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ORIGINAL ARTICLE

Canopy Versus Forest-Floor Nitrogen Addition Alters Nutrient Dynamics but Weakly Affects Litter and Deadwood Decomposition in a Temperate Oak Forest

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Abstract

The decomposition of dead plant matter (leaf litter and deadwood) is a key process for carbon (C) and nutrient cycles in forests. Increased nitrogen (N) deposition due to human activity may affect this process, with important consequences on forest biogeochemistry. Although there is extensive work on leaf litter, the research about the effect of N deposition on deadwood decomposition is still limited. Moreover, most N manipulation studies rely on ground N fertilization, neglecting the canopy, which may influence the quantity and the form of N reaching the forest soil. This study assesses how litter and deadwood decomposition can be influenced by N deposition, using an innovative experimental design, in which N (20 kg N ha^{-1} $year^{-1}$) is applied above the canopy (treatment ''above'') or on the forest floor (treatment ''below'') during a three-year (36-month) field experiment. Litter decomposition was studied with the litterbag method; deadwood decomposition was determined by incubating blocks of deadwood (sapwood and heartwood) at different decay stages. Neither N treatments influenced the decomposition rates or carbon (C) loss patterns of litter and deadwood. Remaining N in litter and deadwood was not affected by treatments, except for decay class IV of the sapwood, where N decreased (release) under the below-canopy treatment but showed a net increase in total N content under the above-canopy treatment and in the control. The dynamics of Na, P, and S in the litter differed between the treatment below and the other treatments. Together, despite unchanged mass loss and C loss these treatment-specific nutrient responses suggest that canopy-mediated N delivery can modulate early biogeochemical trajectories of decomposing litter and deadwood even when bulk decay rates remain unaffected over the short term. However, further research is needed to assess the effect of N deposition on deadwood decomposition in the long term, especially considering the slow

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decay of heartwood.

Key words: N addition; deadwood; nutrient release; oak trees; carbon cycle; mountain forests.

Introduction

Human activities have increased the release of reactive nitrogen (N) into the atmosphere, intensifying N deposition rate onto terrestrial ecosystems (Galloway and others, 2004). Most forest ecosystems are limited by N availability, especially temperate and boreal forests (LeBauer and Treseder, 2008). The N limitation of forests can be alleviated by the additional N supplied through atmospheric deposition, which enters the N cycle and increases N availability within the ecosystem (Fowler and others, 2015; Zhu and others, 2015). This process influences both the N and carbon (C) cycles (Fowler and others, 2015; Reay and others, 2008). Since primary production is related to N availability to plants, N deposition potentially enhances biomass accumulation and C sequestration in the ecosystem's above- and below-ground compartments (De Vries and others, 2006; Schulte-Uebbing and de Vries, 2017). Furthermore, N deposition may affect C sequestration in the forest soil, driven by changes in microbial communities and by decreasing plant and soil organic matter decomposition (Frey and others, 2014; Xia and others, 2018).

The decomposition of plant organic matter is a key process within biogeochemical cycles, since it is responsible for the transfer of nutrients into the soil, connecting above-ground primary productivity to soil processes (Chapin and others, 2011). Plant organic matter decomposition represents the first step toward soil organic matter formation and hence C accumulation. The decomposition rate of organic matter depends on numerous factors, including environmental conditions, such as precipitation and temperature (Du and others, 2020), and soil parameters (e.g., pH and moisture content) (Fravolini and others, 2018). The relationship between soil characteristics and decomposition is mutual. For instance, plant residues decomposition improves soil water retention (Piaszczyk and others, 2019b) and influences the soil and microbial C/N (Kim and others, 2017). Additionally, the decomposition rate of deadwood or leaves increases with substrate quality (Lombardi and others, 2013) which is related to N content, lignin content, C/N, and lignin/N (Du and others, 2020; Melillo and others, 1982; Suseela and Tharayil, 2018). Indeed, deadwood decomposition is slower compared to leaf litter decomposition (Bani and others, 2018), largely because wood rich in lignocellulosic compounds is typically denser and poorer in nutrients than leaf litter and may contain decay-resistant extractives (especially in heartwood), which reduce substrate accessibility and slow microbial processing. Deadwood decomposition rates vary strongly with both wood traits (e.g., wood density and nutrient status) and microclimatic conditions such as moisture and temperature, resulting in residence times that commonly span years to decades. (Harmon and others, 1986; Boddy, 2001; Weedon and others, 2009).

In forests under increased N deposition, the incorporation of extra N into fresh leaves may influence the N content and, therefore, the C/N of litter at the beginning of the decomposition process (Berg and Matzner, 1997; Månsson and Falkengren-Grerup, 2003; Van Diepen and others, 2015). In addition, an increase in lignin content in fresh leaves may occur (Liu and others, 2016). Furthermore, N deposition seems to enhance the decomposition of high-quality litter (Liu and others, 2016; Xia and others, 2018), while the decomposition of low-quality litter or the later stages of decomposition can be inhibited (Tu and others, 2014; Xia and others, 2018). A recent meta-analysis reported an overall small decrease (~ 2–3%) in decay rates under N addition, with responses contingent on litter quality and experimental context (Wu and others, 2023). Particularly, the N deposition may interfere with lignin-degrading enzymes (Xia and others, 2018) and combine with lignin and phenols to create even more recalcitrant compounds, thus inhibiting the efficiency of decomposers (Berg and Matzner, 1997). Indeed, the soil lignin content under N deposition increases (Liu and others, 2016), which may contribute to C accumulation in the soil. However, other studies report that the addition of organic N may promote C emissions from soil, converting it into a C source (Du and others, 2014).

Although the processes related to deadwood decomposition are well known (cf., Zell and others, 2009), the role of N deposition is unclear. Increased N deposition is reported to have positive effects (Bebber and others, 2011; Wu and others, 2019), negative effects (Qiao and others, 2016), or very low/no influence (Chen and others, 2016; Maestrini and others, 2014; Wu and others, 2020; Wang and others, 2026) on this process. According to Bebber and others (2011), N deposition may promote saprotrophic microbial communities, which in turn enhance deadwood decomposition. Moreover, an increase of N concentration in wood tissues may decrease the lignin/N ratio and increase substrate quality (Kaakinen and others, 2007). On the other hand, Qiao and others (2016) observed the opposite effect in a laboratory incubation experiment. Uncertainties are also due to the heterogeneous nature of wood: The decomposition of sapwood and heartwood may respond differently under N deposition.

Moreover, most N manipulation studies have simulated an increase in N deposition by applying fertilization directly to the forest floor. This method neglects the presence of the canopy, which is an active part of the forest and of the N cycle (Bortolazzi and others, 2021). Tree canopy may partially absorb atmospheric N (Wortman and others, 2012), affecting the quantity and quality of N reaching the forest floor (Adriaenssens and others, 2012; Draaijers and others, 1997). Consequently, N from deposition is not fully and immediately available to decomposer communities on the forest floor, being partially absorbed by the leaves (Liu and others, 2016; Ferraretto and others, 2022; Da Ros and others, 2023; Da Ros and others, 2024). The leaf-adsorbed N can return to the soil only later, with litterfall and litter decomposition. This can modify N inputs to decomposing plant materials, altering their decomposition rates (Adriaenssens and others, 2012; Guerrieri and others, 2015; Bortolazzi and others, 2021; Guerrieri and others, 2021; Wang and others, 2026).

Another limitation of many experiments on N deposition is that they used high N application rates, exceeding 100 kg N ha^{-1} year^{-1}, which are similar to agricultural fertilization rates and are around an order of magnitude larger than background rates, representing unrealistic scenarios of increased N depositions (Bebber 2021). In the present study, litter and deadwood decomposition were investigated under increased N deposition, simulated by N fertilization, in a temperate deciduous oak forest. To overcome the limitation of other studies, where the potential interaction of the canopy with N deposition was not considered, the experiment was designed to include plots where fertilization is applied either to the forest floor (''traditional method'') or above the canopy (''innovative method''). In this way, we aimed to assess whether the presence of the canopy influences the effect of N deposition on deadwood and litter decomposition. For both treatments, a relatively low N application rate was applied to simulate a realistic scenario of current or potential future N deposition rates in temperate forests.

Additionally, the patterns of C and N content in plant residues decomposition, as well as nutrient content, were explored to evaluate how the N addition affects the release of nutrients and the storage of C. Considering that leaf litter decomposition was studied using litter collected from trees subjected to different treatments, we could verify if the N fertilization could alter its decomposition by means of a change in litter quality at the beginning of the decomposition process, and particularly an increase of litter N content in fertilized plots due to the higher N availability for the plants. Therefore, the tested hypotheses were the following: I) Increased N deposition, simulated by N addition, enhances litter and deadwood decomposition and nutrient loss; II) the N application below the canopy exerts a different effect on the decomposition process than the N application above the canopy; and III) the effect of increased N deposition on leaf litter decomposition is due to an increase in litter N content due to a higher N uptake in the fertilized plants, in particular in those fertilized from above.

Materials and Methods

Experimental Site and Application of Experimental Treatments

The study was performed in the experimental site of Monticolo (Bolzano, Italy; 46°25′35″ N; 11°17′55″ E) located in a broadleaved forest stand at 530 m.a.s.l. The annual mean temperature in the site is 11.4°C, and the mean annual precipitation is 800 mm. The forest is part of a protected natural reserve with no prior experimental manipulations (Minikaev and others, 2025). The soil is acid brown and originated from porphyritic quartz rock. Soil texture is 45% sand, 46% silt, and 9% clay; topsoil pH is 4.6 (Minikaev and others, 2025). The soil layer is shallow, usually $<$ 20 cm, with presence of emerging rocks. The forest stand is composed of 94% by even-aged sessile oak (*Quercus petraea* (Matt.) Liebl.) trees, with a mean age, at the beginning of the experiment, of 65 years. Other sporadic species are Scots pine (*Pinus sylvestris* L.), lime (*Tilia cordata* Mill.), sweet chestnut (*Castanea sativa* Mill.), European hop-hornbeam (*Ostrya carpinifolia* Scop.), and silver birch (*Betula pendula* Roth) (Giammarchi and others, 2020). At the beginning of the experiment, the stand density was 1177 trees ha^{-1}, mean diameter at breast height was 16.7 cm, and mean height was 12.7 m (Supplementary Figure S4).

During the experiment, air temperature and precipitation were measured in an open area in the site, with an air temperature probe (model CS215, Campbell Scientific, Logan, UT, USA) and a tipping bucket rain gauge (model 52,202, Young Company, Traverse City, MI, USA) connected to a HOBO Micro Station data logger (Onset Computer, Bourne, MA, USA). Precipitation and air temperature patterns are illustrated in Supplementary Figure S1. The annual precipitation in the period of incubation was 462 mm in 2016, 672 mm in 2017, 630 mm in 2018, 834 mm in 2019, and 834 mm in 2020.

The experimental design consists of nine plots of a 12-m radius, three for each treatment. The plots were randomly distributed in a 200-m-long area to minimize the variation of stand conditions. A buffer distance of 10 m was established between plots, to avoid the drifting of fertilization during applications. The treatments are unfertilized plots (control); fertilization above the canopy (''above'' treatment); and fertilization on the forest floor (''below'' treatment). The fertilization has been performed since 2015 (still ongoing) and occurred five times per year, during the growing season from May to September, at monthly intervals.

From a survey conducted in 2017 (see paragraph 2.3.1), the volume of coarse woody debris (CWD) in the experimental plots was 11 $m^3\ ha^{-1}$ on average. CWD was mainly old stumps, dead downed trees or branches, and standing dead trees (55, 42, and 3% of the total, respectively), which accounted for 59, 26, and 15% of the total CWD volume, respectively. Mean length for dead downed trees or branches was 191 cm, while mean height for standing dead trees and stumps was 659–17 cm, respectively. Most of the CWD was in class 4 (88% of the total), while only 10% were in class 3 and the remaining in class 1 or 2. When it was possible to visually identify the species, most of the dead wood in the plots belonged to Quercus plants, even if some pine, birch, and chestnut logs were also present.

The fertilization was applied as an NH_4NO_3 solution (4.3 g N/l), and the annual fertilization rate in the above and below plots was 20 kg N ha^{-1} $year^{-1}$, which is equivalent to more than three times the background N deposition (Marchetti and others, 2002). This N application rate, relatively low in comparison with other studies (Maestrini and others, 2014; Wu and others, 2023; Roy and others, 2023), was chosen to simulate realistic scenarios of increased N deposition. The water provided annually with the fertilizer solution was equivalent to a precipitation of 0.46 mm, hence negligible when compared to the mean annual precipitation.

The fertilization above the canopy is performed through a FALCON® 6504 rotating sprinkler (Rain Bird SNC, Aix-en-Provence, France), which can spray the fertilizer solution on the entire plot area (12-m radius), ensuring an even and consistent watering along the entire radius. The uniformity of distribution was confirmed by preliminary trials performed in an open area, where water was sprayed and the amount of water released was measured at different distances from the sprinkler (data not shown). The sprinkler was assembled on a telescopic pole (Fireco S.R.L., Gussago, Brescia, Italy) reaching 15–18-m height, according to the tree height in each plot. The pressure is ensured by a gasoline-powered pump (Officine Carpi S.R.L., Poviglio, Reggio Emilia, Italy). The fertilization on the forest floor is performed manually, with a water hose and a spray nozzle. To ensure uniformity of distribution, each plot was divided into eight equal-area sectors and an equal volume per sector was applied to each sector using a flow meter mounted on the hose.

Litter Decomposition

Litter Collection

In 2014, three litter traps (22 cm-diameter metal rings with bottom-closed nets on 1.30 m poles) were installed in each experimental plot (control and treated), for a total of 27 traps installed in total in the nine experimental plots. Litter traps were emptied monthly from September to December 2015 and 2016. The litter collected from litter traps installed in each plot was sorted out and oven-dried at 40°C for 48h and carefully mixed to produce a bulk litter sample from each plot, which was stored at room temperature until it was used for litterbags preparation.

At the same time as litterbags were being prepared, a subsample of oak leaf litter from each bulk sample was oven-dried at 65°C for 48h for moisture content determination. The remaining oak leaf litter, after litterbags preparation, was ground at 2 mm with Pulverisette 19 large grinder (FRITSCH GmbH, Idar-Oberstein, Germany) and carefully mixed. A smaller subsample was taken from the ground litter and further ground to a fine powder with a ball mill (Retsch MM400, Verder Scientific, USA) and used for chemical analysis. Litter C and N content was determined with a Flash EA 2000 elemental analyzer (Thermo Fisher Scientific, Germany). Content of the other nutrients was determined with an inductively coupled plasma optical emission spectrometer (ICP-OES, Spectro Arcos, Ametek, Germany).

Litterbag Preparation

Only dry sessile oak leaf litter was used for litterbags preparation. Following Magill & Aber (1998) and Ventura and others (2010), 36 square litterbags (17 × 17 cm, 2 mm nylon mesh, hot-melt sealed) were filled with plot-specific litter collected the previous year: 10 g in 2016 (equivalent to 357 $g\ m^{-2}$ production) and 9 g in 2017 (307 $g\ m^{-2}$). Dry weights were corrected for moisture content.

Deployment and Sampling

Four bags were laid on the soil surface in every plot in January 2016 (series A) and January 2017 (series B). Using two consecutive-year series captures possible shifts in leaf traits induced by enhanced N availability and accommodates interannual climatic variability. One randomly chosen bag per plot was retrieved after 6 months and after 1, 2, and 3 years. Contents were cleaned of soil, oven-dried (65°C, 24h), weighed for mass-loss determination, finely ground, and analyzed for C, N, K, Na, P, and S content.

Deadwood Decomposition

Initial Survey and Sampling

In 2017, the presence of standing dead wood, snags, dead downed trees, coarse woody debris, and stumps was surveyed in each plot. All the standing components with diameter at breast height ≥ 5 cm and lying components with minimum diameter of 5 cm were measured. A threshold height of 1.3 m was used to distinguish stumps (less than 1.3 m) from snags (higher than 1.3 m). The volume of standing and downed dead trees was computed by double-entry volume equations based on diameter and height or length. All downed oak stems and coarse debris were classified in situ using the Müller-Using & Bartsch (2009) four-class system:

I— recently dead, bark, and branches intact;
II— partial bark loss, some crooked branches, longitudinal cracks appearing;
III— deep longitudinal cracks, branches partly decomposed;
IV— advanced decay, bark absent, wood collapsing.

From one log per decay class found in the site, near but outside the experimental plots, a transverse slice was taken to the laboratory. Using an electric saw, sapwood and heartwood were separately cut into ~ 2 × 1 × 1 cm blocks. The exact dimensions of each block were measured with a gauge after cutting and used to calculate sample volume (and density), so analyses were based on measured, not nominal, block size. One block from every decay class × wood type was ground for initial C and N content determination.

Field Incubation

In February 2017, five blocks of each decay class and wood type were enclosed in 0.5 cm-mesh plastic nets and placed on the forest floor of every plot (5 blocks per class × 4 decay classes × 2 wood type × 3 treatments × 3 replicated plots per treatment, for a total of 360 blocks). One block of each combination was collected at 6, 12, 18, 24, and 36 months, oven-dried (105°C, 24h), and weighed. Sapwood of all classes and heartwood of classes I, II, and IV were ground for C and N analysis (except the 36-month samples).

Chemical Analysis of Litter and Wood

The C and N content in litter and deadwood was determined with an elemental analysis (Flash EA 2000 Organic Elemental Analyzer, Thermo Fisher Scientific). The content of other nutrients was determined in fresh and decomposing leaf litter with an inductively coupled plasma optical emission spectrometer (ICP-OES, Spectro Arcos, Ametek, Germany).

Data Elaboration and Statistical Analysis

Statistical analysis was performed with R (version 3.6.1). For both litter and deadwood, remaining mass measured at each time t (*Mt*) was divided by the initial weight of each sample (*M0*) and multiplied by 100, to obtain the remaining mass as % of the initial value (Adair and others, 2010). In the same way, the remaining amounts of N and C (as % of initial values) in decaying litter and wood were calculated multiplying the remaining weight by the C and N content of the collected samples and dividing by the initial C and N amounts in samples at the beginning of the experiment. Furthermore, the C/N was calculated at every sampling time as the ratio between C and N content.

Trends of remaining amounts of biomass, C, and nutrients over time, for litter and deadwood samples, were fitted using linear (Equation 1), single-exponential (Equation 2), or quadratic models (Wieder and Lang 1982; Maestrini and others, 2014; Ventura and others, 2019).

$$\mathrm{Mt} = 100 + kt \quad (1)$$

$$\mathrm{Mt} = 100e^{-kt} \quad (2)$$

$$\mathrm{Mt} = 100{+}k_1t^2 + k_2t \quad (3)$$

where Mt is the remaining mass at the time *t (days)*, and *k, k_1, and k_2* are the decomposition constants (days^{-1}). The decomposition rate was calculated with the minpack-lm package (CRAN).

For the remaining content of nutrients, linear, quadratic, and exponential models were tested as well. The model used was chosen based on the coefficient of determination R^2, root mean square error (RMSE), and Akaike information criterion (AIC) (Supplementary Tables S1 and S2).

The two litter series (A and B) were analyzed separately. Differences among treatments were assessed using linear models, after linearization of the exponential curves when needed. Time, treatment, and interaction were considered factors in the models. When quadratic models were used to describe the trend of remaining nutrient content in the litter, comparison of the trends observed in the different treatment was assessed with an F-test (Zar, 2019).

For deadwood, initially, the analysis was performed considering time, treatment, decomposition class, and wood part as factors in the same linear model, together with their two-way interactions. As a significant interaction was detected between wood part and decay class, the analysis was carried out separately for sapwood and heartwood. Differences among treatments and decay classes were assessed by including them in the model, along with time and their interactions.

In addition, differences among treatments for all dependent variables (remaining mass, remaining C, remaining N, and C/N) were assessed at each single date and each series for litter, at every decay class for deadwood. Percent values were subjected to angular transformation before ANOVA. The homogeneity of variance and the normal distribution were tested. When homogeneity of variance was not satisfied, ANOVA was corrected with the weighted least squares.

Results

Litter Decomposition

The initial N and C contents, as well as the C/N, were different in the two-litterbag series (Figure 1). However, no significant differences were observed among treatments for these parameters, and no interaction between treatment and year was detected. On average, the initial litter N content was lower in series A (0.65 ± 0.008%) than in series B (0.75 ± 0.02%). On the contrary, the initial C content was higher in series A (46.88 ± 0.05%) than in series B (45.2 ± 0.2%). Consequently, also the C/N was higher in series A (72 ± 1) than in series B (60 ± 2), respectively. The initial P content did not differ between years or treatments (Supplementary Figure S2). However, the content of the other examined nutrients (K, Na, S) showed a statistically significant difference between series, but not among treatments. Series A exhibited lower K and higher Na and S content than series B (Supplementary Figure S2).

The trend of mass loss did not differ between the two series (Figure 2a-b). In series A, the mass loss in the first incubation period was more rapid, with a loss of more than 20% in the first 146 days, while series B followed a more gradual mass loss. However, after three years of incubation, the mass remaining for series A and B was similar (on average 47–43% of the initial value, respectively). Within each series, the treatments did not significantly affect the decomposition rate k (Supplementary Table S1).

The C loss followed an exponential decrease. The decomposition rate for C was higher in series A (average rate = $1.04{\cdot}10^{-3}$) than in series B (average rate = $7.35{\cdot}10^{-4}$) but did not differ between treatments within each series (Figure 2c-d).

In series A, the remaining amount of N in the litterbags increased linearly over time (Figure 2e), reaching 131% of the initial value after 1105 days. In series B, the trend of remaining N was better represented by a quadratic model as it increased after 741 days and subsequently decreased (Figure 2f). For both litterbag series, the treatments did not lead to statistically significant differences in the trend of the remaining N or in the values at each sampling time.

The C/N decreased exponentially during the litter decomposition; at the end of the incubation, the C/N was 23.9 ± 0.4 in series A and 23.2 ± 0.5 in series B. The trend of the C/N in the decomposing litter showed no significant differences, neither between series nor between treatments (Figure 2g-h).

Trends of the other nutrients, expressed as remaining value with respect to the initial content, are illustrated in Figure 3 (e–h). The remaining K followed an exponential trend in both series A and B (Figure 3a-b), and no significant effect of treatments was observed. The remaining Na presented two different trends in the two-litterbag series (Figure 3c-d). In series A, it followed a negative

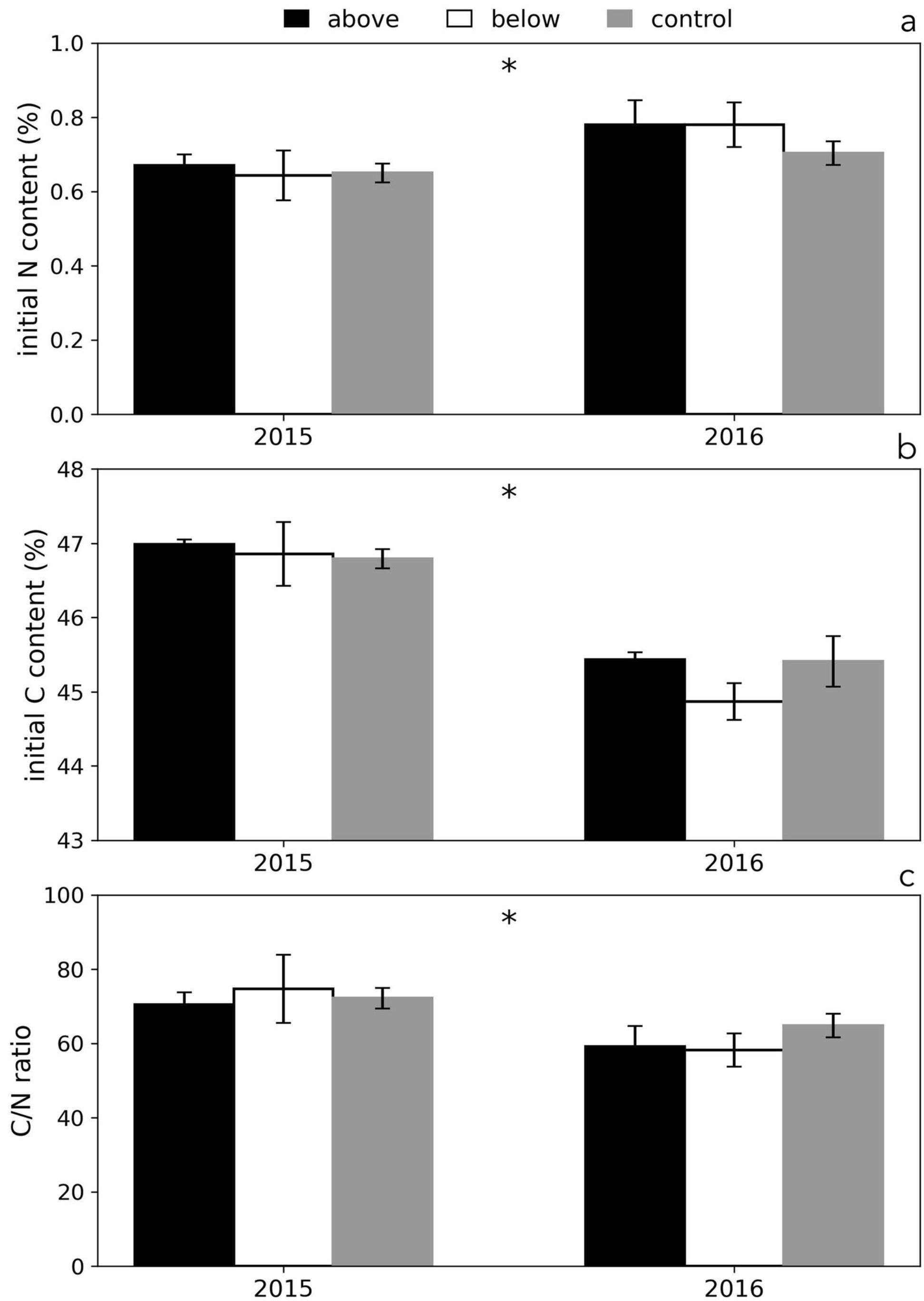


Figure 1. Initial concentration of (**a**) N, (**b**) C, and (**c**) C/N in the leaf litter in 2015 (series A) and 2016 (series B). The symbol * indicates a statistically significant difference between the years (no significant effect was observed among treatments within each year, and no interaction between year and treatment was detected). Bars represent the mean; the vertical bars represent the standard error of the mean (n = 3).

linear model, while in series B it followed a quadratic model, since it initially increased and decreased afterward. In both series, a significant effect of the treatments was observed, but the effect was different according to the series. In series A, the remaining amount of Na was on average higher in the treatments above and below than in the control, but no differences were observed between the two treatments. In series B, the treatments were completely different from each other. The remaining P followed a linear trend (Figure 3e-f). The treatments showed a statistically significant differ-

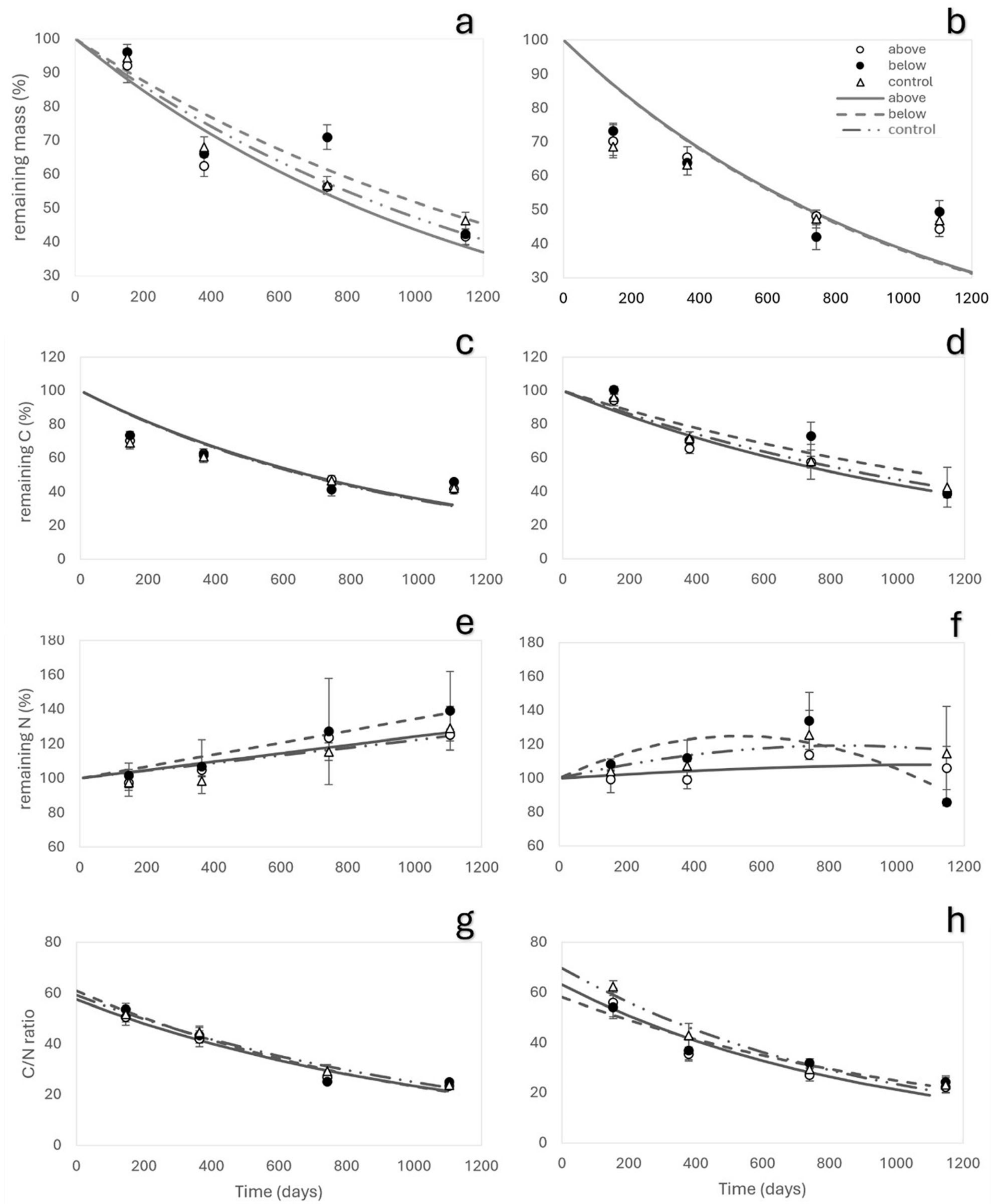


Figure 2. Remaining amount of mass for each treatment over time in series A (**a**) and series B (**b**). The lines represent the decomposition model for each treatment. Variation of C content (**c**, **d**), N content (**e**, **f**), and C/N (**g**, **h**), expressed as percentages of their initial values, in series A (**c**, **e**, **g**) and series B (**d**, **f**, **h**). Data points represent the mean; vertical bars represent the standard error of the mean (n = 3).

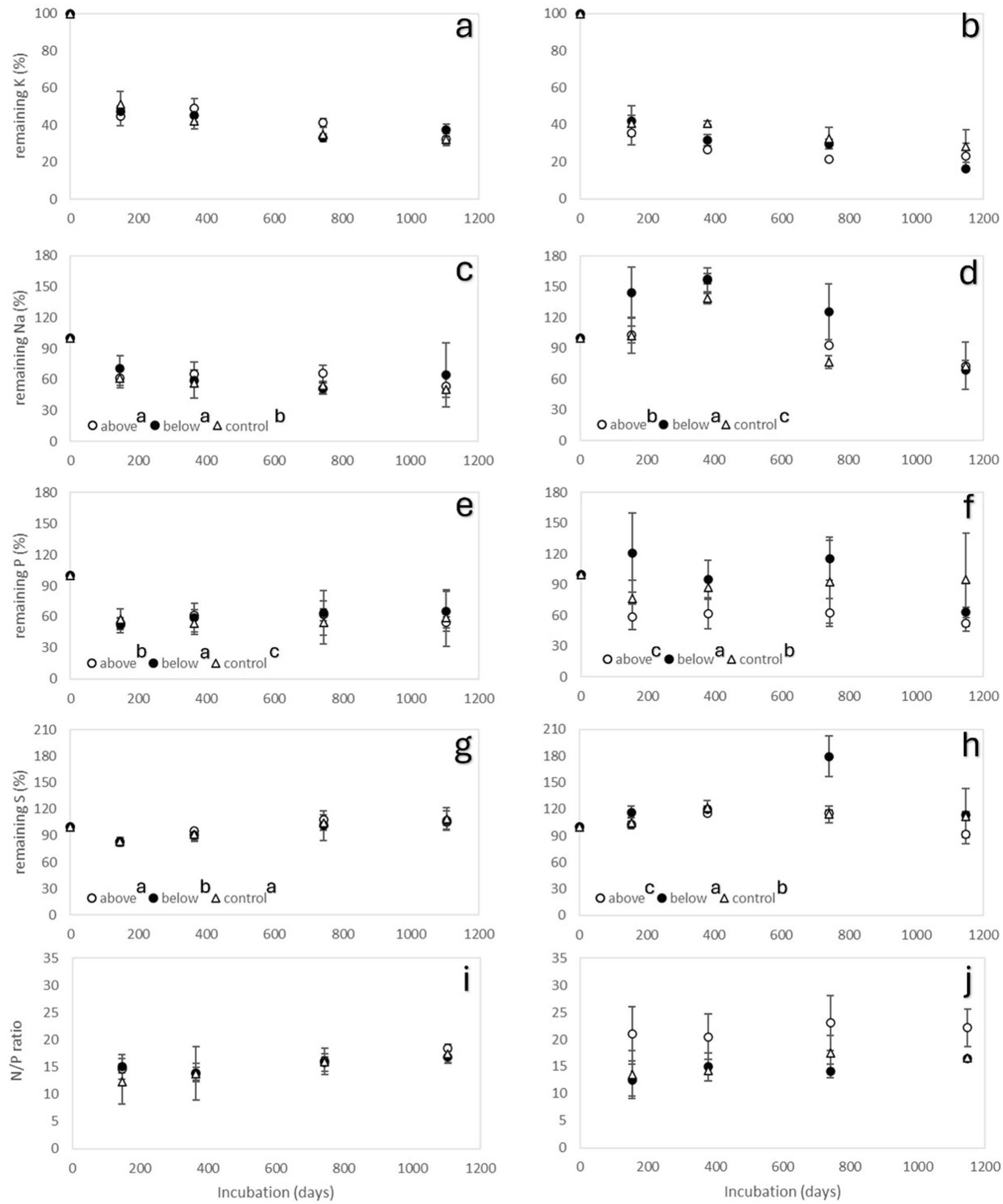
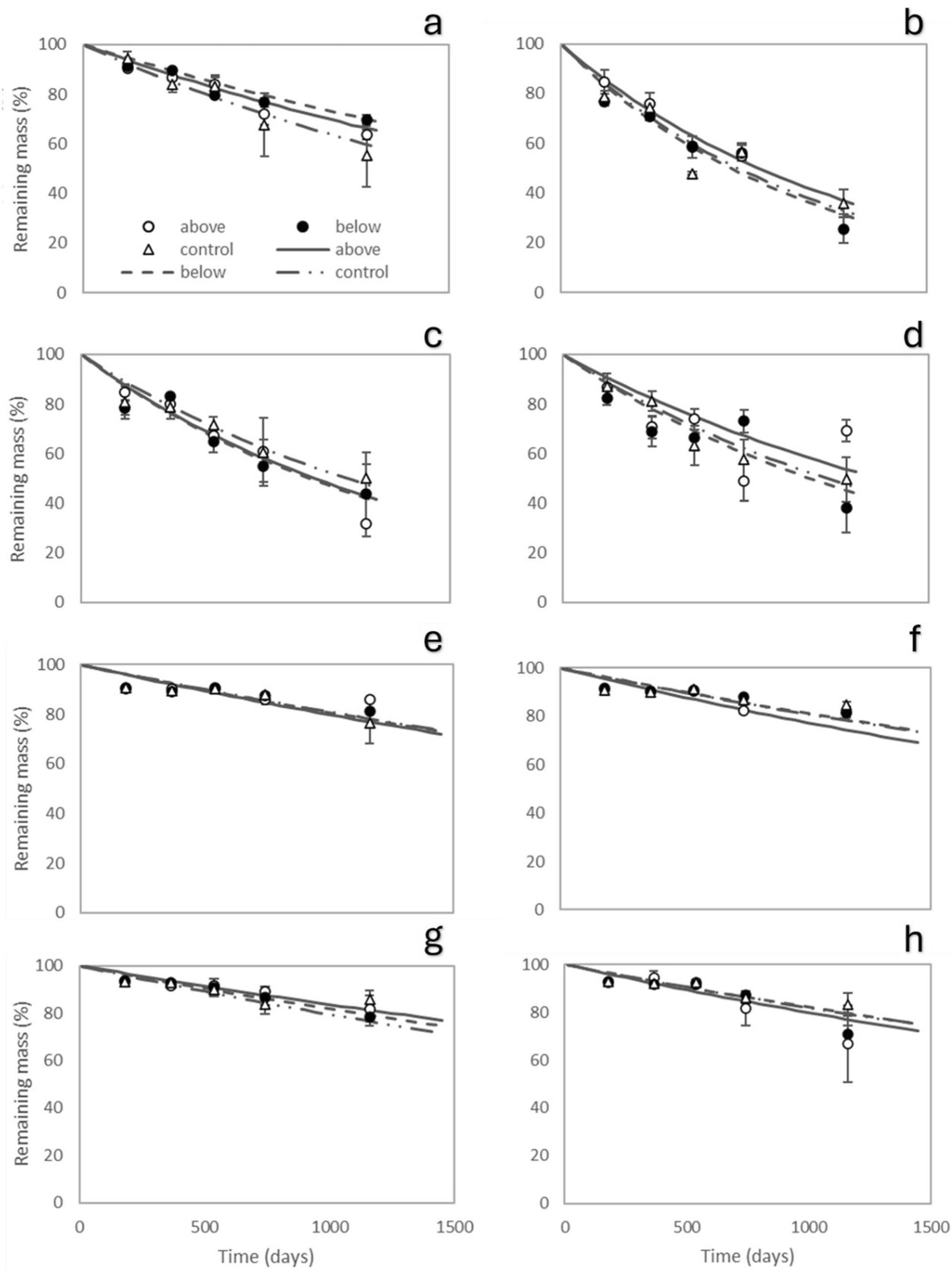


Figure 3. Variation of remaining K (**a**, **b**), Na (**c**, **d**), P (**e**, **f**), S (**g**, **h**), and N/P ratio (**i**, **j**) in the litterbags of series A (**a**, **c**, **e**, **g**, and **i**) and series B (**b**, **d**, **f**, **h**, and **j**). Different letters in the legend indicate statistically significant differences among mean values in the different treatments, for each macronutrient and for each series. Data points represent the mean of three replicates; vertical bars represent the standard error of the mean (n = 3).


a
b
c
d
e
f
g
h
Remaining mass (%)
100
80
60
40
20
0
above
below
control
above
below
control
0
500
1000
1500
Time (days)

◀**Figure 4.** Variation of dry mass weight for each treatment in sapwood (**a–d**) and heartwood (**e–h**), divided into decomposition classes: class I (**a**, **e**), class II (**b**, **f**), class III (**c**, **g**), and class IV (**d**, **h**). Data points represent the mean of three replicates; vertical bars represent the standard error of the mean (n = 3).

ence in both series. In series A, the remaining P decreased in the order below > above > control, with significant differences between treatments. In series B, the remaining P was on average higher in the treatment below than in the control, while in the treatment above it was even lower (Figure 3e-f). The remaining S was better fitted by a linear model in series A and by a quadratic function in series B (Figure 3g-h). In series A, the average remaining S was not statistically different in the above and control treatments, while in the treatment below it was significantly lower. In series B, the treatments differed among each other, in the order below > control > above. The N/P ratio increased significantly during litter decomposition in both series A and B, which did not show any statistically significant difference (Figure 3i-j). The treatments did not induce any significant difference in none of the series.

Deadwood Decomposition

On average, sapwood exhibited a higher initial N content (0.18 ± SE 0.01%) than heartwood (0.08 ± 0.005%), while initial C content was not different between the two wood parts, resulting in 44.9 ± 0.27% and 45.2 ± 0.22%, respectively. Consequently, the C/N was lower in sapwood (245 ± 15) than in heartwood (587 ± 31).

The remaining mass data were fitted by the single-exponential model (Equation 2). Mass loss occurred more quickly in sapwood than in heartwood, with the decomposition rate (k) for sapwood ranging between $3.07 \cdot 10^{-4}$ and $9.97 \cdot 10^{-4}$ days^{-1} and for heartwood between $1.80 \cdot 10^{-4}$ and $2.55 \cdot 10^{-4}$ days^{-1} (Supplementary Table S2, Figure 4). These correspond to 0.112–0.364 year^{-1} (sapwood) and 0.0657–0.0931 year^{-1} (heartwood).

For sapwood, k differed statistically between the different decay classes, since classes II and III had a higher decomposition rate, while class I showed a lower decomposition rate (Supplementary Table S2). The heartwood showed differences among decay classes, as well (Supplementary Table S2). Treatments did not significantly affect the wood decomposition rate of any of the examined classes.

The remaining C in the sapwood decreased linearly over time (Figure 5). No differences in the rate of C loss were observed among the decay classes, and no effect of the treatments was observed on the C loss rate within each class. In the heartwood, the remaining C did not change significantly during incubation for classes I and II (Figure 5a, c), but only in class IV (Figure 5d). For both sapwood and heartwood, the rate of C loss did not differ across decomposition classes, nor was it affected by treatments within each class.

The remaining N in the sapwood increased with the incubation time, with no statistically significant differences among classes (Figure 5e-h). Within each class, the treatments showed no statistically significant difference, except in class IV, in which the slope of the remaining N trend in the treatment above differed significantly from that in the treatment below (Figure 5h). The slopes of the treatment above and the control were positive, while the treatment below had a negative slope. In the heartwood, the remaining N did not change significantly with incubation time in classes I and II but increased only in class IV (Supplementary Figure S3). Within classes, treatments showed no significant difference.

The C/N in the sapwood followed a linear decrease over time (Figure 6a-d). The trends did not differ among decay classes. However, the C/N at 180 days was significantly higher in class IV than in class III, while classes I and II were not significantly different from the others (Figure 6a-d). The treatment did not affect the trend of the C/N in classes I, II, and III, while a difference was observed in class IV, where the treatment below did not vary during the incubation (Figure 6d).

The C/N followed a linear trend in the heartwood as well (Figure 6e-h). The trend differed among classes. Class I varied at a significantly slower pace than class IV. On day 180, significant differences were observed among decay classes. Values in classes III and IV were significantly higher than in class II (Figure 6f, g, h).

Discussion

Litter Decomposition

The fertilization treatments did not affect litter's N content or C/N, contradicting our third hypothesis. A positive effect of N addition or N deposition on foliar N concentration in N-limitation conditions is generally observed (You and others, 2018; Månsson and Falkengren-Grerup, 2003), but under N saturation the effect could be reversed (Braun and

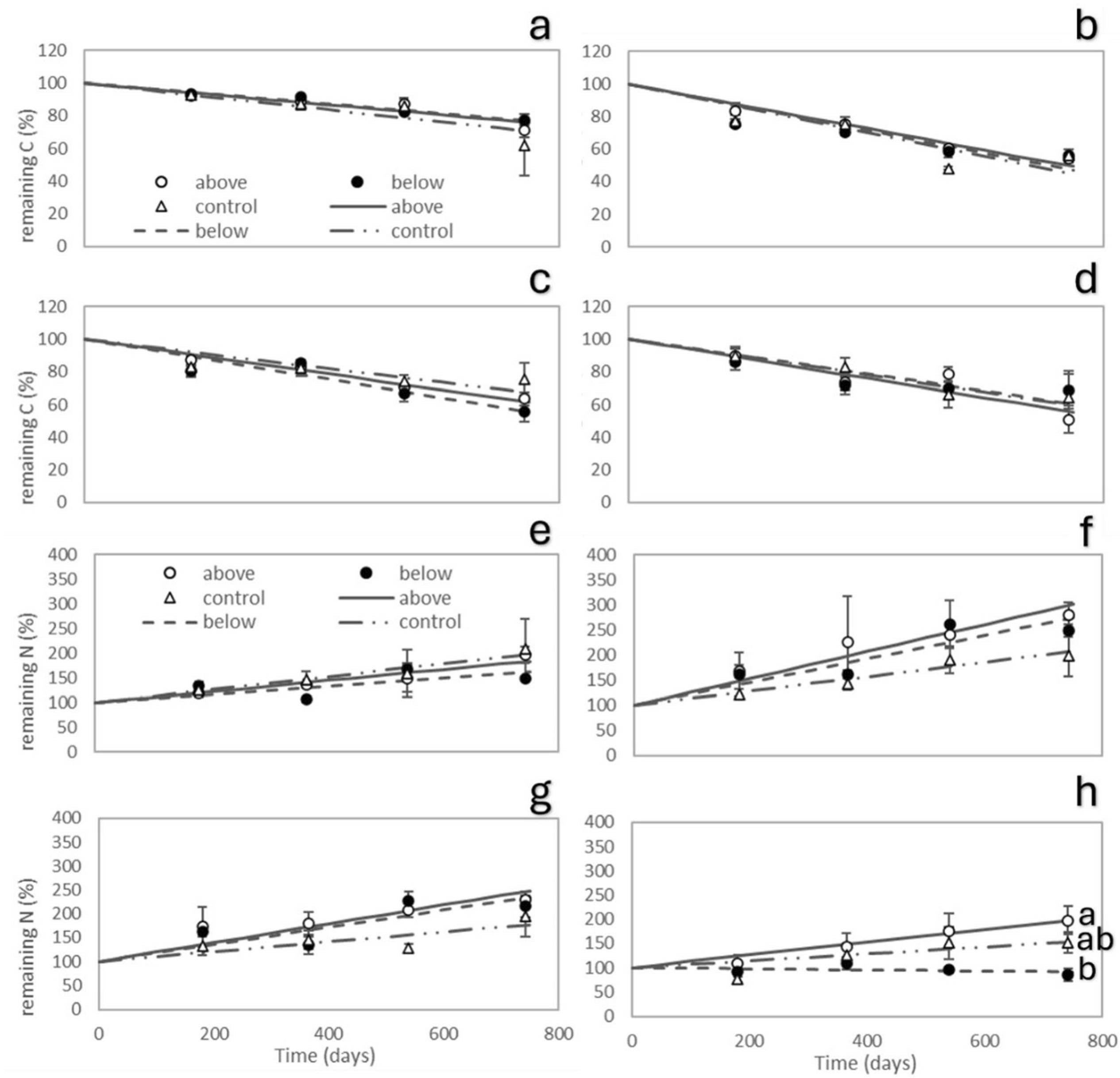


Figure 5. Variation of C content (**a–d**) and N content (**e–h**), as percentage of the initial value, in the sapwood for each treatment, divided into decomposition classes: class I (**a**, **e**), class II (**b**, **f**), class III (**c**, **g**), and class IV (**d**, **h**). Data points represent the mean of three replicates; vertical bars represent the standard error of the mean (n = 3).

others, 2020). Zheng and others (2020) did not record a significant effect of N addition on foliar N concentration. Previous studies performed in Monticolo (Giammarchi and others, 2020; Da Ros and others, 2023) found that N fertilization did not increase the foliar N content, even if 13% of canopy-added N was assimilated by oak leaves. This was related to the relatively short experimental duration; an oak adult high-forest may need more time to shift its N cycle in response to added N. Canopy N absorption may also have been counterbalanced by a lower root N uptake in the same plants, leaving the leaf N content unaffected. However, a higher content of leaf N does not necessarily result in a higher N concentration in the litter, because of N reallocation from leaves to the reserve organs before leaf fall (Liu and others, 2016; Ferraretto and others, 2022).

No detectable effect of N fertilization on litter decay was found at the applied rate over three years, contradicting our first hypothesis. Previous studies (Craine and others, 2007; Hobbie and oth-

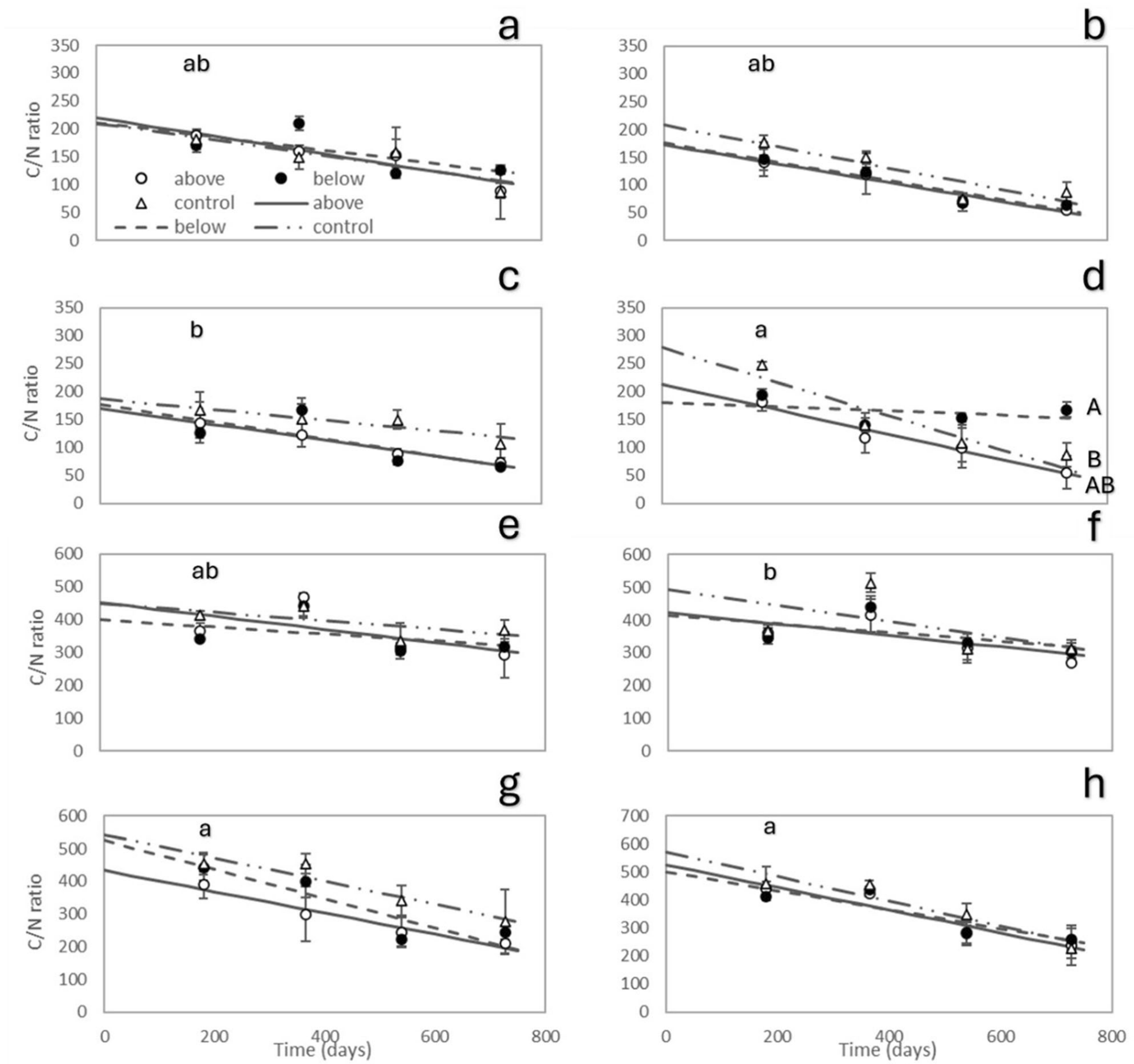


Figure 6. Variation of the C/N during the incubation in sapwood (**a–d**) and heartwood (**e–h**), divided by decomposition class and treatment. For sapwood: class I (**a**), class II (**b**), class III (**c**), and class IV (**d**). For heartwood: class I (**e**), class II (**f**), class III (**g**), and class IV (**h**). The letters above day 180 represent the statistical significance of differences in C/N among classes. The capital letters in (**d**) represent the statistical significance of differences in the C/N trend among treatments. Data points represent the mean of three replicates; vertical bars represent the standard error of the mean (n = 3).

ers, 2012) found that N addition may accelerate litter decomposition in the initial stage, as N addition enhances the activity of enzymes associated with the degradation of accessible C, while in the late decomposition stage N addition inhibits the degradation of lignin (Craine and others, 2007; Tu and others, 2014; Xia and others, 2018). Contrasting effects on litter decomposition are also reported for N deposition (Chen and others, 2019). Recently, Wu and others (2023) reported an increase in litter decomposition rate due to N addition in short term in situ experiments, attributed to elevated N and P concentrations, and reduced C/N and lignin/N ratios in plant litter. However, the effect of N addition was neutral when the decomposition time was between two and three years and negative for longer periods.

The trend of remaining N denoted N immobilization by the microbial community during litter incubation. However, a difference was observed between the two-litterbag series, with constant immobilization of N in series A, while series B started to lose N in the last year of decomposition. This can be explained by the higher precipitation amount observed during the incubation of series B (2189 mm) in comparison with series A (1740 mm). Precipitation and N release can in fact be positively correlated (Santonja and others, 2019). The more rapid N release from the second series may also be due to its higher initial N content and lower C/N, which is a key factor for litter decomposition (Wu and others, 2025).

Over the three years of experiment, N fertilization did not increase in the duration or intensity of N immobilization. This suggests an absence of N limitation for the microbial community, which could obtain sufficient N for its growth from alternative N sources. This was confirmed by soil nutrient content and enzymatic activity measured in the same site, suggesting a relative P limitation rather than N limitation (Minikaev and others, 2025). Previous studies reported non-significant (Li and others, 2015) or positive (Zheng and others, 2017) effect of N addition on litter N immobilization, which depends also on litter quality (Parton and others, 2007). Other explanations for the absence of treatment effect may include the loss of N by leaching in the below-canopy treatment and N uptake from canopy or re-volatilization in the above treatment (Da Ros and others, 2023), which may have reduced the availability of the N provided by fertilization for the microbial community. However, the remaining N in the second litterbag series followed a different trend after the first two years, indicating that the effect of the treatment may become relevant if the incubation period is extended.

While many studies have explored the dynamics of N and C in decomposing plant material, other nutrients have received less attention, although some of them, for example K, can be released in high quantity and, therefore, may play a significant role in plant nutrition (González-Rodríguez and others, 2018; Ventura and others, 2010). In Monticolo, the fast decrease of K in the first period of decomposition was observed also in previous studies (Du and others, 2020; Ventura and others, 2010; Alvarez and others, 2008). The remaining Na followed a quadratic trend in series B. This trend diverges from what observed in a tropical forest, where Na amount in the litter of two species showed a clear decrease (Vinh and others, 2020). The remaining P did not decrease significantly over time, in contrast with Ventura and others (2010), who observed a general decrease of this element by almost 20% in three years, and with Alvarez and others (2008), who observed a decrease of P amount by 53% in oak leaves in six months. Du and others (2020) reported that the P release did not start immediately, but it was low in the first six months, after which it intensified. This result was observed also by Zhuang and others (2020), who found an initial increase of P in the litter of *Michelia wilsonii* (Finet and Gagnep.), followed by a decrease. This decreasing trend was inhibited by N fertilization (40 kg N ha^{-1} $year^{-1}$). The quadratic trend of S shown in the litter of series B was also found by Ventura and others (2010), who observed an initial accumulation, followed by a decrease of the remaining S amount after *circa* one year. On the other hand, Alvarez and others (2008) reported a clear S release from leaves of three tree species in the first six months of decomposition, also in agreement with results obtained in a tropical forest (Vinh and others, 2020).

Most importantly, fertilization treatments affected the remaining amounts of Na, P, and S. Indeed, in the fertilized plots, a higher remaining amount of Na and P was found on average, while remaining S shows differences between the two-litterbag series. Furthermore, differences between the fertilization method were also detected, depending on the specific element and litterbag series. This indicates that the application method produced different results, partially supporting our second hypothesis.

Deadwood Decomposition

The N content and the C/N of the sapwood observed in the present study align with those reported by Noll and others (2016) for *Quercus* spp. (0.21 ± 0.10 and 263 ± 71, respectively), while the N content and the C/N of the heartwood are lower (0.12 ± 0.05 and 410 ± 76, respectively). A higher N content in sapwood than in heartwood was reported by Meerts (2002). It should be mentioned that only one block was used to determine C and N content of the deadwood at different stages. We acknowledge that relying on one sample for elemental analysis may not consider the variability of element content of the biomass. However, the block used for determination of initial C and N content was taken from the same wood slice used to obtain the incubated blocks, to minimize the potential differences with the blocks incubated in the field.

The lower decomposition rate observed for heartwood can be explained by its higher lignin content, lower cellulose content (Bertaud and Holmbom, 2004), higher content of phenols and tannins (Scheffer, 1966), and higher C/N (Weedon and others, 2009). In fact, a lower fungal biomass was found in the heartwood by Noll and others (2016). Decomposition also differed among decay classes, with the slowest rates in class I and faster rates in the more advanced classes, in agreement with Lagomarsino and others (2021). In both wood parts, the C/N at day 180 differed among decay classes. It was unexpected to record a comparatively higher C/N in decay class IV, since the C/N tends to decrease with decomposition (Piaszczyk and others, 2019a). However, the difference was limited to the first sampling time.

The application of N did not alter deadwood mass loss or C loss, contradicting hypothesis I also for wood decomposition. This is in agreement with Maestrini and others (2014), who found no effect on deadwood decomposition under N fertilization rate equivalent to 21 kg N ha^{-1} year^{-1}. Likewise, Chen and others (2016) observed that deadwood decomposition in tropical forests was enhanced by P fertilization, but did not respond to N fertilization, even at higher rate (100 kg N ha^{-1} year^{-1}). Both Chen and others (2016) and Wu and others (2020) concluded that P availability was the primary limitation to decomposition. However, these studies did not distinguish between sapwood and heartwood. Indeed, to the authors' knowledge, the present study is the first to examine the effect of N deposition on sapwood and heartwood separately. Considering the peculiarity of the two wood parts, differentiating between heartwood and sapwood is particularly relevant in decomposition studies.

The general impact of increased N deposition on forests seems to be an increase in net primary productivity (Townsend and others, 1996) and C accumulation (Magnani and others, 2007; Sutton and others, 2008; Lu and others, 2021; Liu and others, 2024). This is attributed also to a decrease in soil respiration, due to degradation of soil organic matter and dead plant material, even if effects are quite variable according to the biome and climate region (Janssens and others, 2010; Liu and others, 2024). In the site and timeframe examined in the present study, changes in deadwood decay are unlikely to explain short-term increases in ecosystem C storage under elevated N inputs; other compartments (e.g., soil organic matter) may contribute more strongly and warrant targeted investigation. Other studies evidence positive or negative effects of N on deadwood degradation: Wu and others (2019) observed an increase in decomposition of coarse wood debris after addition (60 kg N ha^{-1} year^{-1}); similar results were found by Bebber and others (2011) under addition of 2.8 kg N ha^{-1} year^{-1}. On the other hand, a decrease of deadwood decomposition under N fertilization was observed by Qiao and others (2016) in a subtropical forest. Roy and others (2023) observed that N increased mass loss in deadwood of gymnosperms, but reduced or unaffected mass loss in angiosperms such as *Fagus* and *Quercus*. These results indicate that there is no clear effect of N addition on the deadwood decomposition; studies on the topic are scarce and use different methods. Furthermore, results differ according to the biome (tropical, temperate, or boreal forests). This suggests that several factors may influence the effect of N deposition on deadwood decomposition, and further research is necessary to understand these factors and the underlying processes.

Nevertheless, in highly decayed sapwood (class IV) N decreased under the below-canopy treatment but accumulated under the above-canopy treatment and in the control. This shift between N immobilization and release partially supports our first and second hypothesis, regarding nutrient dynamics in deadwood. Decaying wood is a N-limited environment, because of its low N content. Therefore, significant amounts of N must be taken up during the degradation of deadwood (Hossen and others, 2024).

The N content of deadwood reflects the balance between N accumulation through microbial processes such as N_2 fixation and N losses through leaching or other pathways (Smyth and others, 2016). The extra N provided in the below treatment may therefore have shifted the equilibrium toward losses instead of accumulation in the deadwood of class IV. We cannot assess the mechanisms by which this effect occurred only in the most advanced decomposition stage; further analysis is needed to clarify them. However, this provides another indication that the presence of the canopy can interfere with N deposition and change its effect on biogeochemistry of deadwood, stressing the importance of including it in N manipulation studies. Furthermore, the occurrence of N immobilization indicates that the effect of this extra N on deadwood may be evident only in the long term. Considering also the slow degradation rates of deadwood in oak forests, prolonged studies are critical to better understand the dynamics of deadwood decomposition in deciduous oak forests under increased N deposition. These results deviate from the trend observed for leaf litter, wherein N addition was anticipated to augment the remaining N (Chen and others, 2019).

Conclusion

The marginal effect of N addition on decomposition of leaf litter and deadwood observed at this site and over the three-year observation window suggests that an increase in N deposition at the simulated rate (20 kg N ha^{-1} $year^{-1}$) has limited short-term effects on C storage in dead biomass in oak forests. However, interesting differences between the treatments, in particular between above- and below-canopy fertilization, were observed for the remaining Na, P, and S in leaf litter. Furthermore, N application method influenced the trend of the remaining N in the more advanced decomposition stage of the sapwood of sessile oak, promoting N immobilization in the treatment above and the control and N release in the treatment below. These results indicate that the interaction with the tree can change the effect of N deposition in forests.

The occurrence of N immobilization suggests also that the effect of N deposition could be evidenced in the long term; prolonged studies are therefore essential to better understand the dynamics of deadwood decomposition in deciduous oak forests under increased N deposition.

The significant differences in decomposition rates and trends observed between sapwood and heartwood highlight the importance of studying these two wood parts separately in deadwood decomposition studies.

Our experiment was conducted with only three replicates per treatment, which is consistent with most of the N manipulation studies performed on forests, given their logistical complexity and time-demanding nature. For this reason, more studies on N deposition, including the interaction with the tree canopy, should be performed and compared, to clarify the effects on litter and deadwood decomposition in forests.

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AUTHOR CONTRIBUTIONS

Bortolazzi A. was involved in investigation, visualization, data curation, formal analysis, and writing—original draft. Da Ros L. took part in investigation, visualization, and writing—review and editing. Rodeghiero M. and Tomelleri E. were responsible for writing—review and editing. Tonon G. and Tognetti R. participated in conceptualization, funding acquisition, supervision, and writing—review and editing. Panzacchi P. contributed to investigation, data curation, and writing—review and editing. Ventura M. performed conceptualization, funding acquisition, investigation, data curation, visualization, supervision, and writing—review and editing.

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DATA AVAILABILITY

The data supporting the findings of this study are available at: https://zenodo.org/records/20070109.

Declarations

Conflict of interest The authors declare that there is no conflict of interest regarding the publication of this manuscript. None of the authors has any financial, advisory, or personal relationships that could be perceived as influencing the work presented in this study.

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