



Nutrients (N, P, K, Na) and warming affect heterotrophic respiration in temperate forest litter

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Abstract

At present, ecosystems are facing changes caused by global warming and anthropogenic impacts on geochemical cycles. Both temperature and nutrient availability affect litter decomposition; however, little is known about their simultaneous effect on litter decomposition in temperate forests, especially for nutrients such as Na and K. To address this perspective, we investigated how changes in N, P, Na and K supply and increased temperature affect litter decomposition measured as respiration. Moreover, the study determines what changes can be expected in the functioning of two forest types of different fertility (deciduous and coniferous). The respiration measurements were conducted in the laboratory in mesocosms filled with litter from deciduous (oak-hornbeam) and coniferous (mixed pine-oak) forests fertilized by N, P, K, and Na. The experiment was conducted at ambient (14 °C; oak-hornbeam and mixed pine-oak litter) and increased temperatures (22 °C; oak-hornbeam litter). The respiration of oak-hornbeam litter increased with increasing temperature, with Q_{10} values ranging from 1.49 to 2.14. Our results showed different responses of respiration to nutrient addition between temperatures and litter types. In oak-hornbeam, at 14 °C, the addition of N, P and K decreased respiration, whereas at 22 °C, such an effect was noted only under N application, and P and Na addition increased respiration. In mixed pine-oak litter at 14 °C, respiration decreased after Na addition, and other nutrients had no effect. Together, our results suggest that forecasting the impact of nutrient deposition on ecosystem functioning should consider temperature rise as a factor altering ecosystem responses to fertilization in future research.

Keywords Decomposition · Global changes · Nutrient cycles · Respiration · Forest litter

Introduction

At present, ecosystems are facing global changes. The most important driver of these changes is increasing global temperature, but another critical factor is unprecedented increases in element inputs (Sistla et al. 2015). Growing human demand for food has led to agricultural intensification, increasing mineral fertilizer use (Sutton and Bleeker 2013). These changes also affect element deposition in nonagricultural environments and thus processes such as plant growth, litter production, and litter decomposition. Litter decomposition is the crucial process in ecosystem

functioning in natural conditions, e.g., it covers most of the plant nutrient requirements (Schlesinger and Bernhardt 2020). It depends mostly on vegetation type (Laskowski et al. 2003), temperature, moisture, soil pH, and the concentration of nutrients (e.g., N, P, or K) (Berg and McLaugherty 2020). The element cycles that are affected by human activity are nitrogen, phosphorus (Galloway et al. 2004; Gilbert 2009; Bobbink et al. 2010; Bennett et al. 2011; Wang et al. 2017), potassium (Sardans and Peñuelas 2015) and, to a lesser extent, sodium (Kaspari et al. 2014).

Nitrogen sources in ecosystems mainly involve three processes: biological fixation, mineralization of dead organic matter, and deposition from the atmosphere (Bobbink et al. 2010). Before the industrial revolution in the nineteenth century (1850), the nitrogen cycle was affected principally by natural processes. However, by 2005, natural processes had decreased because of changes in land use (deforestation and increased agricultural area), and anthropogenic deposition of N had increased by more than 10 times, with further growth

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predicted (Galloway et al. 2004; Bobbink et al. 2010; Wang et al. 2017). Data on phosphorus deposition changes over time are scarce. An approximately fourfold increase in P inputs to the biosphere was estimated as a result of the mining of P compounds for fertilizers (Falkowski et al. 2000), and a 1.0- to 3.5-fold increase in P deposition was observed in a forest in 2010 compared to 1850 (Wang et al. 2017). The overlooked element is potassium, although it is a relatively abundant element in plant tissues and plays a crucial role in water use efficiency (Sardans and Peñuelas 2015). Anthropogenic atmospheric K deposition originates from agriculture and industrial activity, and in some areas, human activities can contribute a higher proportion of K deposition than natural processes (Sardans and Peñuelas 2015). Sodium, the other element of interest, is less important for plants but is necessary for heterotrophs and can affect decomposer activity (Kaspari et al. 2014; Kaspari 2020). For instance, Yia et al. (2015) showed that Na limits detritivore decomposers and that high levels of Na inhibit soil microbes in inland subtropical forests. The Na sources in the environment include oceanic aerosols, rock weathering, and anthropogenic effects, e.g., the common use of road salt (Kaspari et al. 2014).

Recent studies have yielded numerous papers on the impact of nutrient addition on forest ecosystems, but the most commonly used nutrients were N, N + P (Braiss et al. 2015; Li et al. 2015a; Mayor et al. 2015; Kang et al. 2016; Ratliff and Fisk 2016; Schuster 2016) and N, P, and K (Fay et al. 2015; La Pierre and Smith 2016), and only a few studies have provided results for other nutrients (Sardans et al. 2012; Clay et al. 2015; Jia et al. 2015). A wide range of experiments have shown various litter respiration responses to fertilization in forest ecosystems, including increases (Brumme and Beese 1992; Gallardo and Schlesinger 1994; Cleveland and Townsend 2006), decreases (Lee and Jose 2003; Bowden et al. 2004; Burton et al. 2004) and no change (Lee and Jose 2003; Allison et al. 2008; Kang et al. 2016). These variable responses can be attributed to several factors, such as forest composition and age (Lee and Jose 2003), the rate and duration of nutrient addition (Bowden et al. 2004; Mo et al. 2008), and different levels of site fertility (Kang et al. 2016). For example, Allison and Vitousek (2004) suggested that in nutrient-poor systems, nutrient enrichment may preferentially stimulate C loss and thus accelerate litter decomposition.

The observed climatic changes (increase in air temperature) may result in a faster litter decomposition rate, as temperature (in addition to water and other environmental parameters) is one of the main factors affecting litter respiration (Reichstein et al. 2003; Klimek et al. 2020). Similarly, increased deposition of nutrients (Galloway et al. 2004, 2008; Gilbert 2009; Bobbink et al. 2010; Bennett et al. 2011; Wang et al. 2017), whose availability is a limiting factor

in terrestrial ecosystems, may speed litter decomposition because additional input may stimulate microbial activity. Increased temperature and deposition of nutrients may act simultaneously in changing world, which creates the necessity to explore the response of respiration to fertilization in conjunction to the rise in temperature. However, to the best of our knowledge, it has rarely been studied in temperate forests, especially for nutrients such as Na and K. Therefore, the present study aims to investigate how global changes (increased nutrient deposition and temperature) may affect litter respiration and what changes can be expected in the functioning of two forest types (deciduous and coniferous) with different fertility levels and decomposition rates (Laskowski et al. 2003). To address these questions, we measured respiration in deciduous (oak-hornbeam) and coniferous (mixed pine-oak) litter fertilized with N, P, Na and K (four treatments) and without fertilization (control) at ambient (14 °C) and increased temperatures (22 °C). We focused our study on heterotrophic respiration, which includes respiration by soil/litter microorganisms and fauna (Yan et al. 2010; Wang et al. 2017). We hypothesize that (i) nutrient (N, P, Na and K) addition will increase litter respiration (effect of changes in nutrient supply); (ii): an increase in temperature will cause a stronger positive effect of nutrient (N, P, Na and K) addition on respiration (effect of global warming + changes in nutrient supply); and (iii) a stronger positive effect of nutrient (N, P, Na and K) addition will be noted for less fertile coniferous pine-oak litter than for deciduous oak-hornbeam litter.

Materials and methods

Site description and collection of material

Litter samples were collected in the Niepołomice Forest, southern Poland (49°59′–50°07′ N, 20°13′–20°28′ E, 184–212 m a.s.l., (Grodziński et al. 1984)). The forest is divided into two parts: southern, which is formed by mixed pine-oak forest (*Pino-Quercetum*) on podzols and cambisols on sands with mor humus, and northern, dominated by deciduous forest, especially oak-hornbeam (*Tilio-Carpinetum*) on gleysols on clays with mull humus (Kapusta et al. 2003). The dominant tree species in the studied oak-hornbeam forest are oak (*Quercus robur*) and hornbeam (*Carpinus betulus*) with an admixture of lime trees (*Tilia cordata*). The mixed pine-oak forest is characterized by a dominant tree species: pine (*Pinus sylvestris*) with an admixture of oak (*Quercus robur*). The oak-hornbeam litter is characterized by a lower C content (26.5%), N content (1.5%), and C/N ratio (17.2) and a slightly higher pH than the mixed pine-oak litter (C 77%, N 1.9%, C/N ratio 21.1) (Kapusta et al. 2003). The area is characterized by a moderate transient climate.

The mean annual temperature and precipitation for this region are 8.6 °C and 670 mm, respectively, and the growing season lasts from April until September with a mean temperature of 14 °C (Sensuła and Pazdur 2013; Ziernicka-Wojtaszek et al. 2015).

Litter from the oak-hornbeam and mixed pine-oak forests was collected in March 2017 and October 2017, respectively. The collected material was sieved (10 mm mesh) to remove twigs and freshly fallen leaves and was transported to the laboratory (Laskowski et al. 2003).

Experimental design

The respiration measurements were conducted in mesocosms constructed from 12 L buckets filled with sand (1800 g) moistened with 200 g of distilled water (which is the maximal water capacity of the used sand) at the bottom and experimental litter above. The sand layer was separated from the litter with a white geotextile (17 g/m²). The mesocosm (bucket) was covered with geotextile to reduce litter surface desiccation and to allow air exchange. Before starting the incubation, the dry weight of the collected litter was measured by drying five subsamples in an oven at 105 °C for 12 h, and the water content of the litter was estimated. The dry mass of litter used in the experiment (both mixed pine-oak and oak-hornbeam) was 450 g. The water holding capacity (WHC) of the collected fresh litter was measured (Ilstedt et al. 2000), which allowed us to calculate how much distilled water should be sprayed on the litter surface in the mesocosms to achieve 70% WHC. This level of WHC is considered favorable for microorganism activity (Ilstedt et al. 2000).

Litter (from the oak-hornbeam forest and mixed pine-oak forest) was incubated in climatic chambers without light. In the mesocosms, respiration was measured at two temperatures, 14 °C (oak-hornbeam and mixed pine-oak) and 22 °C (oak-hornbeam). The former corresponds to the mean air temperature of the growing season in southern Poland (Ziernicka-Wojtaszek et al. 2015). The latter represents approximately the maximal increase in global temperature estimated by models, which could be 7 °C by the end of the century (Li et al. 2015b). Respiration measurements of the mixed pine-oak litter at 22 °C were not considered because of climatic chamber failure during the experiment.

To investigate the effects of N, P, K and Na addition on litter respiration, the litter surface (0.053 m²) was sprayed with 100 ml of solutions of ammonium nitrate, phosphorus oxide V, potassium chloride, sodium chloride and distilled water (as a control) once after establishing the mesocosms. The amounts of individual elements in 100 ml of solution were calculated to obtain the following doses: nitrogen—10 g N m⁻² (1.71% ammonium nitrate solution), phosphorus—3 g P m⁻² (0.32% phosphorus oxide V solution),

potassium—2.5 g K m⁻² (0.29% potassium chloride solution), and sodium—1.5 g Na m⁻² (0.23% sodium chloride solution), which exceeded two to three times the maximal bulk deposition measured in Poland and Europe (Walna and Kurzyca 2007; Fischer et al. 2010).

In the present experiment, heterotrophic respiration was measured, as the mesocosms contained only litter with the organisms living in it, and plants and roots were excluded. In the experiment, 75 mesocosms were used: 2 (litter type) × 5 (nutrients: control, N, P, K, Na) × 5 repetitions (at 14 °C) + 1 (litter type) × 5 (nutrients: control, N, P, K, Na) × 5 repetitions (at 22 °C).

Respiration measurements

After 6 days of incubation of the mesocosms in the climate chambers, respiration was measured using a carbon dioxide probe GMP343 (Vaisala, Helsinki, Finland). The mesocosm (bucket) was closed with a cover with the hole in the center where the probe was inserted. Every measurement lasted 120 s, during which the amount of CO₂ evolved from the litter was measured. Measurements were taken once a week (every 6–8 days) for 4 weeks in each type of forest litter. (There was a lack of respiration measurements on the sixth day of the experiment for oak-hornbeam litter at increased temperature.) To maintain constant litter moisture, the water loss from the mesocosms was supplemented after respiration measurements by spraying the surface of the litter with distilled water.

Litter properties: pH and organic matter content

To investigate whether nutrient addition affects litter properties, at the end of the whole experiment, 45 samples of litter were collected (15 for each treatment: 5 nutrient treatments × 3 repetitions). The pH of the litter was determined in distilled water and a solution of potassium chloride using a calibrated pH meter (ELMETRON, Zabrze, Poland). The organic matter content in the litter was measured using the LOI (loss-on-ignition) method (De Vos et al. 2005). The litter samples were dried at 105 °C and then burned in an oven at 550 °C for 8 h.

Data analysis and statistics

The effects of temperature on litter respiration are described by Q_{10} , which was calculated according to Eq. (1) (Balsler and Wixon 2009):

$$Q_{10} = \left(\frac{R_2}{R_1} \right)^{10/(T_2 - T_1)} \quad (1)$$

where R_1 represents the respiration at lower temperature; R_2 represents the respiration at higher temperature; T_1 is the value of lower temperature; and T_2 is the value of higher temperature.

The effects of nutrient additions on microbial respiration were estimated using the ln-transformed response ratio (Zhou et al. 2017a). The response ratio (RR) allowed comparison between the temperatures and types of litter, as the collection and respiration measurements of oak-hornbeam and mixed pine-oak litter were carried out at different times. RR is defined as $\ln(X_t/X_c)$, where \ln is the natural logarithm, X_t is the respiration of the nutrient treatment, and X_c is the respiration of the control. An RR higher than 0 shows an increase in microbial respiration due to nutrient addition, and a value less than 0 shows a decrease in microbial respiration. To determine the significance of nutrient addition, 95% confidence intervals were calculated. When the 95% confidence intervals overlap with 0, the effects of nutrient addition are not significant (Zhou et al. 2017a). RR analyses were performed using Microsoft Excel (Microsoft, Redmond, WA, USA).

The cumulative emissions of CO_2 from each mesocosm for the entire duration of the experiment were calculated by multiplying the average emissions by the number of hours between two consecutive sampling dates and summing the results (Chadwick 2005; Moral et al. 2012; Shah et al. 2016). The percentage change in CO_2 release from the litter as a result of increased temperature for each nutrient treatment was calculated with the following equation:

$$\%C_{\text{CO}_2} = \frac{CE_2 - CE_1}{CE_1} \times 100\% \quad (2)$$

where CE_1 is the cumulative emission at lower temperature and CE_2 is the cumulative emission at higher temperature.

The statistical analysis was performed using R 4.0.3 software (R Core Team 2020) with the lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2017), car (Fox and Weisberg 2019) and rstatix (Kassambara 2021) packages. To test differences in litter respiration between different nutrient treatments and between temperatures, a set of general linear mixed models (GLMMs) was used. In the GLMM for mixed pine-oak litter, the mesocosm was a random effect, and nutrient treatment was a fixed effect. The model also included the day of measurement (we measured respiration 5 times) as a continuous variable. The GLMM for oak-hornbeam litter additionally included the temperature as a fixed effect and the nutrient treatment \times temperature interaction. To test the differences between treatments in litter pH value, organic matter content and cumulative CO_2 emission, a set of general linear models (GLMs) was used. In the GLMs, nutrient treatment and temperature (in the case of oak-hornbeam litter) were fixed effects. The GLM for cumulative CO_2 emissions

additionally included the nutrient treatment \times temperature interaction. Graphics were prepared in Microsoft Office Excel (Microsoft, Redmond, WA, USA) and R with ggplot2 (Wickham 2016) and emmeans (Lenth 2020) packages and edited using InkScape 0.92.4 (Harrington et al. 2004–2005).

The missing respiration data for oak-hornbeam litter were extrapolated using prediction of the GLMM and used in calculation of means, Q_{10} values and response ratio.

Results

Effect of temperature on litter respiration

Respiration decreased with time in both the oak-hornbeam ($\chi^2 = 200.18$, $p < 0.0001$, Fig. 1a) and mixed pine-oak litter ($\chi^2 = 6.94$, $p = 0.008$, Fig. 1b). For the oak-hornbeam litter, the GLMM showed that respiration was higher at 22 °C than at 14 °C ($\chi^2 = 11.56$, $p < 0.001$, Table 1; note that this table shows the means calculated from raw data and from the predictions of GLMM for oak-hornbeam in the case of missing data). This result is also reflected in the amount of CO_2 released from the litter during the 28 days of measurements (cumulative emission) ($F = 82.86$, $p < 0.001$, Fig. 2a), which was approximately 34% higher for the control and N treatments, 85% higher for P, and 57% higher for Na and K at 22 °C than at 14 °C. The mean temperature coefficient (Q_{10}) in the oak-hornbeam forest ranged between 1.49 and 2.14 (Table 1).

Effect of nutrient addition on litter respiration

GLMMs showed that nutrient addition had no effect on respiration either in oak-hornbeam litter ($\chi^2 = 2.01$, $p = 0.734$) or in mixed pine-oak litter ($\chi^2 = 4.48$, $p = 0.345$). Similarly, the GLMs showed no effect of nutrient addition on cumulative CO_2 emissions ($F = 1.54$, $p = 0.211$ for oak-hornbeam litter; $F = 1.47$, $p = 0.248$ for mixed pine-oak litter). Statistical models for oak-hornbeam litter did not reveal a significant interaction between nutrient treatment and temperature for either respiration ($\chi^2 = 8.13$, $p = 0.087$) or cumulative CO_2 emissions ($F = 2.14$, $p = 0.095$). However, based on the RR results, for oak-hornbeam litter incubated at 14 °C, the addition of N, P, and K decreased respiration, and the addition of Na had no effect (Fig. 3a). At 22 °C, N addition decreased respiration, and P and Na addition increased respiration with no effect of K fertilization (Fig. 3b). The only effect detected for mixed pine-oak litter incubated at 14 °C was decreased respiration due to Na addition (Fig. 3c). For oak-hornbeam litter at 14 °C, the highest amounts of CO_2 were released from the control and Na treatments, and the lowest amounts were released from the P and K treatments (Fig. 2a). In contrast, at 22 °C, the highest cumulative

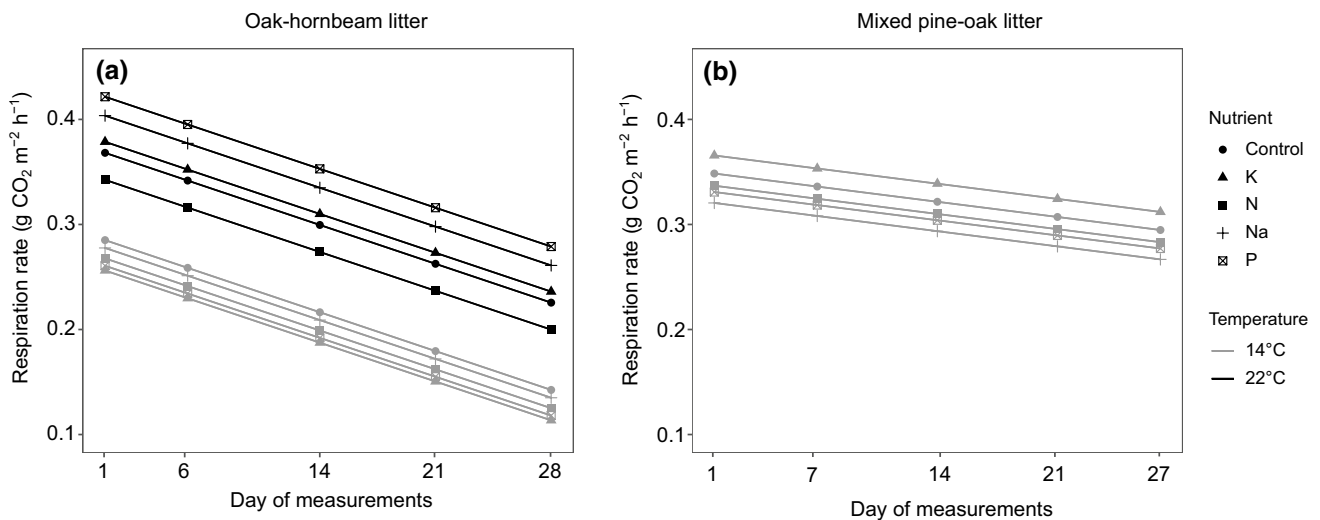


Fig. 1 Respiration in **a** oak-hornbeam litter at ambient and higher temperatures and **b** mixed pine-oak litter at ambient temperature in the control, nitrogen (N), phosphorus (P), sodium (Na), and potassium (K) treatments estimated by GLMMs. Note that the litter of each

forest type was collected at different times. In general, respiration was higher with increased temperature in oak-hornbeam litter and decreased with time in both litter types. The graphs show means estimated from GLMMs

Table 1 Mean (\pm SE) litter respiration ($\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) and Q_{10} values

Nutrient	Oak-hornbeam litter		Q_{10}	Mixed pine-oak litter	
	14 °C	22 °C		14 °C	22 °C
Control	0.216 \pm 0.015	0.300 \pm 0.019	1.50	0.321 \pm 0.018	–
N	0.199 \pm 0.014	0.274 \pm 0.019	1.49	0.310 \pm 0.014	–
P	0.192 \pm 0.011	0.353 \pm 0.020	2.14	0.304 \pm 0.018	–
Na	0.209 \pm 0.013	0.335 \pm 0.017	1.80	0.294 \pm 0.015	–
K	0.187 \pm 0.010	0.310 \pm 0.013	1.87	0.339 \pm 0.018	–

The values were calculated for the entire duration of the experiment from raw and extrapolated data (in the case of missing measurements) predicted from the GLMM for oak-hornbeam. Note that the litter of each forest type was collected at different times

emission was observed in the P-treated litter, and the lowest was observed for the N-treated litter (Fig. 2a). For mixed pine-oak litter, the highest cumulative emission was noted for the K treatment and the lowest for the Na treatment (Fig. 2b).

Litter properties at the end of the experiment

The mean (\pm SE) organic matter content at the end of the experiment was 64.4 \pm 1.6% in the oak-hornbeam litter and 81.5 \pm 0.8% in the mixed pine-oak litter. No differences were found in the organic matter content between temperatures ($F=3.82, p=0.062$) or between nutrients ($F=1.03, p=0.410$) in oak-hornbeam litter. In mixed pine-oak litter, nutrient treatments differed in organic matter content

($F=4.23, p=0.029$), with N, Na and K treatments having approximately 6% higher organic matter content than the control.

In the oak-hornbeam litter, the pH values were higher at 22 °C than at 14 °C ($F=44.61, p<0.001$ for pH(H₂O) and $F=103.37, p<0.001$ for pH(KCl)). Moreover, in general, nutrients caused a decrease in pH ($F=5.83, p=0.002$ for pH(H₂O) and $F=4.95, p=0.005$ for pH(KCl), Table 2; note that this table shows the means calculated from raw data), with significant results between all nutrient treatments (N, P, Na, K) and the control for the pH measured in H₂O and between all nutrients, except N and the control for the pH measured in KCl. For the mixed pine-oak litter, all nutrient treatments were characterized by a similar pH [$F=0.45, p=0.771$ for pH(H₂O) and $F=2.91, p=0.078$ for pH(KCl)].

Discussion

Our results showed that a temperature increase of 8 °C (over the control at 14 °C) increased respiration and thus the release of CO₂ from decomposing oak-hornbeam litter, which is in agreement with common knowledge. The calculated Q_{10} values between 1.49 and 2.14 are close to the values presented by Guo et al. (2017) and Chen et al. (2019) and lower than those reported by Sun et al. (2014). The lower Q_{10} values noted for the control and N-fertilized litter and higher values for the treatments with P, Na, and K suggest a faster decomposition rate of forest litter fertilized with P, Na, and K under global warming than under current climatic conditions.

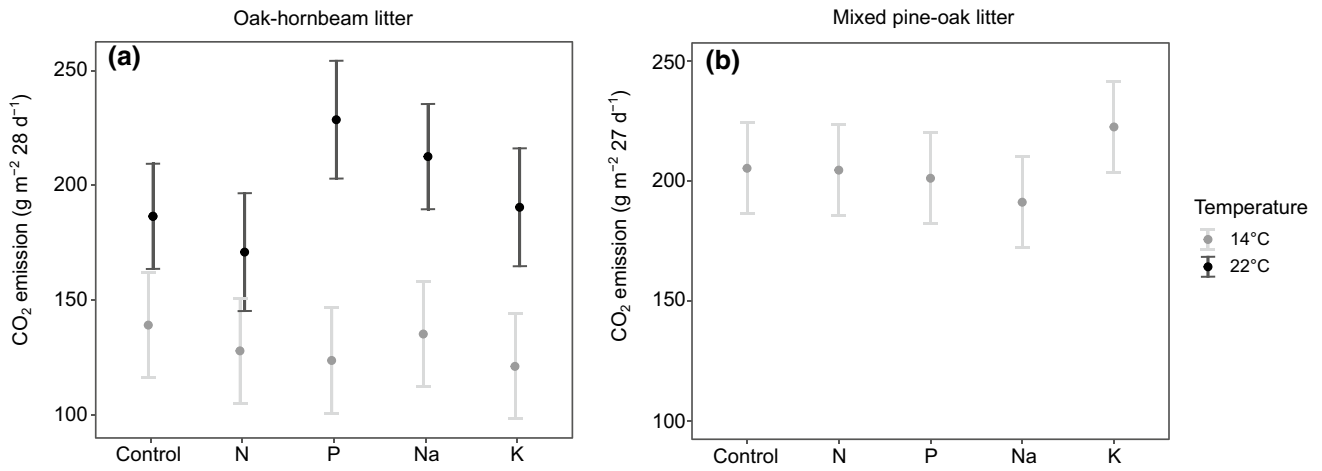


Fig. 2 Cumulative CO₂ emissions released during the experiment from **a** oak-hornbeam litter at ambient and increased temperatures and **b** from mixed pine-oak litter at ambient temperature in the control, nitrogen (N), phosphorus (P), sodium (Na), and potassium (K)

treatments. Note that the litter of each forest type was collected at different times. The graphs show means with 95% confidence intervals estimated from GLMs. Cumulative CO₂ emissions were higher at increased temperature for oak-hornbeam litter

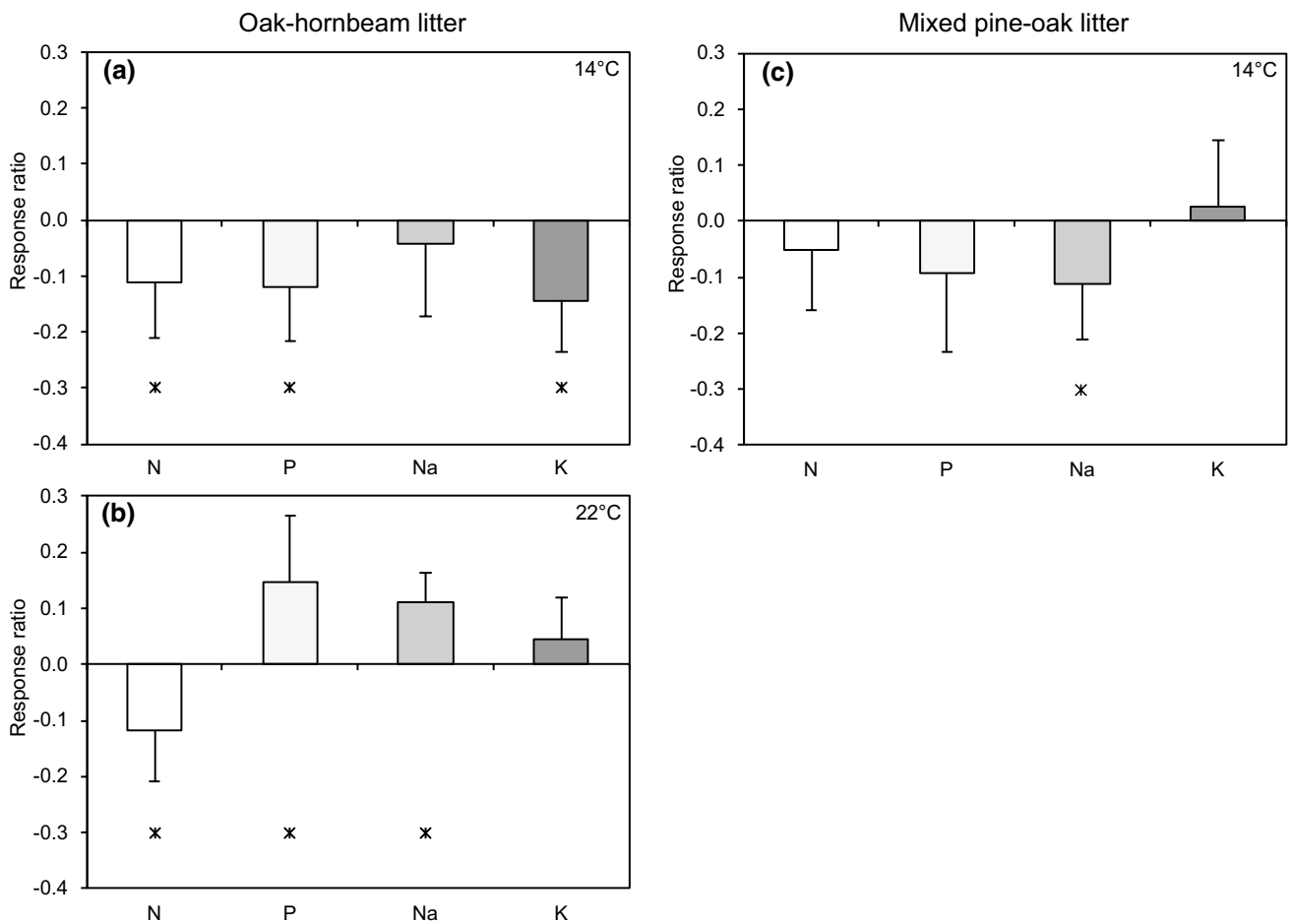


Fig. 3 Response ratios (mean ± CI) of respiration in oak-hornbeam litter **a** at ambient and **b** increased temperatures and **c** in mixed pine-oak litter at ambient temperature calculated for the nitrogen (N),

phosphorus (P), sodium (Na), and potassium (K) treatments. “*” below a marker denotes a significant effect of nutrient addition on respiration in relation to the control ($\alpha=0.05$)

Table 2 Mean pH values (\pm SE) of two litter types, oak-hornbeam and mixed pine-oak, measured at the end of the experiment

Treatment	pH	Oak-hornbeam litter		Mixed pine-oak litter	
		14 °C	22 °C	14 °C	22 °C
Control	pH(H ₂ O)	4.85 \pm 0.08	5.14 \pm 0.12	4.72 \pm 0.12	–
	pH(KCl)	4.36 \pm 0.09	4.74 \pm 0.03	3.78 \pm 0.05	–
N	pH(H ₂ O)	4.65 \pm 0.03	4.97 \pm 0.01	4.76 \pm 0.05	–
	pH(KCl)	4.25 \pm 0.05	4.72 \pm 0.09	3.98 \pm 0.03	–
P	pH(H ₂ O)	4.65 \pm 0.04	4.89 \pm 0.04	4.69 \pm 0.05	–
	pH(KCl)	3.99 \pm 0.08	4.61 \pm 0.07	3.82 \pm 0.10	–
Na	pH(H ₂ O)	4.65 \pm 0.06	4.82 \pm 0.08	4.66 \pm 0.08	–
	pH(KCl)	4.17 \pm 0.05	4.57 \pm 0.02	3.76 \pm 0.01	–
K	pH(H ₂ O)	4.71 \pm 0.03	4.91 \pm 0.05	4.78 \pm 0.02	–
	pH(KCl)	4.17 \pm 0.03	4.48 \pm 0.09	3.81 \pm 0.03	–

The values calculated from raw data. Note that the litter of each forest type was collected at different times

In our experiment, for both litter types, oak-hornbeam and mixed pine-oak, respiration did not differ between nutrient treatments (control, N, P, K and Na). However, when we related the respiration of the litter fertilized with nutrients to the control, as shown by the RR index, we observed that nutrient addition influenced litter respiration. This index also allowed us to compare responses to nutrient addition between the oak-hornbeam and mixed pine-oak litter despite different litter collection times, although different seasonal changes in litter characteristics could have affected respiration. Thus, in the next part of the discussion, we will address the results obtained from this measure.

Contrary to our expectation (hypothesis i), we did not find positive effects of nutrient addition on litter respiration at ambient temperature (at 14 °C) in either oak-hornbeam or mixed pine-oak litter. Moreover, we expected a stronger positive effect of nutrient addition in the mixed pine-oak forest with mor/moder-type humus (hypothesis iii) because of the high content of slowly decomposing pine needles and a higher C:N ratio than in oak-hornbeam litter (Kapusta et al. 2003). Respiration in the oak-hornbeam litter was negatively affected by N, P, and K addition, with no effect of Na addition. A reverse pattern was observed in the mixed pine-oak litter, in which only Na decreased litter respiration, and the addition of other nutrients had no effect. Therefore, our results only partially agree with hypothesis iii, as for mixed pine-oak litter, a less limiting effect of nutrient addition on respiration was observed. The difference in response between oak-hornbeam and mixed pine-oak litter may result from the differences in the microbial (fungal) community composition. The decomposition of more fertile deciduous litter is driven by a bacterial-based energy channel, whereas that of less fertile coniferous litter is driven by a

fungal-based energy channel (Wardle et al. 2004), which may affect the response to nutrient addition. For example, nitrogen supply can reduce fungal-specific PLFAs and lower fungi-to-bacteria ratios (Forstner et al. 2019), as well as reduce lignin-degrading enzyme activity and relative abundances of Gram-negative and Gram-positive bacteria (Hobbie et al. 2012). Therefore, alterations in the microbial community may change enzyme production and decomposer efficiency, reducing respiration (Moorhead and Sinsabaugh 2006).

At the higher temperature (22 °C), a negative effect of nutrient addition was found only for N, whereas the addition of other nutrients caused a positive effect (significant for P and Na), which is in agreement with our hypothesis i. The additive effect of nutrient application on litter respiration at higher temperature was shown as the amount of CO₂ released over 28 days. Whereas respiration in the control and N increased by approximately 34% over those at ambient temperature, in the case of other elements, the values were much higher: 57% (K and Na) or even 85% (P). The latter results agree with our expectations that at increased temperature, there will be a stronger positive effect of nutrient addition (hypothesis ii).

The most commonly studied elements are nitrogen and phosphorus. In our research, the impact of these two elements on the respiration of the oak-hornbeam litter differed. Nitrogen addition decreased respiration at both temperatures (ambient and higher), and this result agrees with observations in other studies. Meta-analyses of the impact of N fertilization on litter respiration showed a 15% (Janssens et al. 2010) and 10% decrease in CO₂ release (Zhou et al. 2017b), whereas an increase in litter respiration was observed in only 6 of 36 experiments (Janssens et al. 2010). Nitrogen fertilization decreases microbial biomass and diversity (especially for fungi) as well as the ratio of fungi to bacteria (Jian et al. 2016; Yue et al. 2016; Zhou et al. 2017b; Forstner et al. 2019), which in turn drives reductions in soil respiration and decomposition (Riggs and Hobbie 2016). Carbon stabilization into more slowly decomposing fractions may occur because of N inhibition of oxidative enzyme activity (Hobbie et al. 2012). For instance, nitrogen addition stimulates hydrolase activities but inhibits the activities of phenol oxidase and peroxidase (Zhou et al. 2017b). Nitrogen addition lowers the pH of deciduous litter, which can affect microbial activity and therefore C storage (Lu et al. 2011). Note that this agrees with our results showing that N addition decreased pH and respiration in oak-hornbeam litter.

While N lowered respiration at both temperatures, P addition lowered respiration at ambient temperature but accelerated respiration at increased temperature. The former observation is contrary to our expectation but is consistent with the data of Thirukkumaran and Parkinson (2000), who observed a negative effect of P addition on the microbial

biomass and respiration rate of pine litter, and DeForest (2019), who demonstrated that chronic P addition inhibited litter decomposition in *Quercus* spp. temperate forest. DeForest (2019) suggests that the “microbial mining” hypothesis may explain the suppressive effect of P on forest litter respiration. This hypothesis states that if any nutrient is the most limiting factor, then increases in the availability of that nutrient will inhibit decay because of decreased “mining” of litter by microbes (DeForest 2019). In other words, if P is a limiting factor, microbes decompose more litter to meet the demand for this element, whereas supplying litter with P results in lower “mining” for this element and therefore a slower decomposition rate. A reversed pattern (consistent with hypothesis i) was observed at increased temperature, in which P addition accelerated the respiration rate. This could result from an increased metabolism of microorganisms and therefore a higher demand for both energy (C) and P. Supply with P increased respiration more than increase caused by the effect of temperature. Consistent with our results, the data from tropical forests, where P in soil is scarce, showed that the addition of this element at 33 °C resulted in higher microbial activity (Hui et al. 2020).

Elements that are less studied or neglected in the literature related to nutrient cycles are K and Na (Kaspari et al. 2008; Sardans and Peñuelas 2015; Kaspari 2020). Our results showed a negative response of respiration to K addition in the oak-hornbeam litter at ambient temperature but no effects at higher temperature. Despite the fact that potassium plays an important role in fungal osmoregulation (Camenzind et al. 2019), evidence has shown that fungal abundance is not affected by K addition (Camenzind et al. 2018). Moreover, Moro et al., (2014) demonstrated that microorganisms are not limited by K, even in soils with low K availability.

Sodium addition in our research had no effect on respiration in oak-hornbeam litter at ambient temperature but increased respiration at higher temperature. Literature data from tropical and subtropical regions showed that sodium addition did not affect fungal growth or respiration (Kaspari et al. 2014; Camenzind et al. 2018). However, respiration may differ between various fungal strains (Camenzind et al. 2018). Data on microbial decomposers demonstrated a negative impact of high doses of Na on microbial activity (Jia et al. 2015; Ji et al. 2020) but a parallel increase in microbial biomass and activity at low doses (Jia et al. 2015).

The input of nutrients into the environment changes not only the concentration of a given element in the litter but also the stoichiometric ratio between this and other elements and therefore may affect microbial activity and composition (Sterner and Elser 2002; Sinsabaugh et al. 2008, 2009). For example, a change in the input of N or P into the environment results in changes in the stoichiometric ratio between both elements. A low N:P ratio promotes bacteria, and a high N:P ratio promotes fungi, which may impact

nutrient dynamics and litter decomposition (Güsewell and Gessner 2009). The addition of elements in our experiment could alter the natural stoichiometry in the studied litter. Moreover, a change in temperature causes a change in the metabolic rate of microbes and thus also their demands for elements, which can become limiting because of disturbed ratios between elements. In addition to the differences in the microbial community caused by different thermal optima of organisms and forest types (Allison et al. 2010; Schindlbacher et al. 2011), this could explain the different responses of respiration to the addition of elements at each temperature.

Conclusions

Overall, our research showed that both an increase in temperature and nutrient deposition affected litter respiration and therefore possibly the carbon sink. Our results suggest that an increase in nutrient deposition under present climatic conditions in oak-hornbeam forests in the temperate climatic zone may increase the carbon sink in the forest floor. In contrast, in mixed pine-oak forests, the additional deposition of N, P, and K fertilizers should not affect carbon deposits in litter under the present climatic conditions, and the addition of Na fertilizer may increase the carbon sink in the forest floor. Under global warming, an increase in N deposition in oak-hornbeam forests in temperate climatic zones may increase the carbon sink in the forest floor, whereas P and Na fertilization may strengthen the amount of CO₂ released from litter. However, as we measured only heterotrophic respiration, these interpretations should be taken with caution because an increase in plant production due to the influx of nutrients (N, P, K) results in an increased inflow of dead organic matter to the forest floor (Wang et al. 2017). Increased production of litter with simultaneous inhibition of its decomposition can increase carbon deposits in the ecosystem. Together, our results suggest that forecasting the impacts of nutrient deposition on ecosystem functioning should consider temperature rise as a factor altering ecosystem responses to fertilization in future research.

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Authors' contributions AR contributed to the study conception and design. Material preparation, data collection and analysis were performed by ES. The first draft of the manuscript was written by AR and ES, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Competing interests The authors declare no competing interests.

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