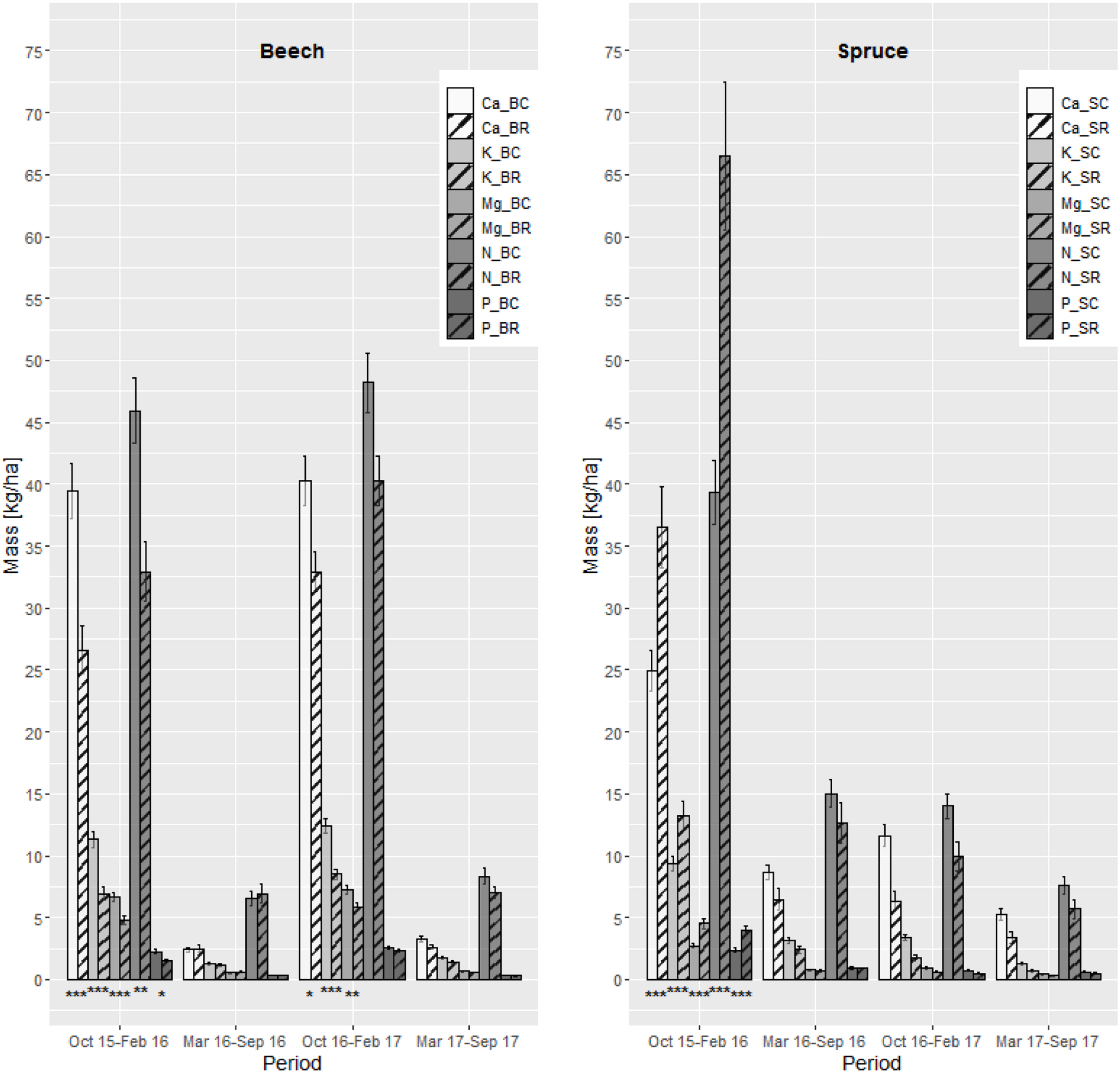

Fig. 3. Main nutrient masses in the foliar litter per hectare, categorized by tree species, treatment, and period. Thin error bars represent the standard errors of the means. BC: Beech Control, BR: Beech Roof, SC: Spruce Control; SR: Spruce Roof. Significant differences between the roof and control plots are marked with asterisks (*: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$).

conditions. Conversely, for Norway spruce, our results revealed the highest needle losses on roof plots, indicative of poorer growth conditions compared to control plots. Hansen et al. (2009) further documented average total litterfall in the range of 3200–3700 kg ha^{-1} yr^{-1}. Although the study periods slightly differ, the litter biomass values observed in our study generally fell outside this range on both control and roof plots for the two tree species. These discrepancies underscore the distinct foliar litterfall dynamics observed: Norway spruce exhibited high needle losses driven by drought susceptibility, while European beech demonstrated a capacity to adapt and sustain foliage production under water scarcity.

4.2. *Nutrient contents of the foliar litter (Q2 and Q4)*

4.2.1. *General nutrient classification and translocation patterns*

Our study reveals detailed patterns in nutrient contents and translocation between European beech and Norway spruce, influenced by nutrient type and observation period. However, Jacobsen et al. (2003) reported that nutrient contents in the foliage and needles (in mg/g dry biomass) decrease in the order N (26.01) > Ca (8.88) > K (8.66) > P (1.46) > Mg (1.25) for European beech and N (13.36) > Ca (6.03) > K (5.70) > P (1.33) > Mg (0.79) for Norway spruce, indicating generally higher nutrient levels in European beech. Similarly, Rademacher (2005) observed significant variability in nutrient contents across tree species, compartments, and forest sites, noting a general decline in nutrient levels from European beech to Norway spruce for most nutrients. An early study by Wolff (1871) documented an autumnal decline in

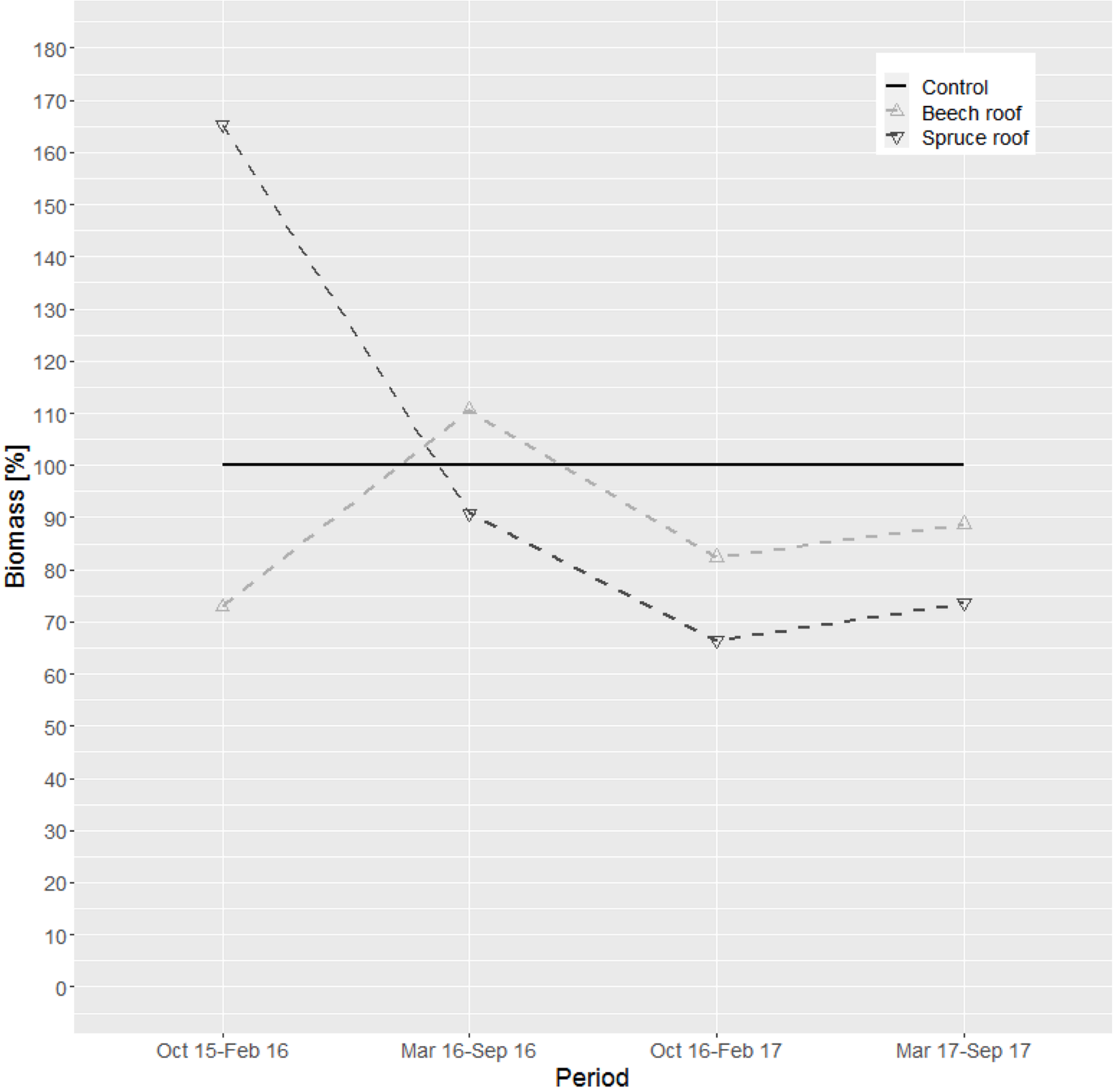

Fig. 4. Percent variance in foliar litter between roof and control plots, categorized by tree species, treatment, and period. The straight line for control plots represents 100 %.

European beech foliage nutrient contents in the order $P > K > Mg$, alongside an increase in Ca. Compared to leaves, foliar litter exhibited lower nutrient levels for K and P but higher levels for Mg and Ca. For Norway spruce, Wolff (1871) reported that needle litter had lower P and Ca contents and higher K and Mg contents compared to green needles. These findings have been corroborated by subsequent research. Nutrient transport within trees is influenced by nutrient mobility in the phloem, affecting seasonal translocation (Helmisaari, 1990, 1992). Bukovac and Wittwer (1957) and Loneragan et al. (1976) classified N, P, and K as mobile nutrients, while Ca is immobile and Mg relatively immobile. Accordingly, Staaf (1982) found that nutrient loss rates during senescence in European beech leaves correlate positively with nutrient contents in the order $N > P > K > Mg > Ca$. Chapin (1980) and Marschner (1995) further noted that mobile macro-nutrients (N, K, Mg, and P) are translocated from senescing leaves, whereas Ca remains immobile, with K being primarily lost through leaching. Guha and Mitchell (1966) observed seasonal trends where Ca and Mg contents are low in early spring but rise throughout the year with minimal translocation in autumn, whereas P and K decrease rapidly after their initial spring peaks, stabilizing before senescence. While these studies broadly support our findings, they underscore the necessity of considering temporal and species-specific variations when analyzing nutrient dynamics. Consistently, these studies illustrate uniform nutrient translocation patterns, primarily driven by nutrient mobility as determined by nutrient-specific chemical properties and seasonal dynamics. Our results largely align with this established knowledge, while emphasizing nuanced variations in nutrient translocation dynamics that are likely shaped by both environmental conditions and study-specific factors.

4.2.2. *Drought-induced senescence and translocation patterns*

Our findings demonstrate that drought-induced stress significantly decreased K contents in abscised leaves and needles, as well as K translocation patterns during both vegetation and non-vegetation periods. Similarly, Ca contents and translocation patterns were influenced by aridity in both species throughout the observation period, with a significant reduction observed only in Norway spruce during the second non-vegetation period. Wilkinson et al. (1990) highlighted the influence of climatic factors, such as temperature and aridity, on nutrient dynamics. Water availability therefore plays a pivotal role in nutrient mobility and plant uptake, as emphasized by da Silva et al. (2011), who underscored its importance in determining soil nutrient absorption and translocation within plants, particularly from roots to shoots. Sardans

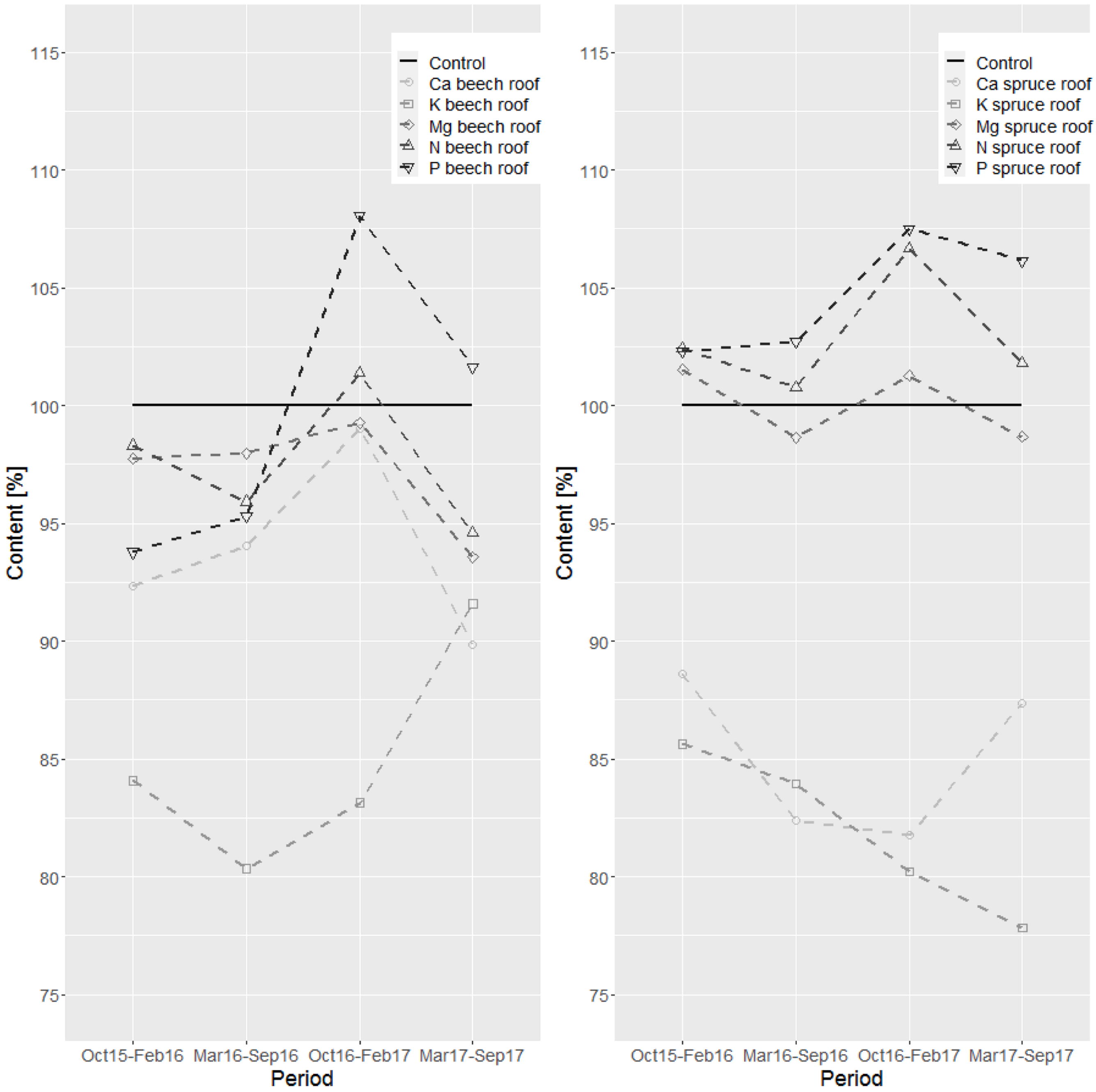

Fig. 5. Percent variance of the main nutrient contents of Ca, K, Mg, N, and P in the foliar litter between the roof and control plots, categorized by tree species, treatment, and period. The straight line for control plots represents 100 %.

et al. (2008) further reported that water scarcity reduces nutrient contents in aboveground biomass by decreasing transpiration, thereby impairing growth in sensitive plants while leading to nutrient accumulation in the soil. However, they also observed that drought can diminish soil nutrient storage capacity, as nutrients become more prone to leaching during heavy rainfall. These findings are consistent with our observations of K translocation sensitivity and uptake in both species and, to a lesser extent, Ca uptake in Norway spruce under drought stress. Prolonged drought likely restricted both the mobility and uptake of K^+ cations, as well as the uptake of Ca^{2+} cations in Norway spruce. Interestingly, Marchin et al. (2010) reported that deciduous species undergoing drought-induced senescence can resorb N, P, and K from senescing leaves, while species lacking such senescence experience substantial nutrient losses through desiccation. In line with this, our findings suggest that European beech and Norway spruce employ adaptive strategies during episodic droughts, characterized by enhanced resorption of K from senescing leaves for storage in other tree organs. This adaptation may help explain the lower K contents observed in foliar litter from roof plots compared to control plots. As the crowns of sample trees in both treatments were exposed to rainfall, K deficiency caused by leaching was evident in both scenarios. However, on the roof plots, the accumulation of dissolved K^+ cations in the soil from precipitation was inhibited during the controlled drying phases, as rainfall was prevented from reaching the ground. Consequently, the higher K contents in the abscised foliage and needles of European beech and Norway spruce in the control plots, compared to the roof plots, may also result from greater concentrations of dissolved, tree-available K^+ cations in the soil solution. Contrary to K and Ca, drought conditions did not significantly

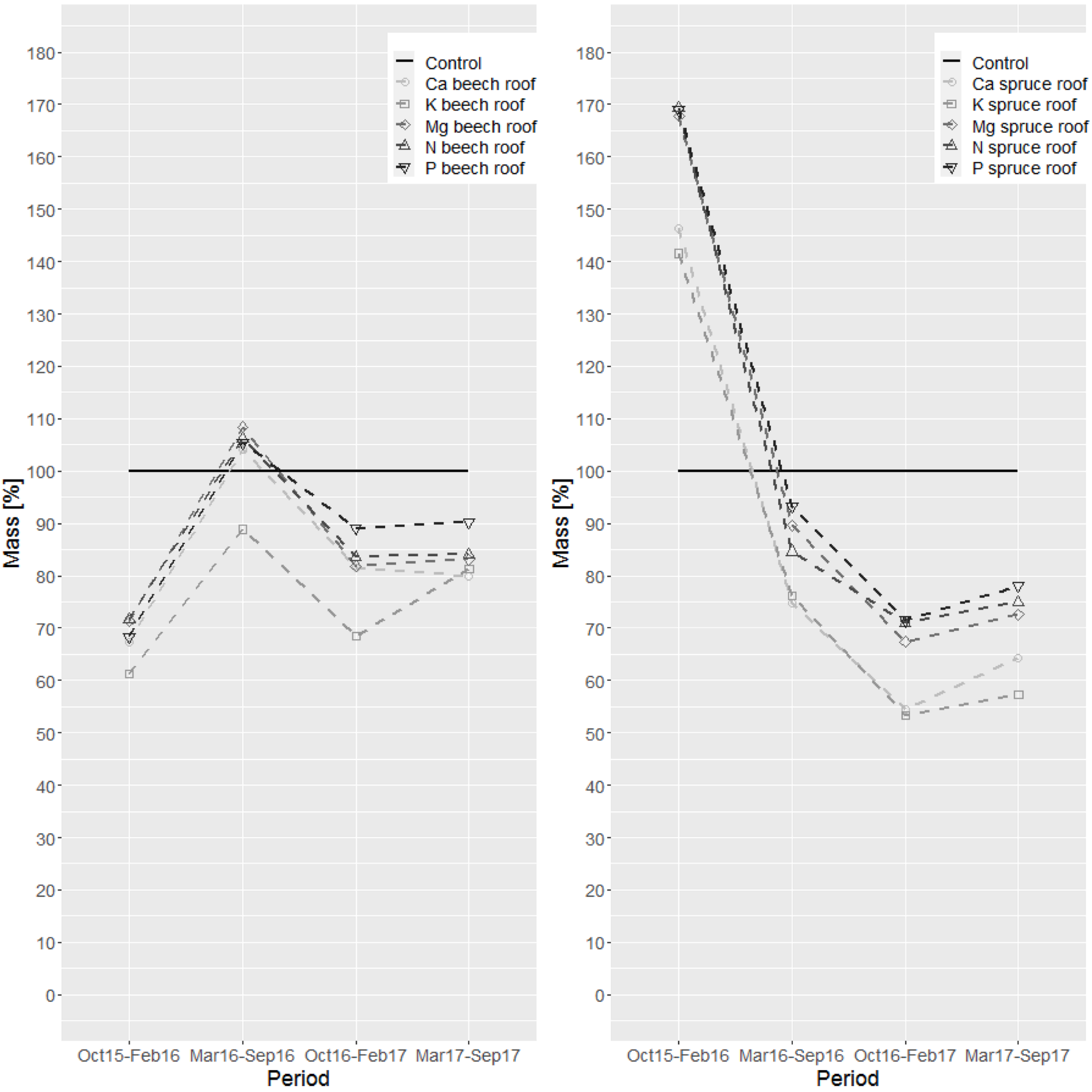

Fig. 6. Percent variance of the main nutrient masses of Ca, K, Mg, N, and P in the foliar litter between the roof and control plots, categorized by tree species, treatment, and period. The straight line for control plots represents 100 %.

affect the foliar contents or translocation patterns of N, Mg, or P throughout the study period, as no statistically relevant differences were observed between control and roof plots for either European beech or Norway spruce. Sardans et al. (2008) reported increased Mg contents in holm oak and strawberry tree leaves under arid conditions, whereas Grabarova and Martinková (2001) found that water shortages caused greater declines in N and Mg contents compared to P and K in Norway spruce during growth periods. For P, Sardans and Peñuelas (2004) observed that a 22 % reduction in soil moisture led to a 40 % decrease in P content in aboveground biomass after three years of rainfall exclusion. Similarly, He and Dijkstra (2014) found that drought stress generally reduced N and P contents in plants but increased N ratios, with short-term drought stress exerting a more pronounced negative effect than long-term drought. These findings contrast with our results, potentially due to variations in the mobility of these nutrients, species-specific drought tolerance mechanisms, or experimental conditions. Furthermore, while Taiz and Zeiger (2006) noted that severe N deficiency due to prolonged drought can result in chlorosis and the abscission of older leaves, no such effects were observed during our monitoring period. Instead, drought-induced leaf and needle senescence in our study likely facilitated nutrient retranslocation, as previously highlighted by Munné-Bosch and Alegre (2004). This process enabled the remaining plant organs to utilize the accumulated nutrients from senescing leaves and needles, potentially mitigating drought-induced nutrient loss. In summary, these findings indicate that the impact of drought on nutrient dynamics is primarily influenced by tree species, seasonal variations, and the chemical characteristics of individual nutrients, further emphasizing the critical role of tree-specific adaptive strategies and nutrient-specific responses in alleviating the effects of episodic drought on forest ecosystems.

4.3. Nutrient masses of the foliar litter and nutrient fluxes (Q3 and Q4)

4.3.1. Evaluation of abscised foliar nutrient masses and nutrient fluxes in response to drought

The nutrient masses in abscised foliage and needles are determined by foliar litter biomass and nutrient contents, with our results indicating a stronger correlation to foliar biomass abscission patterns than to nutrient contents or translocation patterns during senescence. Nutrient inputs also depend on biological, seasonal, and environmental traits, reflecting the growth conditions to which the trees are exposed. Drought stress in European beech resulted in significantly lower abscised nutrient masses of Ca, K, Mg, N, and P during the first non-vegetation period, and Ca, K, and Mg during the second non-vegetation period, with low impact during vegetation periods due to naturally low defoliation rates. Conversely, Norway spruce exhibited significantly higher abscised nutrient masses of these elements during the first non-vegetation period, driven by substantial drought-induced needle loss. Subsequent seasons showed no significant impact from water scarcity, aligning with the foliar biomass abscission pattern. Nutrient cycling in forest ecosystems is mediated by litterfall, throughfall leaching from tree canopies, bulk precipitation, and stem flow, which return nutrients to the forest floor (Hansen et al., 2009; Małek, 2010). Adriaenssens et al. (2012) observed increased throughfall and net throughfall nutrient deposition with canopy depth in the middle and lower canopy of European beech and throughout the entire canopy of Norway spruce. However, in Norway spruce, nutrient levels in throughfall and net throughfall decreased with increasing distance from the stem. Consequently, canopy composition and morphology strongly influence nutrient input patterns (Prescott, 2002), with Norway spruce forests typically contributing higher nutrient inputs than European beech forests due to more pronounced canopy leaching processes (Nihlgård, 1970). Consistent with this, Hojjati et al. (2009) reported that major nutrient fluxes are higher under Norway spruce compared to European beech. In contrast, nutrient inputs from canopy leaching may also lead to reduced nutrient availability for plants by increased soil leaching, which occurs when dissolved nutrients in the soil solution are transported beyond the reach of plant roots by vertical or horizontal water movement, potentially leaving the ecosystem's catchment area (Małek, 2010). Factors such as tree species composition, humus type, temperature, rainfall, and rain quality influence leaching processes (Buldgen and Remacle, 1981; Buldgen, 1982). Houle et al. (2016) monitored nutrient fluxes in a boreal forest ecosystem before, during, and after a severe drought event, finding high throughfall concentrations of Ca, K, Mg, and P during and shortly after the drought, which differed from the long-term norm and resulted in substantial canopy losses. They noted significant net K losses by leaching after the drought, equivalent to nearly 20 years of normal conditions, highlighting drought's impact on K fluxes. Our study similarly suggests high K losses by leaching, with significantly lower K contents in the foliar litter of drought-stressed European beeches and Norway spruces throughout the observation period. For European beech, higher leaching rates on the roof plots compared to control plots were accompanied by reduced abscised foliar biomass. This process likely leads to an accumulation of nutrients in the soil solution through leaching but also diminishes nutrient inputs from foliar litterfall, potentially hindering growth. In contrast, for Norway spruce, higher leaching rates on the roof plots coincided with elevated defoliation rates at the onset of the drought. While this weakens individual trees, potentially increasing mortality rates, the enhanced defoliation provides greater nutrient inputs, benefiting the overall forest ecosystem's nutrition. Macinnis-Ng and Schwendenmann (2015) observed increased litterfall by 72 % during a drought year in a kauri (*Agathis australis*) forest, with a 69 % increase in N inputs, concluding that drought stimulates the N cycle and affects forest N budgets. Norway spruce litter, however, promotes precipitation acidification and the formation of a massive raw humus layer, which binds nutrients and slows nutrient release to the soil (Albers et al., 2004; Kowalska et al., 2016). In contrast, European beech litter forms a less massive moder layer, facilitating faster nutrient release through quicker decomposition (Fabiánek et al., 2009). Wälder et al. (2008) confirmed this for mature European beech and Norway spruce forests in Germany (Solling), noting that Norway spruce needles and litter hinder humus dynamics, while European beech foliage and litter, combined with higher throughfall rates, support humus dynamics. Climatic factors such as temperature, rainfall, humidity, and seasonal variations generally influence litter decomposition rates mediated by animals, fungi, and microbial decomposers (Krishna and Mohan, 2017), while drought conditions specifically decrease decomposition rates, thereby limiting subsequent nutrient release into the soil solution (Santonja et al., 2015). The binding of nutrients in the humus layer may therefore explain why Norway spruce stands exhibit fewer plant-available nutrients than European beech stands. This limitation is further exacerbated by water scarcity, despite higher nutrient inputs resulting from enhanced defoliation. Moreover, the deep root system of European beech enables it to access base cations from deeper soil layers, while its higher transpiration rate, compared to Norway spruce, helps minimize nutrient losses (Berger et al., 2006), ultimately leading to more balanced cation budgets in European beech forests than in Norway spruce forests (Fichter et al., 1998). In summary, our study highlights the intricate nature of nutrient cycling, particularly under drought conditions, and emphasizes the importance of species-specific traits, such as litter decomposition rates and rooting depth, in shaping nutrient availability and retention in soils. A comprehensive understanding of nutrient cycling in forest ecosystems is essential for devising effective conservation and management strategies. The complex interplay between plant physiology, environmental conditions, and ecological processes governs the distribution and availability of nutrients, which are critical for maintaining ecosystem health and productivity in the face of climate change.

4.4. Critique and generalisability

Within each species, the sampled European beeches and Norway spruces are almost equally aged and have similar heights and diameters, with both species growing under comparable climatic, geological, and stand structure conditions. However, there are moderate differences in age, height, and diameter between the two species, despite all sampled trees being mature. These differences, along with slight variations in data acquisition and experimental plot conditions, may contribute to differences in litter biomass, nutrient contents, and nutrient masses. The examined trees represent European beech and Norway spruce forests within the normal range of resource supply found across most Central European forest stands. In this context, "normal" refers to site conditions where both species are competitive, can coexist, and are commonly managed in either monospecific or mixed stands. Although we focused on predominant and dominant trees, growth and nutrient translocation patterns can vary across sites depending on the species, species composition, age, size, forest management practices, and resource availability. Furthermore, the drought-induced stress reactions observed in this study were artificially induced on small-scale experimental plots. This experimental design simulates natural aridity on a much smaller scale, which may not fully replicate the heterogeneity and complexity of larger-scale drought events. As a result, our findings should not be directly extrapolated to other locations with differing climatic or geological conditions or to studies employing different experimental designs. Future research incorporating larger-scale studies and natural drought events would help validate and extend the applicability of these results.

4.5. Conclusions

Water shortages significantly affect litterfall and nutrient translocation patterns through stress-induced leaf and needle abscission. While increased litterfall during drought helps mitigate water loss via reduced transpiration and lowers the maintenance demands of foliage biomass, it also diminishes the number of organs crucial for photosynthesis and growth. Norway spruce and European beech exhibit distinct drought responses due to their differing physiological strategies. Due to water limitations, European beech responds to episodic drought by reducing foliage biomass, either by producing fewer leaves or smaller ones, which may indicate its capacity for acclimation. In contrast, Norway spruce responds to drought by rapidly shedding older needles, with the extent of defoliation depending on drought severity and duration. This strategy renders Norway spruce more vulnerable to prolonged water scarcity, as needle loss is often irreversible, leaving trees weakened and more susceptible to secondary stressors such as insect infestations or windthrow. Consequently, Norway spruce exhibits higher mortality rates under drought conditions compared to European beech. Projected climate change is anticipated to exacerbate these challenges, particularly for Norway spruce, a species historically cultivated extensively in monocultures. To enhance forest resilience, management practices should prioritize reducing the proportion of Norway spruce in favor of mixed-species stands that emulate natural forest communities. Divergent findings across studies underscore the need for further research into species-specific leaf and needle abscission patterns, as well as nutrient translocation dynamics throughout the seasonal cycle under varying growth conditions.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT 4.0 in order to revise language, grammar and tenses. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

CRediT authorship contribution statement

Matthias Ulbricht: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Peter Biber:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Thomas Rötzer:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Enno Uhl:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Karin Pritsch:** Methodology, Formal analysis, Data curation. **Bernhard Michalke:** Formal analysis. **Hans Pretzsch:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no conflicts of interest.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2025.100851.

Data availability

Data will be made available on request.

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