




















RESEARCH ARTICLE

Nitrogen increases early-stage and slows late-stage decomposition across diverse grasslands

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Abstract

1. To evaluate how increased anthropogenic nutrient inputs alter carbon cycling in grasslands, we conducted a litter decomposition study across 20 temperate grasslands on three continents within the Nutrient Network, a globally distributed nutrient enrichment experiment
2. We determined the effects of addition of experimental nitrogen (N), phosphorus (P) and potassium plus micronutrient (K_{μ}) on decomposition of a common tree leaf litter in a long-term study (maximum of 7 years; exact deployment period varied across sites). The use of higher order decomposition models allowed us to distinguish between the effects of nutrients on early- versus late-stage decomposition.
3. Across continents, the addition of N (but not other nutrients) accelerated early-stage decomposition and slowed late-stage decomposition, increasing the slowly decomposing fraction by 28% and the overall litter mean residence time by 58%.

Allison L. Gill and Sarah E. Hobbie should be considered joint first author.

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4. *Synthesis*. Using a novel, long-term cross-site experiment, we found widespread evidence that N enhances the early stages of above-ground plant litter decomposition across diverse and widespread temperate grassland sites but slows late-stage decomposition. These findings were corroborated by fitting the data to multiple decomposition models and have implications for N effects on soil organic matter formation. For example, following N enrichment, increased microbial processing of litter substrates early in decomposition could promote the production and transfer of low molecular weight compounds to soils and potentially enhance the stabilization of mineral-associated organic matter. By contrast, by slowing late-stage decomposition, N enrichment could promote particulate organic matter (POM) accumulation. Such hypotheses deserve further testing.

KEYWORDS

grasslands, litter decomposition, nitrogen, nitrogen deposition, Nutrient Network (NutNet), phosphorus

1 | INTRODUCTION

Human activities are altering element fluxes at a global scale. For example, agricultural and industrial activities have greatly increased global cycling of reactive nitrogen (N; Ackerman et al., 2019), increasing atmospheric N inputs relative to phosphorus (P), and leading to elevated N:P ratios in soils and plants (Peñuelas et al., 2013). Yet, we lack a general mechanistic understanding of how variation in nutrient inputs alters carbon (C) cycling, hampering the development of Earth System Models to accurately forecast global C dynamics in a changing world (Peñuelas et al., 2013). Such understanding is especially lacking for grasslands, which represent c. 30% of non-agricultural global land area and terrestrial net primary productivity (NPP; Chapin III et al., 2011) and store 20% of the world's soil C (FAOSTAT, 2009). The effects of N deposition on grassland C cycling will likely depend on the supplies of other nutrients, since NPP in grasslands is often co-limited by multiple nutrients, with N limitation more prevalent at higher latitudes (Cleland et al., 2019; Du et al., 2020; Fay et al., 2015). On the other hand, grassland surface soil C stocks are relatively insensitive to N and P addition, with strong but unexplained response variability across sites (Crowther et al., 2019; Keller et al., 2022), but increase with short-term addition of K with micronutrients (Crowther et al., 2019). This inconsistency between nutrient effects on plant biomass production (NPP) and soil C accumulation indicates a gap in understanding of nutrient effects on litter and soil organic matter (SOM) decomposition across diverse grasslands.

Past studies of nutrient effects on decomposition in grasslands have been limited in geographic scope or duration. In studies at individual or relatively few sites, N had varied effects (Aerts et al., 2003; Hobbie, 2008; Hou et al., 2021; Hunt et al., 1988; Liu et al., 2006; Liu et al., 2010) and P had neutral effects (Aerts et al., 2003) on decomposition. In a more widespread but short-term study of tea leaf

decomposition (90 days across 21 grasslands), N and P both weakly increased tea leaf decomposition rate and the tissue stabilization factor, a modelled representation of the biochemically transformed residues that persist at late stages of decomposition (Ochoa-Hueso et al., 2020). Meta-analyses combining experiments done at single or few sites to generate synthetic insights into nutrient effects on decomposition have uncovered important among-study patterns (Gill et al., 2021; Knorr et al., 2005; Zhang et al., 2018). However, strong inference from meta-analysis is limited because it combines data from studies using different methods (e.g. substrate types, nutrient treatment levels). Most available studies are of short duration and often lack information on key covariates (climate, soil chemistry, plant productivity). For example, the median study duration in a recent meta-analysis of 334 paired decomposition sequences (from control and associated N-fertilized plots) was 2 years (Gill et al., 2021). In addition, past meta-analyses focused solely on N (with supply rates varying widely among studies); yet nutrients other than N might be expected to influence decomposition or interact with N treatments. While individual studies and meta-analysis provide important insights, generating a general understanding of nutrient effects on grassland litter decomposition requires long-term, geographically distributed experiments that use standard methods and thus overcome the limitations to inference imposed by the diverse methodologies (e.g. substrate, duration, nutrient enrichment rates) inherent in meta-analyses (Borer et al., 2014).

Long-term studies are needed specifically to determine if nutrients have different effects early versus later in the decay process. In forests, N often reduces litter decomposition in its later stages (Berg & Matzner, 1997; Carreiro et al., 2000; Fog, 1988; Gill et al., 2021; Hobbie et al., 2012). Such N inhibition has been attributed to the inhibition of oxidative enzyme activity (Carreiro et al., 2000; Chen et al., 2018; Hobbie et al., 2012; Jian et al., 2016; Waldrop et al., 2004), which may be less strong in grasslands than in forests,

because of their distinct fungal communities with reduced oxidative enzyme capabilities (Sinsabaugh, 2010). On the other hand, if N inhibition of late-stage decomposition results from other mechanisms, such as decreased pH and microbial biomass (Treseder, 2008), or increased decomposer necromass accumulation (Gill et al., 2021), such N inhibition might be expected in grasslands as well as in forests.

Cross-site experiments are needed to determine whether the effects of nutrients on litter decomposition are consistent across geographically diverse sites, or depend on site characteristics such as climate and edaphic factors. Regional analyses of litter decomposition in grasslands found inconsistent relationships with precipitation or temperature (Bontti et al., 2009; O'Halloran et al., 2013), although studies at larger spatial scales found evidence for both (e.g. Tuomi et al., 2009). Nutrient effects on decomposition might be expected to be more pronounced in high rainfall areas where water does not constrain microbial activity, as has been shown for net primary production (Burke et al., 1997; Harpole et al., 2007; La Pierre et al., 2016; Ren et al., 2017), or to depend on ambient soil nutrient supply (Hobbie, 2005).

Here we decomposed a standard oak leaf litter (to avoid any home-field advantage effects, Palozzi & Lindo, 2018) for up to 7 years in a replicated nutrient addition experiment in grasslands across multiple continents that ranged widely in climate and edaphic conditions, to (a) determine the effects of N and P enrichment on different stages of litter decomposition, and (b) address whether and how nutrient limitation of leaf litter decomposition varies geographically. The long duration of the experiment allowed us to determine which empirical decomposition model structures (single, double and asymptotic exponential or Weibull models) best described litter decomposition dynamics, and to specifically determine whether the effects of nutrient addition differed between the early and late stages of decomposition as shown previously for N, primarily in forests (Gill et al., 2021). Unlike in forests, we did not expect N to inhibit the later stages of decomposition in these grasslands because of low oxidative enzyme activity. In addition, we expected that nutrient effects on decomposition would depend on soil resource supply, such that N limitation of decomposition would be common across temperate and alpine regions with young, P-rich soils, but not in areas with high ambient N deposition or N-rich soils. On the other hand, we expected that P limitation would be restricted to sites with highly weathered soils that are low in available P (e.g. Australia) or to areas with high N deposition. Furthermore, we hypothesized that nutrient limitation of decomposition would be strongest in regions with high precipitation or where moisture supply is relatively constant across the year.

2 | MATERIALS AND METHODS

2.1 | Decomposition experiment

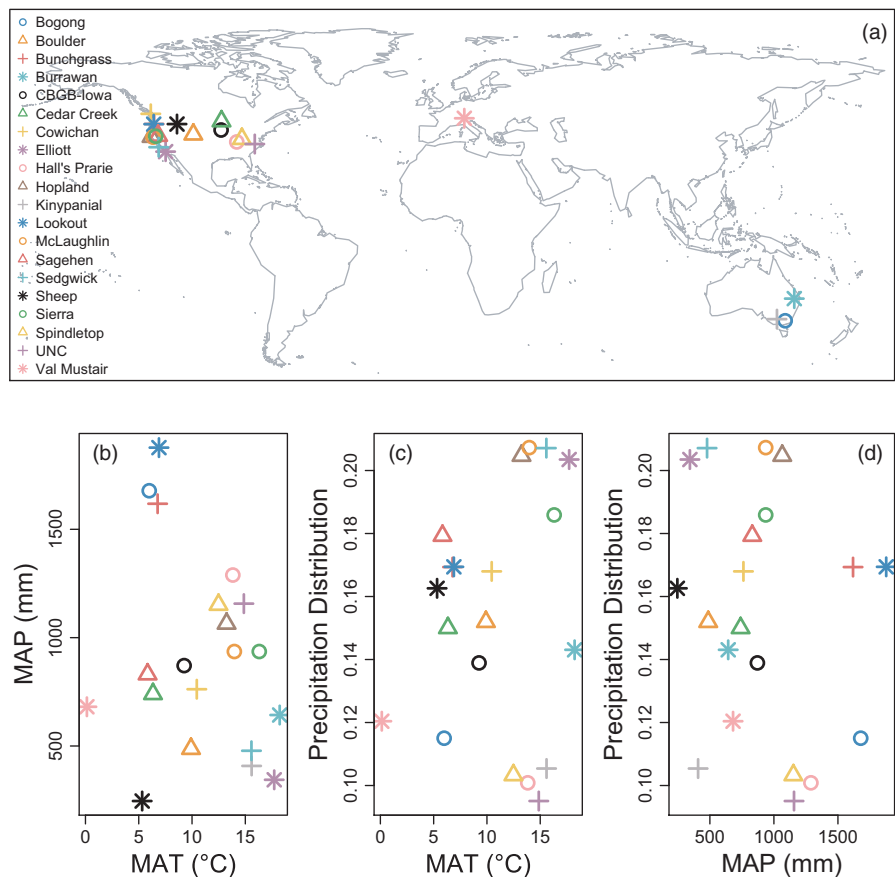
In the Nutrient Network (NutNet) study, experimental plots are fertilized annually in a full-factorial manner as follows: N is added as slow-release urea ($10 \text{ g N m}^{-2} \text{ year}^{-1}$), P as triple superphosphate

($10 \text{ g P m}^{-2} \text{ year}^{-1}$) and K as potassium sulphate ($10 \text{ g K m}^{-2} \text{ year}^{-1}$) with micronutrients (Ca, Mg, S, B, Cu, Fe, Mn, Mo and Zn; single addition at treatment initiation; K_μ). Twenty sites in the United States, Canada, Australia and Europe participated in the present decomposition study, which began <1–2 years following the initiation of fertilization treatments (Figure 1; Table S1). Sites ranged 17-fold in atmospheric N deposition ($1.1\text{--}18.9 \text{ kg N ha}^{-1} \text{ year}^{-1}$), 7-fold in mean annual precipitation (331–1898 mm/year) and 60-fold in mean annual temperature ($0.3\text{--}18.4^\circ\text{C}$). Precipitation and temperature were unrelated across sites, allowing us to explore their independent effects. Treatments were applied to $5 \text{ m} \times 5 \text{ m}$ plots in a randomized block design; for this study, three blocks were used at all sites except Sierra Foothill, where five blocks were used. All necessary permits and permissions were obtained prior to initiating the NutNet experiment.

We selected leaf litter of *Quercus ellipsoidalis* (Table S2) as a common substrate for a long-term decomposition study because its N concentration (0.927%) fell within the range of N concentrations of grassland leaf litter (Wedin & Pastor, 1993), it was readily abundant and, since it does not occur in any of the plots, will not exhibit home-field advantage effects that could confound among-site environmental effects. Additional comparisons of *Quercus* and grassland litter chemistry and decomposition are included in the Supporting Information. Freshly fallen leaf litter of *Q. ellipsoidalis* was collected from several adjacent individual trees in October 2008 at the Cedar Creek Ecosystem Science Reserve, Minnesota, USA. Litter bags ($20 \text{ cm} \times 20 \text{ cm}$, 1-mm mesh fibreglass window screen) were filled with 10 g (dry weight) of sterilized leaf litter autoclaved at 121°C for 15 min. Sufficient bags were constructed to allow annual harvests over 7 years and sent to individual site researchers in September 2009. Bags were strung together in groups of seven and were pinned to the ground (1 string per plot) using landscape staples. Subsamples of initial litter were analysed for (1) C fractions using an ANKOM Fiber Analyzer (Ankom Technology; cell solubles, hemicellulose + bound protein, cellulose and lignin + other recalcitrants; $n = 5$); (2) initial C and N concentrations on a Costech ECS4010 element analyser (Costech Analytical; $n = 5$); and (3) initial concentrations of phosphorus (P), magnesium (Mg), calcium (Ca), manganese (Mn) and potassium (K) by inductively coupled argon plasma emission spectrometry (ICP, Applied Research Laboratory 3560) following digestion in 10% HCl (Munter & Grande, 1981) at the University of Minnesota's Research Analytical Laboratory ($n = 1$; Table S2).

Sites varied in accessibility and the frequency and timing of research visits, thus the date of initial deployment ranged from December 2009 to October 2010. Litter bags were sequentially harvested at approximately annual intervals, and litter was cleaned of any material other than colonizing microbes, dried (65°C to constant mass), weighed and sent to the University of Minnesota for further processing. Harvested litter was ground, milled and analysed for total C and N as above, and a subsample was ashed (600°C for 6 hr) to determine ash-free dry mass (AFDM). Proportion initial mass remaining was converted to proportion initial C remaining for further analyses to account for soil contamination, as soil has low C concentration

FIGURE 1 Distribution and meteorological conditions of 20 Nutrient Network sites included in this study. Sites were located in North America, Europe and Australia. (a) Map of site locations; (b) relationship between site MAT and MAP; (c) relationship between site MAT and precipitation distribution; (d) relationship between site MAP and precipitation distribution. MAT, mean annual temperature (°C); MAP, mean annual precipitation (mm); precipitation distribution (precipitation in wettest month/MAP)



relative to litter. This method is similar to correcting for soil contamination using ash-free dry mass, since they are highly correlated, as confirmed here (across all samples: $\%C = 0.75 + 0.50 \times \%AFDM$, $R^2 = 0.77$, $p < 0.0001$). We handled missing %C data and outlier proportion C remaining values as described in the Supporting Information.

Not all participating sites were able to sample litter bags for the full duration of the study due to investigator turnover, natural disasters (floods, herbivory, fires) and unnatural disasters (e.g. loss of sites to development). In some cases, investigators were unable to visit sites annually. Therefore, the total number of sites included in the final dataset varied from year to year (Table S1). Herein we present data from 20 sites that contributed data from at least three, and up to seven, harvests (Figure S1).

2.2 | Temperature, precipitation, solar radiation and soil physical and chemical properties

To understand variation in decomposition across and within sites as well as interactions between nutrient addition treatments and potential covariates, we considered modelled site-level predictors, including mean annual temperature (MAT), mean annual precipitation (MAP), potential evapotranspiration (PET), aridity index (AI), MAP/PET; Hijmans et al., 2005), precipitation distribution (Precip. Dist., precipitation in wettest month/MAP; unitless), atmospheric

N deposition (Ackerman et al., 2019) and annual top of atmosphere insolation (NASA GISS <https://data.giss.nasa.gov/modelE/ar5plots/srlocat.html>; Hansen et al., 2005). We also considered the following plot-level data: pre-treatment soil %C and %N (determined as above, Crowther et al., 2019); Mehlich 3-extractable P, Mn and base cations (K, Ca, Mg, Na; Waypoint Analytical, Mehlich, 1984); and pH (1:1 soil:water suspension, Waypoint Analytical). Above-ground plant biomass was measured by clipping, drying and weighing all live and dead plant biomass from two 0.1 × 1 m strips/plot at peak biomass annually (2010–2016).

2.3 | Overview of analytical approach

In our analytical approach, we (1) assessed fit of proportion C mass remaining to four different decomposition models (single, double and asymptotic exponential; Weibull) that differ in how they represent decomposing litter (e.g. as a single pool decomposing at one rate vs. as multiple pools decomposing at different rates); (2) fit litter N dynamics to a quadratic function to determine the extent and timing of litter N immobilization during decomposition; (c) analysed the effects of factorial $N \times P \times K_{\mu}$ treatments on parameters obtained from the model fitting described in (1) and (2), using treatment-only mixed-effects models, which included N, P and K_{μ} treatments as fixed effects and site and experimental block as nested random effects; (4) analysed for potential interactive effects of N, P and K_{μ} fertilization and edaphic

and environmental site characteristics on decomposition model parameters, using treatment-covariate models, which included single covariates in mixed-effects models; and (5) used model selection to identify edaphic and environmental variables that most strongly explained cross-site variation in decomposition model parameters.

2.4 | Decomposition model fitting

Having up to seven harvests over 7 years allowed us to fit litter proportion C remaining over time to four alternative decomposition models that vary in their mathematical representation of the biophysical process of litter decomposition and chemical composition of the litter (Cornwell & Weedon, 2014; Olson, 1963; Wieder & Lang, 1982). This allowed us to explore whether nutrients had different effects in the early versus later stages of decomposition. The *single exponential decay model* describes litter as a single pool with a constant decay rate, k_s , and assumes a constant fraction of litter mass is decomposed per unit time, t . The proportion of initial litter C remaining, X , is a function of k_s and t :

$$X = e^{-k_s t}, \quad (1)$$

The *double* and *asymptotic exponential models* divide litter into two pools that decompose at different rates. In the double exponential model, a labile fraction, L , decomposes at rate k_1 , while the remaining slow fraction $(1 - L)$ decomposes at rate k_2 :

$$X = L e^{-k_1 t} + (1 - L) e^{-k_2 t}. \quad (2)$$

In the asymptotic model, A describes the slow fraction, which decomposes at rate zero, while the remaining labile fraction $(1 - A)$ decomposes at rate k_a :

$$X = A + (1 - A) e^{-k_a t}. \quad (3)$$

Although the decomposition rate of A would not realistically be zero, A approximates a fraction of litter for which the decomposition rate is negligible (Berg, 2000).

These first three models represent litter as having one or two discrete 'pools', each with a constant decomposition rate. A fourth model, the *Weibull model*, characterizes litter decay as a continuous distribution of residence times, as might be expected given the diverse chemistry of constituents found in litter. This distribution is described by a scale parameter, β , and a shape parameter, α (Cornwell & Weedon, 2014; Fréchet, 1927; Weibull, 1951):

$$X = e^{-\left(\frac{t}{\beta}\right)^\alpha}, \quad (4)$$

The shape parameter, α , indicates the degree of divergence of decomposition rates between the early versus later stages: $\alpha > 1$ indicates that decomposition is slow early on and then accelerates in the later stages, as might occur if there is a lag period before decomposition

begins, whereas $\alpha < 1$ indicates more rapid early-stage decomposition relative to the later stages, as might occur if more labile constituents decompose first, followed by more complex constituents. When α equals 1, the Weibull model collapses to a single exponential decay model where the instantaneous decay rate is constant and $k_s = \frac{t}{\beta}$.

As the rate of decomposition described by the Weibull model changes continuously with time, we cannot compare individual k values associated with discrete litter pools. We therefore used the Weibull framework to calculate the time to 10%, 25% and 50% mass loss ($t_{1/10}$, $t_{1/4}$ and $t_{1/2}$ respectively) and the litter mean residence time (MRT; Cornwell & Weedon, 2014) as:

$$t_{1-p} = \beta \left(\ln \left(\frac{1}{p} \right) \right)^{\frac{1}{\alpha}}, \quad (5)$$

and

$$MRT = \beta \Gamma \left(1 + \frac{1}{\alpha} \right), \quad (6)$$

where p is the proportion of litter mass remaining at time t and Γ is the gamma distribution.

To determine the most appropriate decomposition models to describe litter decay dynamics, we initially fit decomposition models to pooled data from each site \times treatment combination (3–5 plots per pool) and compared model AIC_c values to assess the capacity of individual decomposition model structures to describe decomposition dynamics across treatments (Burnham & Anderson, 2002). Differences of >3 between model AIC_c values (ΔAIC_c) were used to identify significant differences between model fits. Root mean square error (RMSE) was also compared among models as a second measure of fit. Exponential models were fit using the *mle2* function in the *BBMLE* package (Bolker, 2020) and Weibull models were fit using the *nls* function. To evaluate whether nutrient addition changed which model best fit the data, we compared which model was the best fit to the data for all plots that did versus did not receive N, P or K_{μ} , in three separate contingency analyses.

Three of the four decomposition models (single exponential, asymptotic and Weibull) best described litter decomposition across sites and treatments (see Results), so we then fit each of the three models to the proportion C remaining from all litter bags harvested over time from an individual plot. To identify outliers within the individual plot models and obtain more precise parameter estimates for decomposition models, we calculated the sum of the residual distances between the proportion C remaining at each litter bag harvest and the predicted value in the Weibull model, adjusted for the number of predicted values (n_{Pred}) in each model according to the following relationship:

$$\text{Model Deviance} = \frac{\sum [X_{Pred} - X_{Obs}]^2}{n_{Pred}}. \quad (7)$$

Individual plot models with the highest 2.5% of all deviance scores were evaluated individually for outliers. In these cases, we iteratively removed individual data points and refit Weibull models to identify

predictor sets that resulted in the lowest model deviance. Individual harvest points were removed from 22 of 494 decomposition curves and their removal did not affect analyses presented below. We eliminated entire plots from the analysis when outlier removal reduced the number of harvest points included in the model prediction below three (2% of models fit to three points).

2.5 | Model fitting to estimate changes in litter N dynamics

Nitrogen is often immobilized initially before being released from decomposing litter (StAAF & Berg, 1981). To describe changes in the litter N pool throughout the decomposition period, we fit plot-level changes in litter N pool size through time to quadratic functions with the form:

$$Z = (\beta_1 t + \beta_2 t^2) + \beta_0, \quad (8)$$

where Z is the litter N pool (grams), t is the time since the start of the study (years), β_1 and β_2 are coefficients on the t and t^2 terms, respectively, and β_0 is the initial litter N pool (grams) in each plot. Models were fit to plot-level decomposition sequences. We used the quadratic function to calculate the maximum litter N pool (N_{\max}) and the time to N_{\max} ($t_{N_{\max}}$) during the litter decomposition period. We excluded data from individual litter bag harvests in which the litter C:N ratio fell outside the 95% confidence interval of the mean for each harvest time point. We also excluded plots with three or fewer data points describing litter N pool size.

2.6 | Nutrient effects on litter decomposition

We evaluated the effects of addition of N, P and K_{μ} on parameters describing early (Weibull $t_{1/10}$, $t_{1/4}$ and $t_{1/2}$; asymptotic k_d), late (asymptotic A) and overall (single exponential k_s ; Weibull α , MRT) litter decomposition using general mixed models (NLME R package; Pinheiro et al., 2019) in which site and block were included as nested random effects. These *treatment-only* statistical models were specified as a full-factorial block design in which N, P and K_{μ} treatments were included as separate fixed factors. Treatment-only models were also used to analyse treatment effects on litter N dynamics, N_{\max} and $t_{N_{\max}}$.

Using *treatment-covariate* statistical models, we considered whether inclusion of single covariates—soil pH, soil C (%), atmospheric N deposition rate ($\text{kg N ha}^{-1} \text{ year}^{-1}$), soil P (ppm), soil Mn (ppm), MAT ($^{\circ}\text{C}$), MAP (mm), precipitation distribution, annual insolation (W/m^2) or above-ground biomass (g/m^2)—interacted with nutrient addition treatments or altered the significance of treatment effects. We fit individual three-way ANCOVA models that included N, P and K_{μ} fertilization treatments in factorial combination with each covariate (covariates were considered individually because of the high number of covariates relative to the number of sites; site

and block were included as nested random effects; *lme* function; NLME R package; Pinheiro et al., 2019). All predictor and response variables were log- or square-root transformed to approximate normality, as appropriate.

2.7 | Cross-site variation in litter decomposition

We used model selection to identify predictor variables that best described cross-site variation in decomposition model parameters (Weibull α , MRT , $t_{1/10}$, $t_{1/4}$ and $t_{1/2}$; asymptotic k_d , A ; single exponential k_s). We considered predictors describing climate and edaphic conditions, including MAT, MAP, AI, PET and precipitation distribution; soil C, N, P, Mn and base cation content; soil pH; and modelled N deposition rate. After screening potential predictors for collinearity (Pearson $R > |0.70|$, Table S3; Hmisc R package; Harrell, 2020), we excluded AI, which was highly correlated with MAT; PET, which was highly correlated with MAT and AI; soil N, which was highly correlated with soil C; the sum of the extractable base cations, which was highly correlated with pH; and annual insolation, which was highly correlated with MAT (Pearson's $R > 0.70$). The final set of predictors is presented in Table S3.

We fit individual global mixed-effects models with all potential predictors (MAT, MAP, Precip. Dist., soil C, soil P, soil Mn, soil pH, annual N deposition rate and above-ground plant biomass; Table S3) for each response variable using the *lme* function in the NLME R package (Pinheiro et al., 2019). We then generated a full submodel set from the global model using the 'dredge' function and considered all two-way interactions (MuMIn R package; Nakagawa & Schielzeth, 2013). McLaughlin Natural Reserve and Hopland Research and Extension Center in California, USA, did not report initial soil chemistry, and thus sites were excluded from the model selection analysis, while Val Mustair in Europe was excluded as modelled N deposition data were unavailable. Experimental block nested within site was included as a random effect in each model, but fertilization treatments were excluded from models.

We present the top models with $\Delta\text{AIC}_c < 3$ and conditional model average associated with each parameter. For individual candidate models with $\Delta\text{AIC}_c < 3$, we calculated the variance explained by the fixed effects in isolation (marginal R^2) and that explained by both the fixed and random effects in combination (conditional R^2 ; MuMIn R package; Nakagawa & Schielzeth, 2013). All analyses were conducted using R version 3.5.3 (R Core Team, 2018).

3 | RESULTS

Across all sites and treatments, the median percentage C remaining at the end of the experiment was 36% (Figure S1). Sites with the fastest decomposition were Cowichan, British Columbia; Spindletop Farm, Kentucky; University of North Carolina; and Hall's Prairie, Kentucky (with 4%, 7%, 12% and 14% initial C remaining on average across treatments respectively). Sites with the slowest decomposition were

Sheep Experiment Station, Idaho; Kinypanial, Victoria; and Sagehen Creek Field Station, California (with 55%, 59% and 62% initial C remaining respectively). Formal comparisons of mass loss among treatments and sites were not possible because of different duration of litter deployment across sites. Hereafter, we focus on the analyses of parameters obtained from fitting decomposition models.

3.1 | Decomposition model fits

Using AIC_c to compare model fits, within the exponential decay model family, single and asymptotic decomposition models provided the best fits to the data, whereas the double exponential model was a poor fit to the data (Table S4.A). When we compared the fit of the Weibull decomposition model to that of the exponential decay models, the Weibull model fit the data as well as or better than any exponential model in 61% of all *site* × *treatment* combinations (Table S4.B). Because AIC_c was consistently higher for the double exponential model than the other models, we fit the single, asymptotic and Weibull models to all individual plots. We also assessed model fit using root mean square error (RMSE), a measure of the difference between sample and predicted values within a fitted model that does not reflect model parsimony. Across *site* × *treatment* combinations, the RMSE of the asymptotic (two parameters) and double exponential (three parameters) models were lower than that of the single exponential model (one parameter) in 58% and 73% of all *site* × *treatment* combinations respectively. The RMSE of the Weibull model (two parameters) was lower than the single exponential decomposition model in 100% of *site* × *treatment* combinations.

While neither N, P, nor K_μ changed which decomposition model best fit the data (Table S5.A), the best model to describe litter decomposition differed across sites (Table S5.B). The single exponential model best described the majority of the treatments at 13 sites, the asymptotic model at three sites and the Weibull model at one site. At two sites, the single exponential and Weibull models were the best fit for an equal number of treatments. The double exponential was never the best model for any treatments at any sites.

3.2 | Effects of experimental nutrient addition on early-stage litter decay ($t_{1/10}$, $t_{1/4}$, $t_{1/2}$ and k_a)

In treatment-only statistical models, the addition of N (but not P or K_μ) greatly accelerated early-stage decomposition, decreasing the Weibull time to 10% and 25% mass loss ($t_{1/10}$ and $t_{1/4}$) and increasing the initial decay rate (asymptotic k_a), by 16%, 12% and 23% respectively (Figure 2; Table S6). Similarly, in treatment-covariate models, N fertilization (but neither P nor K_μ) reduced $t_{1/10}$ and $t_{1/4}$ and increased asymptotic k_a (Table S7). However, in contrast to our expectations, N-induced increases in early-stage litter decomposition were not stronger in sites with high P or base cation availability. There were some weak interactive effects of fertilization and other site factors on early-stage decomposition (Table S7), with N more

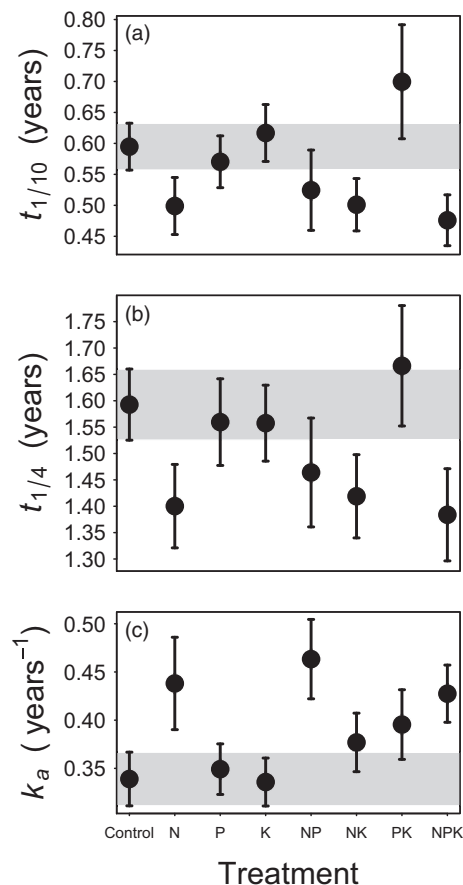


FIGURE 2 Effects of nutrient addition on early stages of litter decomposition. (a) Weibull time to 10% mass loss ($t_{1/10}$), (b) Weibull time to 25% mass loss ($t_{1/4}$) and (c) initial litter decay rate (asymptotic k_a). For visualization purposes, means (SE bars) of untransformed data are shown for each treatment (pooled across sites). Mixed-effects treatment-only model results are shown in Table S6 and treatment-covariate models are shown in Table S7. Shaded region shows mean and standard error in control treatment to make visual comparison among treatments easier

strongly increasing early-stage decomposition (k_a) in sites with low soil Mn content (Figure S2) and pH (Figure S3). K_μ increased $t_{1/10}$ and $t_{1/4}$ in sites with more evenly distributed precipitation (not shown), while P and K_μ increased $t_{1/2}$ and decreased $t_{1/4}$, respectively, in sites with high pH (Figure S3).

3.3 | Effects of nutrient addition on late stage and overall litter decay (α , MRT, k_s , A)

In contrast to the early stages of litter decomposition, in treatment-only models, both N and P, but not K_μ , increased the Weibull MRT, and N decreased Weibull α and increased the fraction of slowly decomposing C (asymptotic A), indicating that N caused rates to slow as decomposition proceeded (Figure 3; Table S6). However, N effects on early- and late-stage decomposition were largely offsetting, as there were no significant main effects of any nutrients on the

single exponential decomposition rate (k_s). Similarly, in treatment-covariate models, N increased Weibull MRT and A (Table S7) and had only a small effect on the single exponential decay model (k_s), increasing it by 6% on average (Figures 3 and 4; Table S7). The decrease in Weibull α with added N, from values >1 to values closer to 1, indicated that N accelerated early-stage decomposition (Figure 4). Phosphorus also generally increased Weibull MRT and sometimes increased the fraction of slowly decomposing C (A), indicating it also tended to slow the later stages of decomposition. Phosphorus also affected litter half-life ($t_{1/2}$) in models that included covariates, but complex $N \times P \times K_{\mu}$ interactions made those effects difficult to interpret (Table S7).

Fertilization interacted with several site factors in its effects on late-stage and overall decomposition dynamics (Table S7). Nitrogen

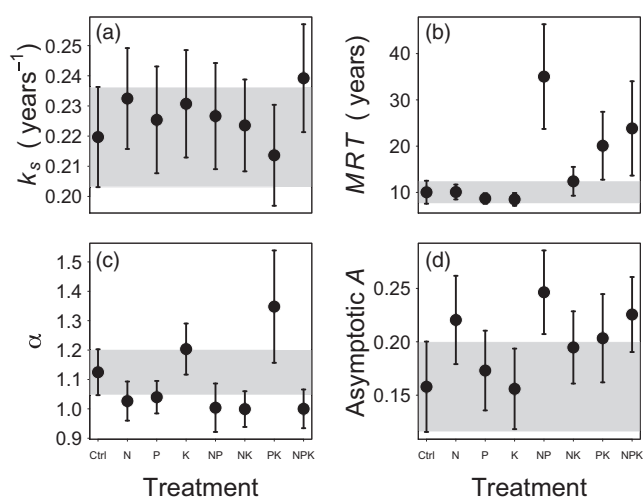
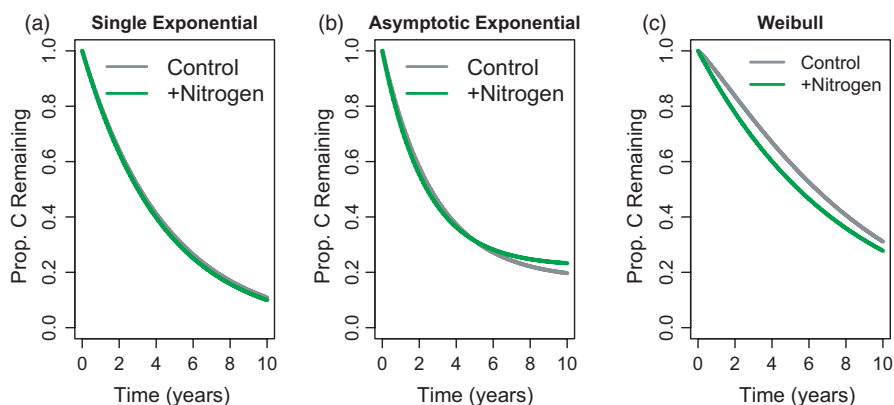


FIGURE 3 Effects of nutrient addition on decomposition parameters describing the entire time course of decomposition. (a) Single exponential k_s , (b) Weibull MRT and (c) Weibull α ; or later stages of decomposition, (d) asymptotic A. For visualization purposes, means (SE bars) of untransformed data are shown for each treatment (pooled across sites). Mixed-effects treatment-only model results are shown in Table S6 and treatment-covariate models are shown in Table S7. Shaded region shows mean and standard error in control treatment to make visual comparison among treatments easier. Ctrl = control

FIGURE 4 Comparison of proportion C remaining over 10 years predicted by (a) single exponential, (b) asymptotic exponential and (c) Weibull models of decomposition between treatments receiving (+N, green line) or not receiving (-N, grey dashed line) N. Model parameters were obtained by averaging across all replicates, sites and appropriate treatments



increased single exponential k_s more at sites with low than high N deposition (albeit weakly, Figure S4). Nitrogen also increased k_s in sites with low Mn (Figure S2), but reduced k_s and Weibull α , and increased Weibull $t_{1/2}$ and MRT, and asymptotic A more where precipitation was more evenly distributed across the year (low Precip. Dist; Figure S5). Finally, N reduced Weibull α and k_s and increased Weibull MRT more at sites with higher above-ground biomass (Figure S6).

Nitrogen was typically immobilized in leaf litter in the initial stages of decomposition. Plots with faster early-stage decomposition (higher asymptotic k_a , lower Weibull $t_{1/10}$) exhibited higher maximum litter N pools (N_{max} , Table S8). Higher N_{max} was also associated with increased litter MRT and asymptotic A, as well as reduced Weibull α . In treatment-only models, N fertilization increased litter N_{max} (N: $p < 0.0001$), as well as the time to the maximum litter N content ($p = 0.031$, Table S9; Figure S7).

3.4 | Variables predicting litter decay dynamics across sites

Later stage decomposition and the total decomposition curve were effectively predicted by climate and atmospheric deposition. In particular, MAT, background N deposition and precipitation variation were modest to strong predictors of Weibull half-life ($t_{1/2}$), parameters describing later stage decomposition (asymptotic A) or parameters describing the entire decomposition curve (Weibull α , MRT; single exponential k_s ; Table S10). Generally, warmer sites had faster decomposition (lower $t_{1/2}$, lower Weibull MRT), sites with more variable seasonal precipitation (higher Precip. Dist.) had slower decomposition (longer Weibull MRT, lower k_s) and sites with higher levels of atmospheric N deposition had faster decomposition (lower Weibull MRT, lower asymptotic A, Tables S7 and S10).

In contrast, climatic and edaphic factors did not explain substantial variation in decomposition model parameters describing the early stages of decay (Weibull $t_{1/10}$, $t_{1/4}$; asymptotic k_a ; Table S10). Less than 10% of the cross-site variation in these parameters was captured by fixed effects, indicating that most of the variation among sites in the initial decomposition rates was caused by unmeasured site factors (Table S10).

4 | DISCUSSION

4.1 | Contrasting effects of N on early- versus late-stage decomposition

In a long-term (7-year) experiment replicated across grasslands spanning diverse biotic, edaphic and climatic conditions, N consistently accelerated early-stage decomposition. This points to N limitation of microbes decomposing the N-poor *Quercus* litter, whereby added N increased decomposer C demand. Neither P nor K_{μ} , alone or in combination with N, limited decomposition in its early stages, in contrast to nutrient co-limitation of NPP in grasslands (Cleland et al., 2019; Du et al., 2020; Fay et al., 2015). Decomposer N demand likely was met via fungal translocation of soil N in control plots (Chigineva et al., 2011; Frey et al., 2000; Xiong et al., 2014), but via fertilizer-supplied N in N-treated plots. Accordingly, litter in the N-fertilized plots exhibited less initial delay of decomposition and greater N immobilization than litter in control plots. Our findings corroborate observations from previous studies across diverse litter types, showing that low-N litter types exhibited lagged decomposition dynamics relative to high-N litter (Cornwell & Weedon, 2014). In addition to alleviating N limitation, N may have affected early-stage decomposition via other mechanisms. A study in semi-arid grassland attributed positive effects of N on decomposition to acidification that increased Mn availability and altered the microbial community (Hou et al., 2021). However, while N fertilization also reduced soil pH in the present study (at 10/20 sites), the magnitude of pH reduction was unrelated to the effects of N on decomposition model parameters (data and analyses not shown).

The current work builds from earlier short-term studies demonstrating widespread N stimulation of early-stage decomposition, but is the first to show this using a long-term experiment in diverse grasslands. A short-term study of decomposing tea leaves across 21 Nutrient Network sites also found positive N effects on early-stage decomposition (Ochoa-Hueso et al., 2020). Unlike the current study, P addition also positively affected early-stage decomposition, perhaps because the relatively high N concentrations in tea increased microbial P demand. In a meta-analysis of N fertilization effects on decomposition in diverse ecosystems, N fertilization reduced $t_{1/10}$ and $t_{1/4}$ and increased Weibull MRT and asymptotic k_a , as found here (Gill et al., 2021). Our findings are also consistent with results from some local to regional cross-site studies, predominantly in forests, showing N stimulation of initial decomposition (Berg & Matzner, 1997; Hobbie et al., 2012).

In contrast to our hypothesis, N inhibited later stage decomposition (increasing asymptotic A and increasing Weibull MRT), as found in many forest studies (Berg & Matzner, 1997; Gill et al., 2021; Whittinghill et al., 2012), and in a short-term grassland study, where N increased the Tea Bag Index stabilization factor (a modelled representation of the biochemically transformed tea leaves that persist at late stages of decomposition; Ochoa-Hueso et al., 2020). The concordance of results presented here with those from forest and short-term grassland studies points to the generality that elevated N slows

late-stage decomposition in terrestrial ecosystems. The inhibition of late-stage decomposition by added N has been attributed to several interrelated mechanisms including the suppression of oxidative enzyme activity; formation of recalcitrant compounds from accumulated microbial necromass or reactions of inorganic N with litter metabolites; Mn limitation; and suppression of microbial biomass by acidification (Berg & Matzner, 1997; Carreiro et al., 2000; Entwistle et al., 2018; Fog, 1988; Gill et al., 2021; Hobbie et al., 2012; Morrison et al., 2018; Treseder, 2008; Whalen et al., 2018; Zak et al., 2008).

We hypothesized that N would not inhibit late-stage decomposition in grasslands because of relatively low plant lignin content, and associated low basidiomycete abundance and lignin-degrading oxidative enzyme activity (Sinsabaugh, 2010). Indeed, meta-analyses published well after our study began showed little evidence that N inhibits oxidative enzyme activity in grasslands (Chen et al., 2018; Jian et al., 2016; Xiao et al., 2018). However, depressive effects of N enrichment on grassland microbial biomass (Ramirez et al., 2012) could have slowed decomposition.

It is also possible that alleviation of microbial N limitation early in decomposition led to necromass accumulation on litter surfaces and contributed to the apparent reduction in late-stage litter because of necromass constituents that decompose more slowly than the plant compounds consumed by those decomposers (Gill et al., 2021; Liang et al., 2019). Increased N immobilization in response to N fertilization, which was associated with reduced rates of late-stage decomposition, provides indirect support for this mechanism. Concurrent measures of enzyme activity and decomposer necromass are needed to distinguish among these potential mechanisms.

Contrasting N effects early and late in decomposition, as found here, have implications for N effects on SOM. Early in decomposition, N could promote litter processing and transfer of low molecular weight compounds to soils, potentially enhancing stabilization of mineral-associated organic matter (MAOM). By contrast, larger slowly decomposing litter fractions could promote the accumulation of particulate organic matter (POM) and total SOM (Cotrufo et al., 2015). Interestingly, a study conducted in nine North American NutNet sites found no effects of N on MAOM or POM (Keller et al., 2022), raising uncertainty about whether differential effects of N over the course of litter decomposition have consistent consequences for SOM.

4.2 | Utility of higher order models in describing litter decomposition dynamics

Multi-parameter empirical models illuminated divergent N effects early vs. late in decomposition. Thus model structure choice influences interpretation of litter decomposition dynamics, with implications for experimental design and hypothesis testing (Cornwell & Weedon, 2014). Single-parameter models readily fit data from experiments with fewer collection points, but may mischaracterize decomposition dynamics that shift through time. Herein, the single exponential model often provided equivalent AIC_c fit to two- or

three-parameter models, suggesting that it sufficiently described the complexity of grassland litter decomposition. However, the Weibull model structure fit the data equally well or better than the single exponential model for 61% of site-treatment combinations, and the asymptotic model fit the data equally well or better for 88%. As the fertilization responses observed here and in other recent syntheses (Gill et al., 2021) emerged only when models allowed decomposition rates to change through time, these higher order model structures deserve consideration in both experimental design and data analysis.

Whether N addition would differently affect *Quercus* litter decomposition relative to native litter at each site due to variation in litter chemistry, lack of home-field advantage effects (Palozzi & Lindo, 2018) or sterilization prior to deployment is unclear. In a study across eight locations at one of our study sites (Cedar Creek), where the litter used here originated, litter of *Quercus elipsoidalis* and *Schizachyrium scoparium*, a dominant C4 grasses in Cedar Creek grasslands and savannas, had similar initial acid non-hydrolysable fractions (lignin and other recalcitrants), N concentrations and rates of decomposition, and responded idiosyncratically to added N in grasslands in the early and late stages of decomposition (Hobbie, 2005, 2008). However, the *Quercus* litter used here had higher concentrations of lignin (Table S2) than would be expected for herbaceous species on average (e.g. Oliveira et al., 2020), which could have accentuated negative effects of N on the later stages of decomposition if the underlying mechanism was related to N inhibition of oxidative enzyme activity.

4.3 | Interactions between nutrient treatment effects and site factors

We found limited support for hypothesized interactions between site factors and nutrient treatments on decomposition, suggesting that N effects (and lack of P and K_u effects) were general across diverse climatic and edaphic conditions. We had expected that nutrients would limit decomposition more in warm, wet regions, yet N limitation of early-stage decomposition was largely independent of climate. However, negative effects of N on late-stage decomposition were strongest in sites where precipitation was more evenly distributed across the year. As the frequency of wetting events regulates nutrient diffusion to litter bags, more consistent precipitation regimes may support elevated N environments throughout the year, contributing to elevated microbial biomass and higher necromass stabilization. Negative N effects also increased with above-ground biomass, which may protect litter from UV radiation and prevent decomposer desiccation, supporting increased necromass stabilization.

Across 20 sites with widely varying geography, results did not support our hypothesis of greater N limitation of decomposition in younger, less weathered sites, and greater P limitation in older, more weathered sites. Instead, N increased early-stage decomposition regardless of soil chemistry and climate, and the only consistent P effect was to increase Weibull MRT.

4.4 | Variation in decomposition across sites

Mean annual temperature, precipitation variability and atmospheric N deposition all contributed to variation in decomposition rates across sites, mostly later in decomposition. Faster decomposition in warmer sites, observed previously in global decomposition syntheses (Gholz et al., 2000; Kwon et al., 2021; Zhang et al., 2008), is expected because of greater biological activity, longer growing seasons and higher nutrient availability. Greater photodegradation in warmer sites could also have contributed to faster decomposition in those sites, given that MAT was highly correlated with annual insolation (Austin & Vivanco, 2006). Faster decomposition in sites where precipitation was distributed more evenly relative to annual precipitation likely reflects the importance of moisture in limiting decomposition in grasslands, especially at times of year when temperatures are favourable (Gholz et al., 2000; Meentemeyer, 1978). Indeed, a manipulation of rainfall variability showed that lower precipitation variability, resulting in higher average soil moisture, led to more rapid decomposition (Walter et al., 2013).

Positive relationships between k_s and N deposition provide further evidence that N limits decomposition across grasslands, and contrast results from a cross-site study of tea leaf decomposition world-wide, which showed negative relationships between atmospheric N deposition and mass loss over 3 and 12 months in temperate sites (Kwon et al., 2021). The effects of N from deposition and fertilizer differed in key ways. First, whereas fertilizer N reduced the initial lag period of slow decomposition, atmospheric N deposition was associated with a longer lag period. This discrepancy could have arisen if long-term effects of chronic N addition were not yet apparent in fertilized plots, which began receiving fertilizer <2 years before litter bags were deployed. For example, N deposition might have altered microbial communities, as seen in long-term (>8 years) fertilization studies (Entwistle et al., 2018; Frey et al., 2004; Hesse et al., 2015; Hou et al., 2021; Whalen et al., 2018), in ways that slowed colonization of litter by decomposer organisms and reduced litter-soil hyphal connections. Other effects of chronic N deposition associated with soil acidification (e.g. reduced base cation supply; Hou et al., 2021) might also have manifested slowly in N fertilization treatments.

While sites with higher N deposition had smaller litter slow pools, N fertilization increased the slow pool. As discussed previously, numerous long-term decomposition studies have demonstrated that N fertilization increases the slow pool (asymptotic A), but fewer studies evaluated the relationships of A with ambient N deposition rates. The rates of N addition in fertilization studies, including ours, are often higher than the highest rates of N deposition in polluted regions (Midolo et al., 2019). Herein, N was added at a rate of 100 kg N ha⁻¹ year⁻¹, whereas the highest rate of N deposition across sites was c. 20 kg N ha⁻¹ year⁻¹. Although the specific mechanism by which added N increased the slow pool is unknown, perhaps its effects only occur at relatively high rates of added N. In addition, modelled N deposition values reflect site precipitation, and site-level variation in moisture availability may independently influence the

slow litter pool size, although site MAP did not directly influence the size of the slow-cycling C pool in this analysis.

4.5 | Unexplained site variation

Initial decomposition rates varied widely among sites, but in ways not explained by measured site climate or edaphic factors. Decomposition of common above-ground substrates was similarly unrelated to climate factors across six grassland sites in the US Central Great Plains (Bontti et al., 2009), and a cross-sites study of decomposing tea leaves similarly found a high percentage of unexplained variation across grassland sites (Kwon et al., 2021). What other factors might have contributed to variation in initial decomposition across sites? Variation in the decomposer community (Prober et al., 2015) and how quickly it colonized the litter could have contributed to site variation in initial decomposition because of variation in metabolic capabilities of microbial decomposers (Bray et al., 2012; Gessner et al., 2010; Glassman et al., 2018; Strickland et al., 2009). Other factors, such as the contributions of soil fauna to decomposition or vascular plant community composition, might also have contributed to site-to-site variation in decomposition (García-Palacios et al., 2013). For example, the site with the highest total decomposition (Cowichan) is dominated by densely growing rhizomatous grasses, whose roots completely encased the litter bags after several years. Previous decomposition trials at this site also exhibited rapid biomass decomposition (Ziter & MacDougall, 2013).

Photodegradation is also important for above-ground decomposition in grasslands and could have contributed to site variation in decomposition dynamics (Adair et al., 2017; Austin & Vivanco, 2006), given that the fibreglass mesh used in this study transmits about 45%–50% of solar radiation (Adair et al., 2017). However, greater above-ground biomass was associated with faster k_s in control plots (but not in plots receiving N), opposite what might be expected if photodegradation contributed substantially to initial decomposition rates. We were unable to evaluate the effects of photosynthetically active radiation (PAR) at the ground surface on decomposition across sites because of lack of data, so we cannot rule this out as a potential mechanism. Nevertheless, variation in irradiance, soil contamination of the litter bags (Adair et al., 2017; Brandt et al., 2010) and position of the bags relative to the ground surface, and standing and fallen vegetation (Lin & King, 2014) could have caused variation in photodegradation and biotic decomposition.

5 | CONCLUSIONS

In a long-term (7-year) study of decomposition of a common leaf litter substrate in a factorial fertilization experiment replicated at 20 grassland sites spanning a wide range of biotic, edaphic and climatic conditions, N fertilization consistently increased early-stage and slowed late-stage decomposition, as often seen in forests. These patterns were discernible because of the long duration of the study,

the large number of sites and the use of decomposition models that could distinguish early- and late-stage decomposition dynamics. These findings corroborate those of Gill et al. (2021) in showing that fitting decomposition data to single exponential models can obscure the effects of environmental factors on decomposition dynamics. Implications of contrasting early- versus late-stage effects of N on litter decomposition for SOM pools and dynamics deserve further empirical study and exploration using ecosystem models.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

S.E.H. and A.L.G. contributed equally; E.T.B., E.W.S., W.S.H., S.E.H. and K.S.H. designed the research; E.T.B., C.R.B., E.E.C., C.M.D., K.F.D., D.S.G., W.S.H., S.E.H., A.S.M., R.L.M., B.A.M., J.L.M., J.W.M., A.C.R., M.S., E.W.S., J.P.W. and L.H.Y. performed the research; P.B.A., E.T.B., C.R.B., E.E.C., C.M.D., K.F.D., A.L.G., D.S.G., W.S.H., S.E.H., A.S.M., R.L.M., B.A.M., J.L.M., J.W.M., A.C.R., M.S., E.W.S., J.P.W. and L.H.Y. contributed to data analysis, collection or interpretation; PBA, E.T.B., E.E.C., C.M.D., K.F.D., ALG, W.S.H., S.E.H., K.S.H., A.S.M., R.L.M., A.C.R., M.S., E.W.S., J.P.W. and L.H.Y. contributed to writing the manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13878>.

DATA AVAILABILITY STATEMENT

Data are archived and available through the Environmental Data Initiative and the Cedar Creek Long Term Ecological Research Program (Hobbie, 2021): <https://www.cedarcreek.umn.edu/research/data/dataset?aige247>, <https://doi.org/10.6073/pasta/2ebd7eaf2fac27e1c7eee9678baa7940>. Code to replicate analyses

and figures are available on Zenodo <https://doi.org/10.5281/zenodo.6366764> (Gill, 2022) and on Github <https://github.com/gill20a/NutNetLitterDecomp>.

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