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Autumn sunlight promotes aboveground carbon loss in a temperate mixed forest

Xingzhi Li^{1,2,3}, Yanan Wang^{1,2,3}, Juanjuan Zhang^{1,2,3}, Thomas Matthew Robson^{4,5}, Hiroko Kurokawa⁶, Huan Peng¹, Li Zhou^{1,3}, Dapao Yu^{1,3}, Jiaojiao Deng^{1,3*} and Qing-Wei Wang^{1,3,6*}

Abstract

Background Photodegradation of plant litter plays a pivotal role in the global carbon (C) cycle. In temperate forest ecosystems, the exposure of plant litter to solar radiation can be significantly altered by changes in autumn phenology and snow cover due to climatic change. How this will affect litter decomposition and nutrient dynamic interacting with forest canopy structure (understorey vs. gaps) is uncertain. In the present study, we conducted a field experiment using leaf litter of early-fall deciduous *Betula platyphylla* (Asian white birch) and late-fall deciduous *Quercus mongolica* (Mongolian oak) to explore the effect of change in autumn solar radiation on dynamics of litter decomposition in a gap and understorey of a temperate mixed forest.

Results Exposure to the full-spectrum of not only significantly increased the loss of mass, C, and lignin, but also modified N loss through both immobilization and mineralization during the initial decomposition during autumn canopy opening, irrespective of canopy structure and litter species. These effects were mainly driven by the blue-green spectral region of sunlight. Short-term photodegradation by autumn solar radiation had a positive legacy effect on the later decomposition particularly in the forest gap, increasing mass loss by 16% and 19% for Asian white birch and Mongolia oak, respectively.

Conclusions Our results suggest that earlier autumn leaf-fall phenology and/or later snow cover due to land-use or climate change would increase the exposure of plant organic matter to solar radiation, and accelerate ecosystem processes, C and nutrient cycling in temperate forest ecosystems. The study provides a reference for predictive research on carbon cycling under the background of global climate change.

Keywords Carbon cycling, Canopy phenology, Snow cover, Climate warming, Solar radiation, Photodegradation

*Correspondence:

Jiaojiao Deng

jiaojiaod@iae.ac.cn

Qing-Wei Wang

wangqingwei@iae.ac.cn

¹ CAS Key Laboratory of Forest Ecology and Silviculture, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China

² University of Chinese Academy of Sciences, Beijing 100049, China

³ Changbaishan Xipo National Field Observation and Research Station for Forest Ecosystem, Baishan 134500, China

⁴ UK National School of Forestry, University of Cumbria, Ambleside LA22 9BB, UK

⁵ Organismal and Evolutionary Biology, Viikki Plant Science Centre (ViPS), University of Helsinki, P.O. Box 65, 00014 Helsinki, Finland

⁶ Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki 3058687, Japan



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Introduction

Plant litter decomposition is the crucial biogeochemical processes that controls nutrient cycling in terrestrial ecosystems (Friedlingstein et al. 2020), impacting carbon (C) sinks, soil fertility, and releases C backflow to the atmosphere. It is widely accepted that the rate of litter decomposition is primarily regulated by climate, initial litter traits, and decomposers (Counteaux et al. 1995, Currie et al. 2009, Waring 2012, Garcia-Palacios et al. 2013). However, recent evidence has identified photodegradation induced by solar radiation as another main driver of litter decomposition and C cycling in a wide range of ecosystems (Marinho et al. 2020; Jiang et al. 2022; Berenstecher et al. 2022; Wang et al. 2022a, b). These researches broaden our knowledge that photodegradation is a ubiquitous contributing driver of decomposition across biomes (Barnes et al. 2022). This suggests that factors altering the exposure of plant litter to solar radiation, or interacting with the role of solar radiation, may affect terrestrial carbon and nutrient cycling in the context of global change (Bernhard et al. 2020; Sulzberger et al. 2019). Such an effect would have important implications for temperate forest ecosystems, which have become the main global carbon sinks (Yang et al. 2023), given that their high seasonality in canopy structure and phenology may contribute to the interannual variation in global C balance.

Solar radiation can directly break down plant litter and release greenhouse gases (GHGs) into the atmosphere without biodegradation (referred to as photomineralization). Photomineralized compounds do easily leach during rainfall (Yao et al. 2022), but also make litter more palatable to microbes and thereby enhance microbial decomposition (referred to as photofacilitation) (Keiser et al. 2021). Photofacilitation can occur on a timescale of days, or even within a single day (Gliksman et al. 2017a). It is well known that ultraviolet (UV) radiation (290–400 nm) and short-wavelength visible light (blue-green, BG, 400–600 nm) are the main spectral regions causing photodegradation. Lignin has been identified as preferentially photodegraded due to its absorbance spectrum (Austin et al. 2016; Austin and Ballare 2010). Therefore, the relative significance of the photodegradation to decomposition rates depends on the spectral regions to which litter is exposed and litter quality (e.g., lignin/N ratio).

There is growing evidence that photodegradation is a cause of litter decay in temperate forest ecosystems, even in areas with relatively low solar radiation, such as shaded undergrowth (Pieristè et al. 2019, 2020a; Wang et al. 2022b, 2021). Forests canopy dynamics (e.g., gap creation, canopy phenology) can modulate litter decomposition rates and nutrient flux by modifying photodegradation.

The reduction in forest canopy closure is the dominant form of disturbance due to changes in land-use (e.g., deforestation and clear felling). Together with climatic drivers, the increase in sunlight exposure gaps facilitates the litter decomposition of leaves, twigs, and logs (Chen et al. 2023; Wang et al. 2022b), and slows litter humification process (Wu et al. 2023), enhancing ecosystem C release. Our recent study has found that exposure to the full-spectrum when a forest gap opens can greatly increase litter decomposition rate by almost 120% across a wide range of species (Wang et al. 2021). Moreover, N is immobilized in the understory during canopy flushing, but released during canopy leaf-fall (Wang et al. 2022b). Together, these findings suggest that seasonal canopy phenology can significantly change the N dynamics during litter decomposition by modulating sunlight reaching the forest floor. Therefore, models of biogeochemical cycling rates in temperate forest ecosystems in response to climate and land-use change could be improved by including variation in solar radiation, as modified by canopy structure and phenology.

At the field scale, controls on initial decomposition are ascribed to micro-environmental factors and changes in litter exposure to solar radiation (Berenstecher et al. 2021; Wang et al. 2022a, b). In drylands, litter decomposition is driven by direct photomineralization in summer when there is little moisture, and by photofacilitation during winter due to increased microbial access to labile carbohydrates when conditions are moist (Berenstecher et al. 2022). However, photofacilitation remains dominant in accelerating litter decomposition rate year-round, because litter in temperate forests is exposed to a heterogeneous radiation and mesic environments with diverse decomposer organisms due to vegetation cover (Neale et al. 2021). In many northern temperate biomes, the size of this photofacilitation effect may partially depend on accumulated solar radiation during the period from canopy leaf-fall to snow cover, since the snowpack can last to the next year's canopy flushing. For example, standing dead leaf litter over winter has a higher decomposition rate (up to double) during the following year than leaf litter covered by the snowpack. With continued climate change, the timing of autumn leaf senescence (leaf-fall phenology) and/or snow cover will be further delayed in temperate regions (Chen et al. 2020; Zani et al. 2020). Litter of early-fall deciduous species (i.e., species that lose their leaves early in the autumn) and the species that live beneath them receives more solar radiation than litter from late-fall deciduous species. This distinction according to autumn leaf-retention strategy may potentially differentiate litter photodegradation rates together with differences in the litter quality of these two functional types of trees. However, little is known about how

autumn solar radiation interacts with canopy structure and phenology to drive litter C turnover and nutrient dynamics in temperate forests in an ecological context.

To address this issue, we conducted a field experiment to investigate the effect of changes in autumn solar radiation on the dynamics of litter decomposition in a gap and understorey of a temperate mixed forest. We selected litter from two dominant tree species with large differences in their autumn leaf-fall phenology: early-fall deciduous species *Betula platyphylla* (Asian white birch) and late-fall deciduous species *Quercus mongolica* (Mongolian oak). Spectral attenuation filter treatments were used to quantify the contribution of photodegradation to litter decomposition. Changes in autumn solar radiation were created by setting up one group of litterboxes with different filters at the beginning of autumn canopy opening (ACO type) and another group at the beginning of winter snow cover (WSC type) in the forest gap and understorey. We hypothesized that: (H1) photodegradation by autumn solar radiation would directly accelerate initial mass and lignin loss, even though the exposure period between leaf-fall and snow-cover is relatively short; (H2) photodegradation by autumn solar radiation may accelerate litter decay during the following growing season, due to photofacilitation from pre-exposure of litter during autumn leaf-fall; (H3) During the initial decomposition period, nitrogen (N) mineralization would predominantly occur in ACO litter due to photodegradation, while nitrogen immobilization predominantly occurs in WSC litter owing to the absence of photodegradation. However, during the growing season, at a later stage of litter decomposition, the dominant process would be nitrogen release in both litter types, regardless of prior photodegradation.

Materials and methods

Site description

The study was conducted in the Changbai Mountain Forest Ecosystem Research Station (CMFER) (42°01′–42°48′N, 127°53′–128°34′E), in Jilin Province, China, which has a temperate continental monsoon climate at an altitude of 750 m. Average climate for a period of 2020–2021 is: annual monthly temperature is –7 to 3 °C, with minimum average of –20 °C in winter and maximum average of 22 °C in summer. Average annual precipitation is 700–1400 mm, of which 60%–70% occurs in June–September. The mature and old-growth forests are mixed forests dominated by broadleaved trees and *Pinus koraiensis*. A 7×7 m plot in the CMFER understorey was established where the natural light environment varies seasonally with canopy phenology. Additionally, a similar-size gap plot was established in an adjacent gap, which provided a homogeneous light environment and

ensured that the soil conditions were similar to those of the understorey plot. Fences were used to protect plots against wild mammals (mainly boars).

Litter collection

Freshly senesced leaves of the early-fall deciduous species *B. platyphylla* (Asian white birch) with low lignin concentration and the late-fall deciduous species *Q. mongolica* (Mongolian oak) with high lignin concentration were collected in September and November 2019, respectively (Table S1). All litter samples were laid flat in newspaper, pressed in a wooden frame and oven-dried at 37 °C to a constant weight. The pressed litter samples were kept in the dark at 25 °C until their transfer to litterboxes.

Experimental design

Based on our previous study, litter materials were placed in a litterbox (Wang et al. 2021). The litterbox frame was made from sterile plastic straws (21 cm long and 18 cm wide, 1.3 cm height; Bihin, Japan). A central pillar was made from a section of plastic straw, which maintained a space in the litterbox preventing the litter touching the filters during decomposition. Litterbox tops consisted of different spectral filters, including: (1) Full-spectrum treatment, with a fully transparent polyethylene filter (Okura, Marugame, Japan), transmitting approximately 95% of the total solar spectrum >280 nm; (2) No-UV treatment, filtering all UV radiation <400 nm (0.2-mm-thick Rosco EColor 226 filter, West lighting, Helsinki, Finland); (3) No-UV-&-Blue-Green (BG) treatment, attenuating all UV, blue and green wavelengths <580 nm (0.2-mm-thick Rosco E-Color 135 Deep Golden Amber filter). In order to allow air, moisture, and microorganisms to interact with the litter, holes with a diameter of 2 mm were drilled into the filter on a 1-cm grid. The bottom of the litterboxes was made of 0.1-mm nylon mesh (19×19 cm), which excludes soil animal incursion. Leaf litter was placed with the adaxial epidermis facing up and fixed flat to the bottom mesh with stainless steel staples (2–8 leaves per litterbox, weighing 1.0 g per species).

Litterbox deployment and collection

In order to evaluate the influence of the autumnal solar radiation on the above-ground carbon turnover, we built two decomposition experiments in October 2020 for ACO type that receives the photodegradation during the autumn, at the beginning of autumn canopy opening, and in December 2020 for WSC type that receives no photodegradation during the autumn, at the beginning of winter snow cover. In each plot, four blocks of litterboxes were randomly pinned to the soil surface (Fig. 1A). Temperature and solar radiation were recorded using HOBO (Onset Computer Corporation, MX2202, Bourne,

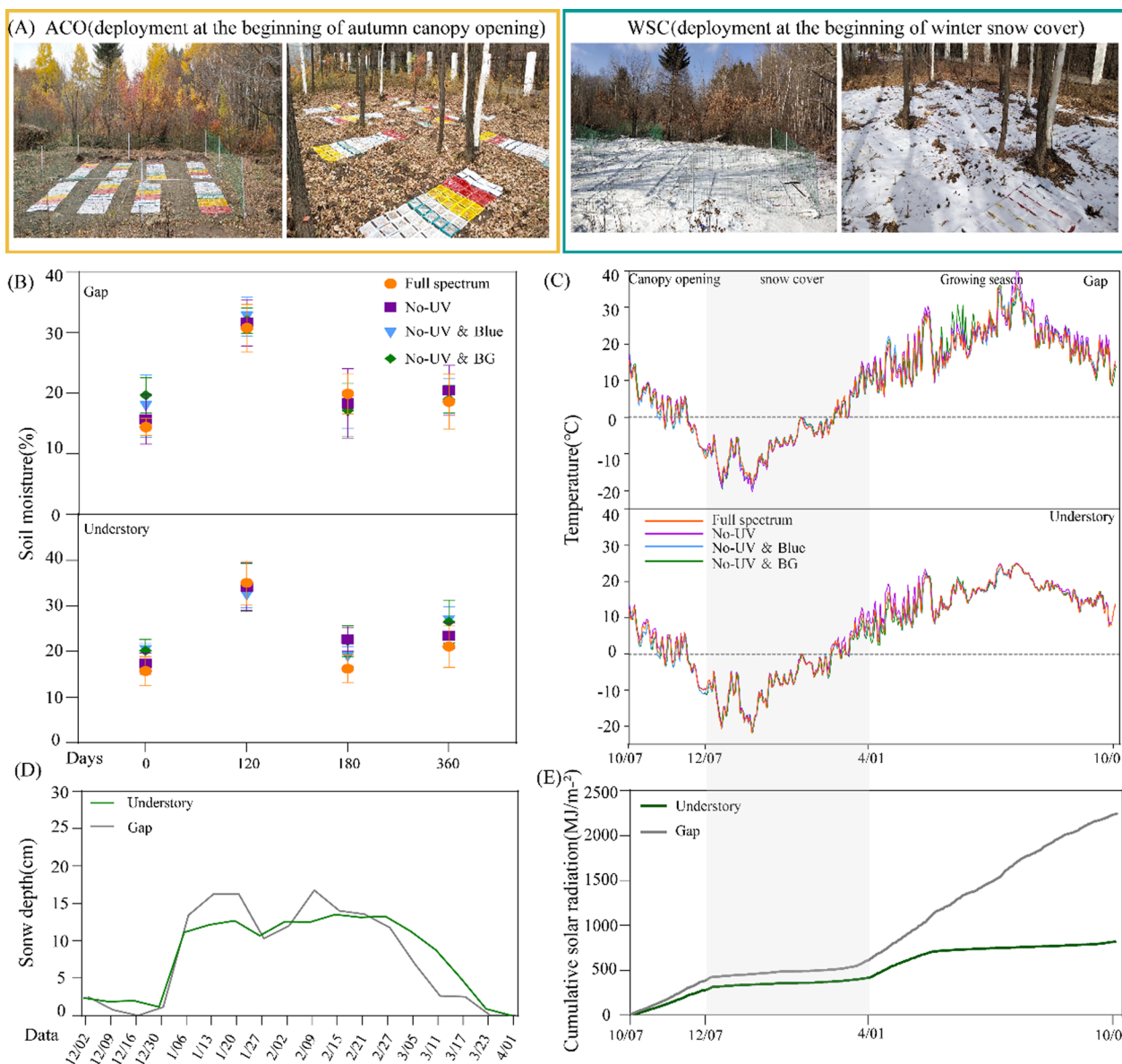


Fig. 1 Field experiment site and microclimate. **A** Litterboxes were randomly pinned to the soil surface in four blocks in the plots of the forest gap and understory in October 2020 (litterboxes placed at the beginning of autumn canopy opening, ACO) and December 2020 (litterboxes placed at the beginning of winter snow cover, WSC); **B** Soil moisture under litterboxes in the gap and understory; **C** Daily mean temperature in litterboxes; **D** Snow depth in plots; **E** Cumulative solar irradiance received by litter in the gap and understory

MA, USA). The depth of snow cover was measured every week. Plots were checked every 2 weeks and any debris on the litterboxes were cleaned. Soil moisture content was measured using the drying method.

Based on the estimated timing of leaf fall and snow accumulation in the Changbai Mountain region over the years, we designed two key time points for deployed litterboxes, ACO litterboxes were randomly collected after 60, 180, and 360 days of the field experiment (6 December 2020, 4 April and 1 October 2021) according to the

canopy phenology and snow cover. WSC litterboxes were randomly collected after 120, and 300 days of the field experiment (4 April and 1 October 2021). After retrieving the litterboxes, any non-litter material, e.g., soil and dust, was gently cleaned from the litter surface and litter was oven-dried at 37 °C to a constant weight. A total of 288 litterboxes were used in the experiment (ACO: 2 species × 3 filter treatments × 2 plots × 4 collection times × 4 replicates; WSC: 2 species × 3 filter treatments × 2 plots × 2 collection times × 4 replicates). The ash-free

dry mass was determined after samples were treated in a muffle oven (550 °C for 5 h).

Litter trait measurements

Leaf mass per area (LMA) was determined using Fiji software (www.fiji.sc, IMAGEJ) based on the litter area and oven-dried weight of scanned leaves. Total C and N content were quantified using an elemental analyzer (Vario MACRO Cube, Germany). The lignin content was determined using an improved acetyl-bromide procedure (Fukushima and Hatfield 2001). Soluble sugar and starch contents were assessed through anthrone colorimetry. The litter initial traits are shown in Table S1.

Statistical analyses

The ash content was used to determine the ash-free dry weight of the litter mass and the biochemical contents (C, N and lignin). We used the following equations to calculate the mass loss ratio (M) and nutrient loss (Q) per unit mass during the process of the experiment.

$$M = (1 - X_t/X_0) \times 100\%$$

$$Q = 1 - (X_t \times Y_t)/(X_0 \times Y_0) \times 100\%$$

X_0 and X_t are dry mass, and Y_0 and Y_t are nutrient contents at the beginning of the experiment and at time t , respectively.

In order to examine each phase's decomposition dynamics, we calculated the loss ratio (%/day) of mass, C, N, and lignin.

$$\text{Loss}(\%/day) = (Q_t - Q_{t-1})/\Delta T$$

where Q_t , Q_{t-1} are the loss ratio of nutrient mass at time t and the previous time ($t - 1$), respectively. ΔT is the number of days between the two collection times.

We calculated the spectral response ratio of litter mass and nutrient (C, N, lignin) loss at each harvest, in order to clarify exactly which spectral regions were important for decomposition.

$$\text{Response ratio (RR)} = (Q_i - Q_j) / |Q_j|$$

where Q_i , Q_j are the mass and nutrients loss of litter in the filter treatment i and j , respectively.

The contrasts between the treatments transmitting solar radiation: >280 nm vs >580 nm, >280 nm vs >400 nm, >400 nm vs >580 nm, gave the effect of full-spectrum, UV, blue & green, respectively. As the RR value (e.g. RR_{uv}) increases above 0.0, more mass and nutrient loss increase, as attributable to each specific spectral region, e.g. litter that received or did not receive UV radiation.

Linear mixed effects models (LMM) were used to test the effects of canopy structure deployment time, filter treatment and their interactions on mass and nutrient (litter C, N and lignin) loss. Furthermore, least significant difference (LSD) was used to conduct multiple comparisons ($p < 0.05$). To evaluate the effect of autumn solar radiation on lignin loss, we performed t -test comparisons between ACO and WSC groups. Correlative relationships between lignin loss in the early stages of decomposition and changes in mass loss during the growing season were evaluated by linear regression using RStudio with ggplot2.

Results

Climate characteristics

Soil moisture among different filter treatments did not vary significantly both in the forest gap and understorey (Fig. 1B). The temperature was similar between the filter treatments within the plot, but was higher in the forest gap (mean value was 22.4 °C) than in the understorey (mean value was 16.7 °C) (Fig. 1C). The snowpack formed at the beginning of December and melted at the end of March, with the maximum depth 17 cm in the gap and 14 cm in the understorey (Fig. 1D). Cumulative solar irradiance during the experiment was higher in forest gap than understorey (Fig. 1E): the dose received by ACO and WSC litter was 832.83 and 515.66 MJ m⁻² in the understorey, respectively, and 2133.09 and 1729.09 MJ m⁻² in the gap, respectively.

Response of initial litter decomposition to change in autumn solar radiation

Initial litter decomposition (the first 60 and 120 days of decomposition for ACO and WSC, respectively) of both Asian white birch and Mongolian oak were driven by canopy structure, filter treatments, deployment time, and their interactions (Table 1). In general, ACO litter deployed just before snow cover had a higher mass loss rate, which up to 2.1 times than that of WSC litter, irrespective of species; ACO litter decayed faster in full-spectrum and No-UV treatments than No-UV&BG treatment (except for Asian white birch in the understorey) (Fig. 2A). ACO litter was more prone to lignin loss than litter mass and mass loss, particularly in the forest gap, and these processes occurred faster than that in WSC litter (Figs. 2A, B, 3A, B). However, WSC litter also exhibited a significant variation in lignin loss among filter treatments, with the exception of Mongolian oak in the understorey (Fig. 2B). N loss in ACO litter followed a similar pattern to that of lignin loss, however, N tended to be immobilized in WSC litter (Fig. 2D); for example, N loss in WSC litter of Mongolian oak was much lower in No-UV&BG treatment than other two filter treatments.

Table 1 Linear mixed-effects model (LMM) results of three fixed factors (canopy structure, filter treatments, and deployment time) and their interactions on mass and nutrient (C, N, and lignin) loss of *Betula platyphylla* and *Quercus mongolica* litter during the period from the autumn canopy opening to the winter snow cover (non-growing season)

Factor	DF	Mass loss		Lignin loss		C loss		N loss	
		χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>
<i>Betula platyphylla</i>									
Filter treatment (Ft)	3	11.25	0.004	572.19	< 0.001	27.28	< 0.001	218.99	< 0.001
Canopy structure (Cs)	1	36.66	< 0.001	56.31	< 0.001	0.91	0.341	30.21	< 0.001
Deployment time (Dt)	1	586.05	< 0.001	837.31	< 0.001	911.64	< 0.001	6316.62	< 0.001
Ft×Cs	3	10.12	0.006	72.24	< 0.001	5.42	0.067	100.27	< 0.001
Ft×Dt	3	40.99	0.014	248.73	< 0.001	8.52	0.014	175.99	< 0.001
Cs×Dt	1	0.72	0.390	34.81	0.007	80.79	< 0.001	27.35	< 0.001
Cs×Dt×Ft	3	0.68	0.710	23.32	< 0.001	5.65	0.079	113.43	< 0.001
<i>Quercus mongolica</i>									
Filter treatment (Ft)	3	34.96	< 0.001	294.99	< 0.001	9.34	0.009	239.23	< 0.001
Canopy structure (Cs)	1	4.11	0.042	49.28	< 0.001	1.53	0.828	2.17	0.141
Deployment time (Dt)	1	926.71	< 0.001	153.76	< 0.001	106.06	< 0.001	2279.93	< 0.001
Ft×Cs	3	1.24	0.567	20.88	< 0.001	13.69	0.001	34.60	< 0.001
Ft×Dt	3	38.16	< 0.001	102.95	< 0.001	3.93	0.140	4.46	0.108
Cs×Dt	1	17.72	< 0.001	16.02	< 0.001	0.12	0.740	0.00	0.988
Cs×Dt×Ft	3	1.126	0.569	12.49	0.002	7.05	0.029	0.88	0.645

p-values in bold indicate statistically significant differences ($p < 0.05$)

The majority of spectral response ratios (RR) for mass loss were positive for ACO litter irrespective of canopy structure and litter species (Fig. 4). Asian white birch had higher values of $RR_{\text{full-spectrum}}$ (0.16) and $RR_{\text{blue\&green}}$ (0.10) in the gap, and $RR_{\text{full-spectrum}}$ (0.10) and RR_{uv} (0.10) in the understorey. For Mongolian oak, the $RR_{\text{full-spectrum}}$ and $RR_{\text{blue\&green}}$ were higher (0.35 and 0.26 in the gap, and 0.25 and 0.23 in the understorey). $RR_{\text{full-spectrum}}$ and $RR_{\text{blue\&green}}$ were higher than RR_{UV} in most of cases. These results indicated that the full-spectrum significantly accelerated mass and lignin loss, and most of this effect was accounted by blue-green light rather than UV radiation for ACO of both species (Fig. 4A, B). Notably, positive RR values of lignin loss were also found for WSC litter of two species (Fig. 4B), even though the incubation started from the beginning of the winter snow cover, implying that photodegradation occurred in WSC litter.

Legacy effect of autumn solar radiation on litter mass loss during the growing season

The litter mass loss of Asian white birch and Mongolian oak varied significantly depending on canopy structure, filter treatments, deployment time, and their interactions during the growing season (Table 2). Both ACO and WSC litter experienced higher mass loss in full-spectrum and No-UV treatments compared to the No-UV&BG treatment in the forest gap, but not in the understorey, regardless of species (Fig. 5A). Their positive values of

RR (Fig. 6A) suggest that litter decomposition processes were promoted by photodegradation when litterboxes were re-exposed to solar radiation (especially blue-green light) during the growing season.

However, the relationships between mass loss for ACO and WSC indicated that ACO litter lost mass faster than WSC litter (Fig. 7A), suggesting there is a role for legacy effect of autumn solar radiation. For Asian white birch, the values of $RR_{\text{full-spectrum}}$ (1.34) and $RR_{\text{blue\&green}}$ (1.53) in ACO litter were higher than those in WSC litter (0.49 and 0.33) in the gap, and the difference between ACO and WSC was 83% and 119%, respectively. Such differences for Mongolian oak were 51% for $RR_{\text{full-spectrum}}$ and 42% for $RR_{\text{blue\&green}}$ (Fig. 6A, S3). Blue-green light was the main spectral region driving the legacy effect on litter decomposition during the subsequent growing season.

Legacy effect of autumn solar radiation on litter nutrient loss during the growing season

Canopy structure and filter treatments, interacting with deployment time, significantly affected litter nutrient loss in two tree species during the growing season (Table 2). Similar to litter mass loss, ACO and WSC litter showed faster lignin and C loss under full-spectrum and No-UV treatments than those under No-UV&BG treatment during the growing season in the forest gap, but not in the understorey (Fig. 5B, C). RR values indicated that blue-green light is the main spectral region accounting for

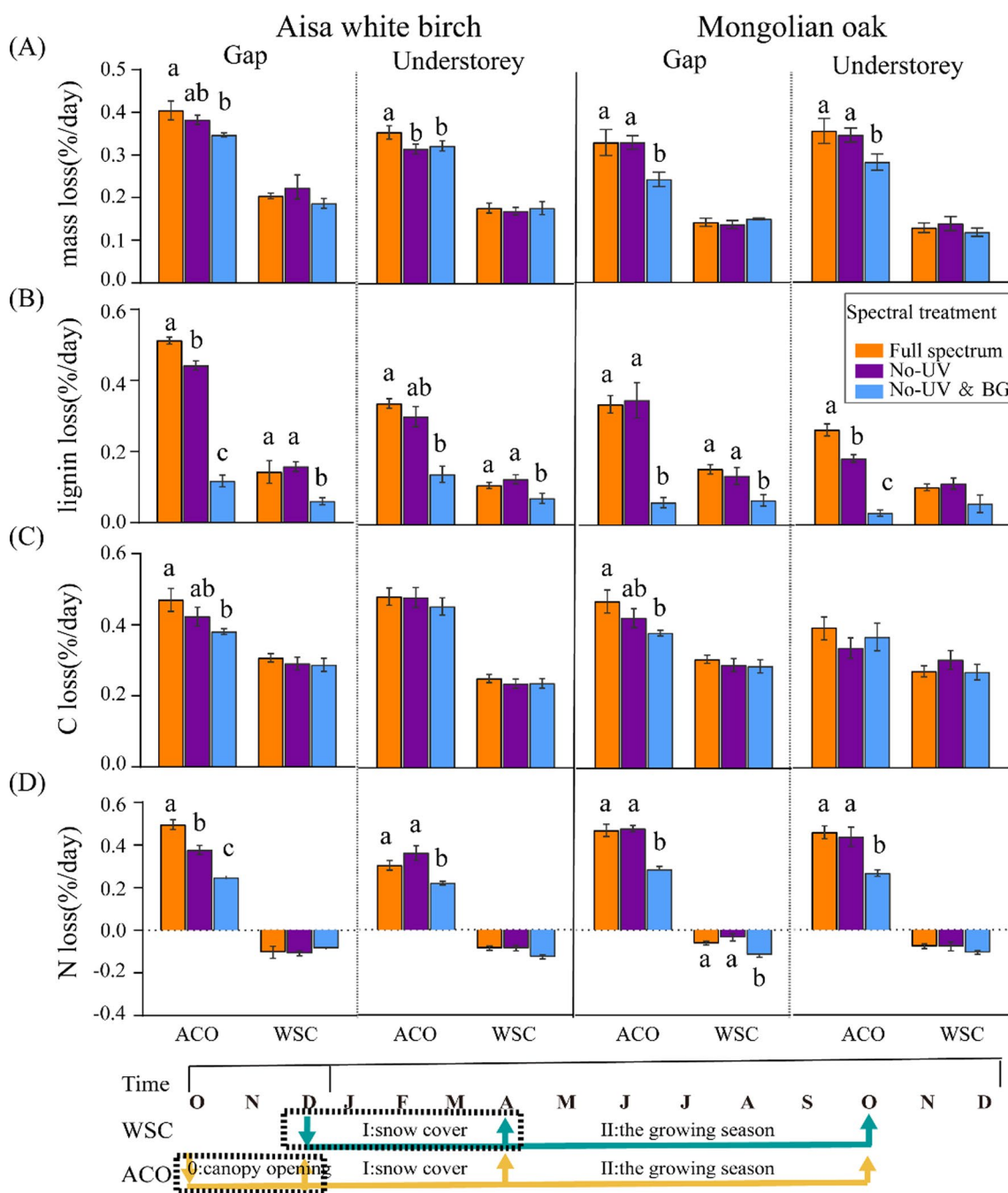


Fig. 2 Litter mass and nutrient loss under filter treatments during the initial decomposition. **A** Mass loss, **B** lignin loss, **C** C loss, and **D** N loss of *Betula platyphylla* (Asian white birch) and *Quercus mongolica* (Mongolian oak) under different filter treatments in the forest gap and understorey during the autumn canopy opening (ACO-0) and winter snow cover (WSC-I), which were highlighted with dotted rectangles. ACO and WSC represent litterboxes placed at the beginning of autumn canopy opening and at the beginning of winter snow cover, respectively. Different lowercase letters denote significant differences among different filter treatments ($p < 0.05$). ACO: Phase 0, forest canopy opening; I, snow cover; II, the growing season. WSC: Phase I, snow cover; II, the growing season

photodegradation during the growing season (Fig. 6B, C). Legacy effects of autumn solar radiation on lignin and C loss were particularly distinct for Asian white birch litter

of high quality (low lignin/N ratio, Table S1). Furthermore, lignin loss in ACO litter during the initial decomposition was positively correlated with mass loss during

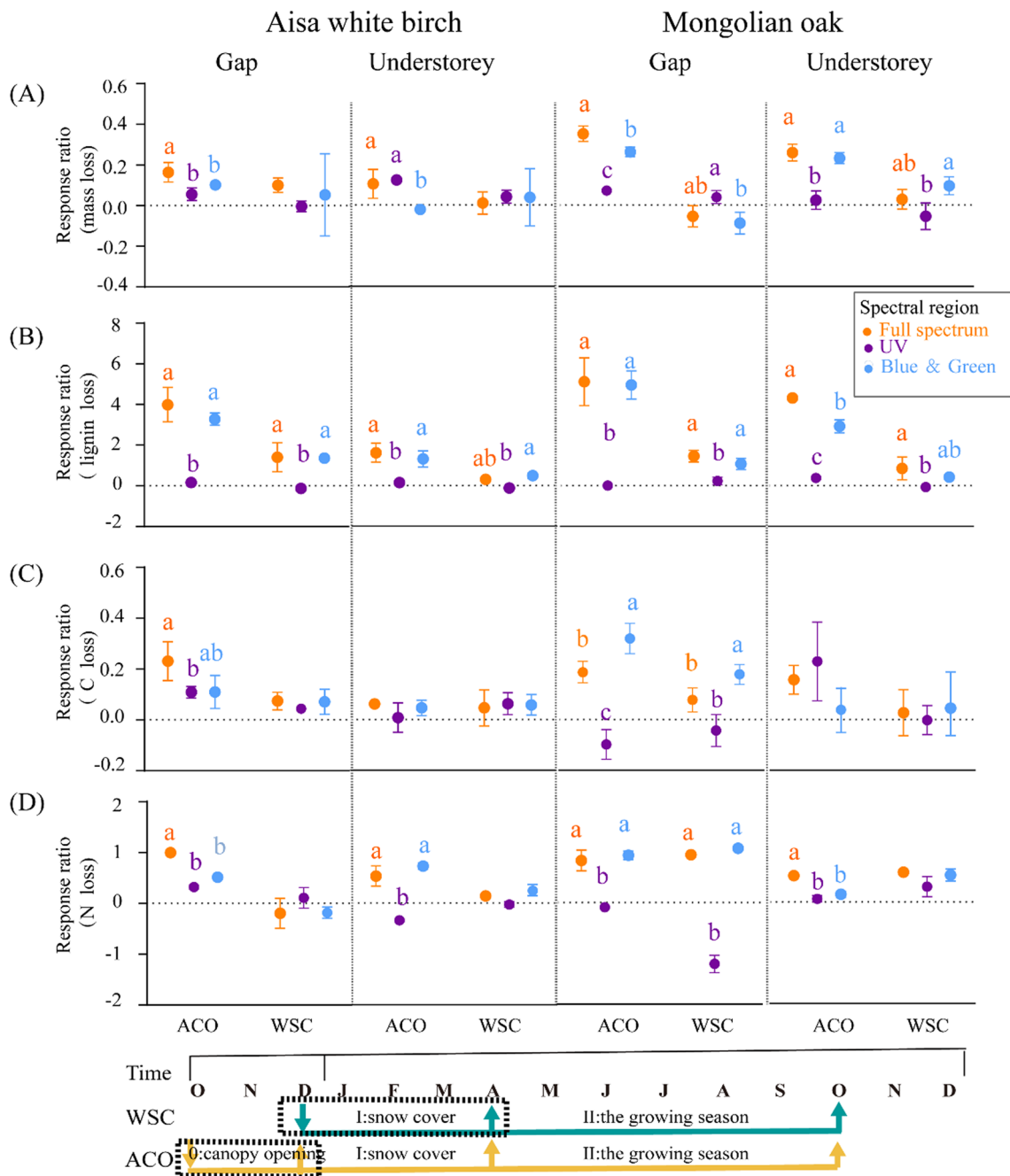


Fig. 3 The response ratio of litter mass and nutrient loss to solar spectral regions during the initial decomposition. **A** Mass loss, **B** lignin loss, **C** C loss, and **D** N loss of *Betula platyphylla* (Asian white birch) and *Quercus mongolica* (Mongolian oak) in the forest gap and understorey during the autumn canopy opening (ACO-0) and winter snow cover (WSC-I), which were highlighted with dotted rectangles. ACO and WSC represent that litterboxes were placed at the beginning of autumn canopy opening and at the beginning of winter snow cover, respectively. Different lowercase letters denote significant differences among different filter treatments ($p < 0.05$). ACO: Phase 0, forest canopy opening; I, snow cover; II, the growing season. WSC: Phase I, snow cover; II, the growing season

the second growing season, irrespective of species, while such a relationship for WSC litter was not detected (Fig. 8). This confirms that legacy effects of autumn solar

radiation were related to lignin photodegradation driven by blue-green light.

Although N loss varied among treatments consistently with lignin loss (except for WSC litter of Mongolian

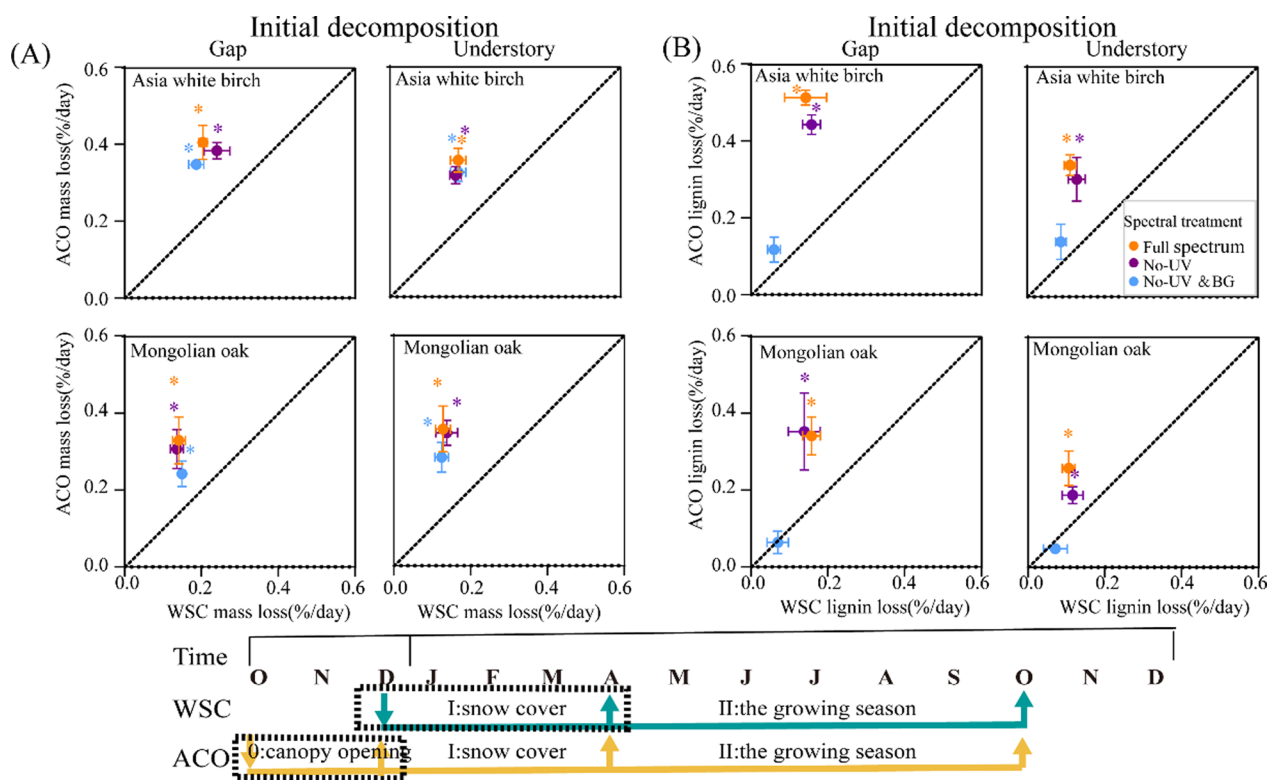


Fig. 4 1:1 line of litter mass and lignin loss with or without the exposure to autumn solar radiation during the initial decomposition. **A** Differences between ACO and WSC mass loss were analyzed under gap and understory; **B** Differences between ACO and WSC lignin loss were analyzed under gap and understory. ACO and WSC represent that litterboxes were placed at the beginning of autumn canopy opening and at the beginning of winter snow cover, respectively. ACO: Phase 0, forest canopy opening; I, snow cover; II, the growing season. WSC: Phase I, snow cover; II, the growing season

oak) (Fig. 5D), *RR* values of N loss from ACO litter were slightly higher than those of WSC litter (Fig. 6D). This suggests that legacy effects of autumn solar radiation were relatively weak for N loss during the growing season.

Discussion

Short-term photodegradation by autumn solar radiation accelerates initial decomposition

Photodegradation by autumn solar radiation was found to directly accelerate initial mass loss rates up to 16% and 10% for Asian white birch and 35% and 25% for Mongolian oak in the gap and understory, respectively (Figs. 2A, 4A) (H1). This effect was apparent despite a relatively short exposure period (60 days) between canopy opening and formation of the snowpack. Visible blue-green light was the main spectral region driving initial decomposition (Fig. 4A). This result aligns with previous findings that sunlight is an important contributor to C turnover through photodegradation even when solar irradiance under vegetation cover is relatively low (Pieristè et al. 2020b; Wang et al. 2021), or when a short

exposure period is considered (Lin et al. 2018), or even within a single day (Gliksman et al. 2017b). This finding implies that photodegradation occurs when litter is exposed to solar radiation irrespective of duration, time of year, or ecosystem in question.

Lignin, as a photosensitive component of leaf litter, was the target of photomineralization by solar radiation (particularly blue-green light, because of its strong absorbance) in the early decomposition (Fig. 4B), which is consistent with previous studies (Austin and Balzare 2010). Its partial breakdown through photodegradation is important for later biodegradation by fungal enzymes at a later stage of decomposition (Keiser et al. 2021). Moreover, the extent of lignin degradation in response to photodegradation was observed to be more pronounced in Mongolian oak than Asian white birch which has a lower initial lignin content (Table S1). This observation suggests that alterations in leaf-fall phenology among tree species with differing initial characteristics may potentially influence the significance of photodegradation in decomposition processes and

Table 2 Linear mixed-effects model (LMM) results of three fixed factors (canopy structure, filter treatments, and deployment time) and their interactions on mass and nutrient (C, N, and lignin) loss of *Betula platyphylla* and *Quercus mongolica* litter during the growing season

Factor	DF	Mass loss		Lignin loss		C loss		N loss	
		χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>
<i>Betula platyphylla</i>									
Filter treatment (Ft)	3	108.85	<0.001	31.88	<0.001	128.62	<0.001	104.71	<0.001
Canopy structure (Cs)	1	321.75	<0.001	233.35	<0.001	273.47	<0.001	370.47	<0.001
Deployment time (Dt)	1	92.43	<0.001	0.01	0.660	60.14	<0.001	24.28	<0.001
Ft×Cs	3	94.84	<0.001	8.68	0.013	100.82	<0.001	14.97	<0.001
Ft×Dt	3	42.94	<0.001	12.33	0.002	34.86	<0.001	19.14	<0.001
Cs×Dt	1	4.77	0.029	3.64	0.777	2.42	0.119	78.22	<0.001
Cs×Dt×Ft	3	76.44	<0.001	14.50	0.001	11.45	0.043	5.85	0.054
<i>Quercus mongolica</i>									
Filter-treatment (Ft)	3	295.53	<0.001	36.33	<0.001	81.35	<0.001	5.83	0.054
Canopy structure (Cs)	1	433.91	<0.001	34.37	<0.001	274.43	<0.001	38.31	<0.001
Deployment time (Dt)	1	6.92	0.0085	23.84	0.058	0.30	0.586	10.47	0.001
Ft×Cs	3	258.32	<0.001	5.67	0.059	57.87	<0.001	25.60	<0.001
Ft×Dt	3	22.43	<0.001	0.50	0.779	3.03	0.220	18.15	<0.001
Cs×Dt	1	39.61	<0.001	2.94	0.122	13.10	<0.001	3.40	0.065
Cs×Dt×Ft	3	4.90	0.087	14.31	<0.001	1.55	0.46	7.37	0.025

p-values in bold indicate statistically significant differences ($p < 0.05$)

subsequent carbon cycling within ecosystems in the context of climate change.

Interestingly, lignin content in WSC group also changed significantly among filter treatments (Figs. 2B, 4B). It was found that in situ solar radiation can be transmitted through the snow cover to a depth of 20–24 cm (about 10% of photosynthetically active radiation reaches a depth of 7 cm in the snowpack) (Robson and Aphalo 2019). Our results might imply that solar radiation penetrating through the snowpack can still accelerate litter decomposition during the winter when biodegradation may scarcely progress due to very low temperatures. Nevertheless, to better understand how spectral irradiance drives the C cycle under snow, further research is needed.

Pre-exposure to autumn solar radiation has a positive legacy effect on litter decay in the next growing season

We found that ACO litter lost mass faster than WSC litter (Fig. 3A), suggesting that initial photodegradation by autumn solar radiation has a positive legacy effect on litter decomposition in the next growing season (H2). Particularly in the forest gap, the legacy effect of full spectrum sunlight on mass loss could be increased by 83% and 51% for Asian white birch and Mongolia oak, respectively (Fig. S1). The most likely explanation of this effect is that photofacilitation of litter pre-exposed to solar radiation accelerates the degradation of lignin. This may

occur through an increase in the availability of labile carbohydrates (saccharification) and microbial enzymatic activity of the litter (Méndez et al. 2022). Similar to tropical and subtropical regions, over-winter standing dead litter decays faster in the following year than litter that falls to the ground in the autumn (Jiang et al. 2023). In Mediterranean ecosystems, solar radiation doubles litter C loss through direct photochemical mineralization in the dry summer and its positive legacy accelerates biotic degradation in the winter (Berenstecher et al. 2020). This pattern of photoprimering followed by photofacilitation suggests that changes in vegetation cover or phenology due to climate change and/or land use will generally alter C loss from above-ground litter through sunlight exposure.

Precipitation (or moisture) may be a significant abiotic factor determining the legacy effects of photodegradation on litter decomposition. The fragmentation of recalcitrant compounds not only increased microbial degradation in cool and moist understorey, but also promotes leaching during the growing season. This can be particularly important in temperate continental monsoon climates, such as our study site where precipitation is relatively frequent during the summer. Day et al. (2022) found that exposure to sunlight nearly doubled litter mass loss, and accelerated decay by 2.6 times if precipitation was supplemented (Day et al. 2022). A recent meta-analysis indicates that photodegradation

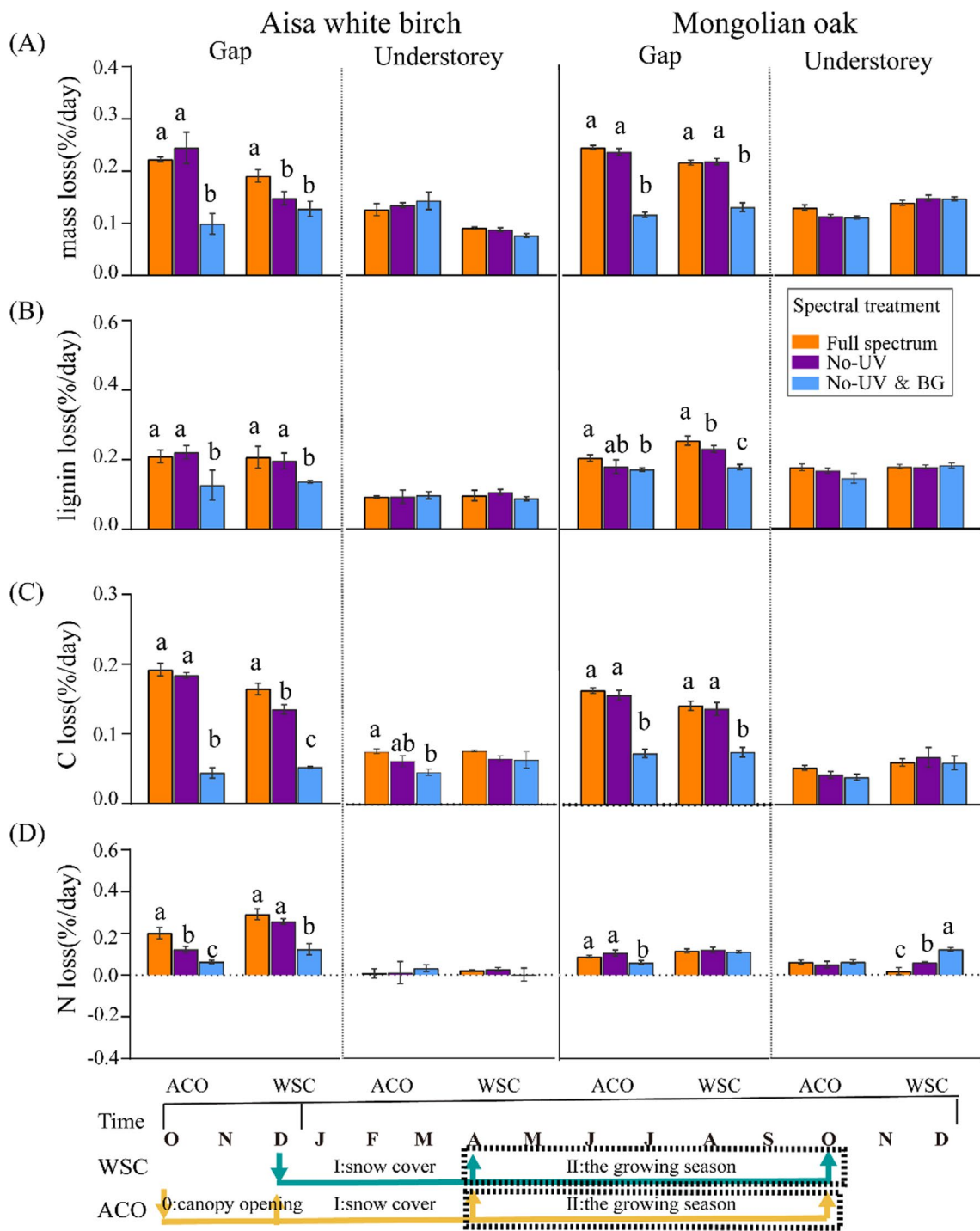


Fig. 5 Litter mass and nutrient loss under filter treatments during the following growing season. **A** Mass loss, **B** lignin loss, **C** C loss, and **D** N loss of *Betula platyphylla* (Asian white birch) and *Quercus mongolica* (Mongolian oak) under different filter treatments in the understory and gap at the ACO-II and WSC-II phase, which were highlighted with dotted rectangles. ACO and WSC represent that litterboxes were placed at the beginning of autumn canopy opening and at the beginning of winter snow cover, respectively. Different lowercase letters denote significant differences among different filter treatments ($p < 0.05$). ACO: Phase 0, forest canopy opening; I, snow cover; II, the growing season. WSC: Phase I, snow cover; II, the growing season

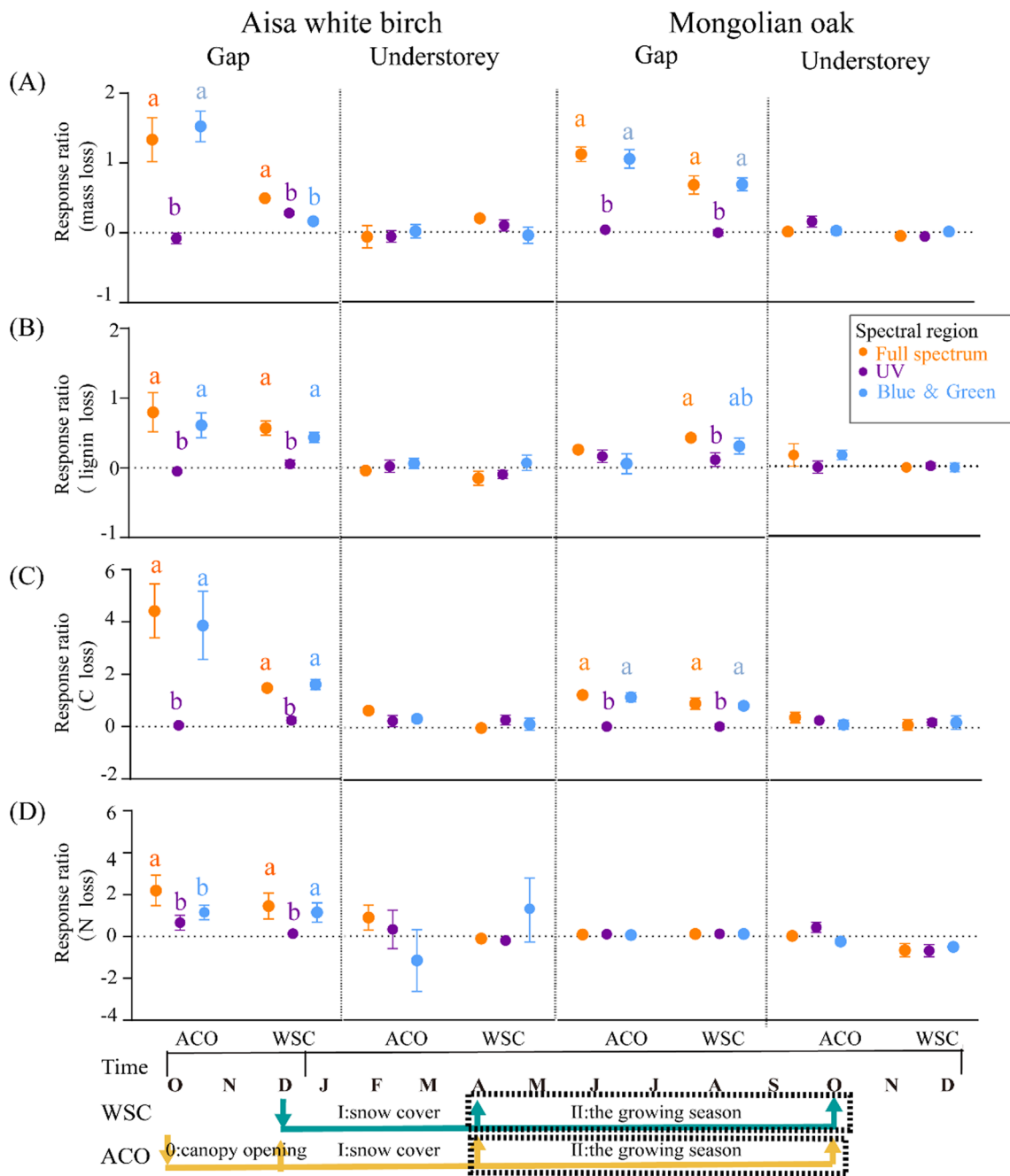


Fig. 6 The response ratio of litter mass and nutrient loss to solar spectral regions during the following growing season. **A** Mass loss, **B** lignin loss, **C** C loss, and **D** N loss of *Betula platyphylla* (Asian white birch) and *Quercus mongolica* (Mongolian oak) in the forest gap and understorey at the ACO-II and WSC-II phase, which were highlighted with dotted rectangles. ACO and WSC represent that litterboxes were placed at the beginning of autumn canopy opening and at the beginning of winter snow cover, respectively. Different lowercase letters denote significant differences among different filter treatments ($p < 0.05$). ACO: Phase 0, forest canopy opening; I, snow cover; II, the growing season. WSC: Phase I, snow cover; II, the growing season

is similar in arid and humid regions (with precipitation levels below 200 and above 800 mm) (Liu et al. 2023). This suggests that the photodegradation pathways of litter would shift from photomineralization to

photofacilitation with increasing precipitation through leaching and microbial regulation. Therefore, long-term field experiments that cover the main biotic and abiotic factors are essential for predicting litter decomposition

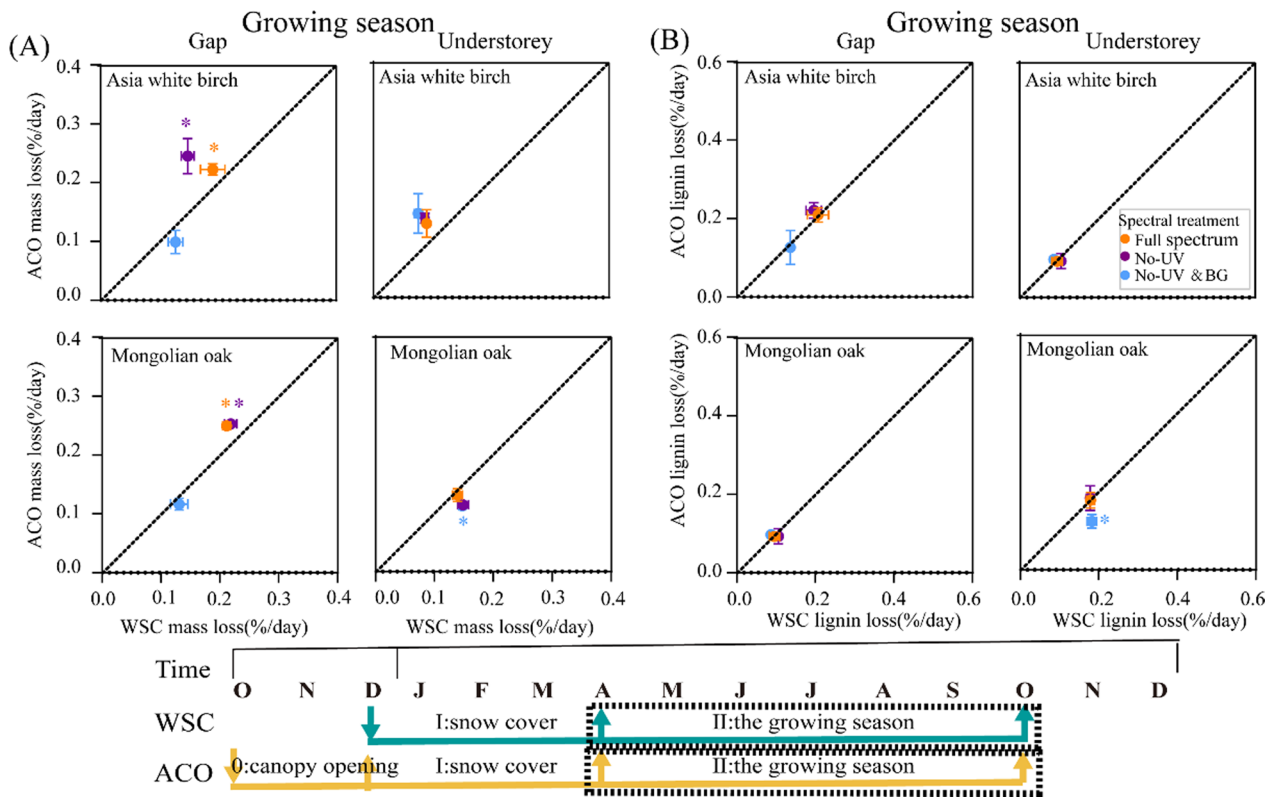


Fig. 7 1:1 line of litter mass and lignin loss with or without the exposure to autumn solar radiation during the following growing season. **A** Differences between ACO and WSC mass loss were analyzed under gap and understorey; **B** Differences between ACO and WSC lignin loss were analyzed under gap and understorey. ACO and WSC represent that litterboxes were placed at the beginning of autumn canopy opening and at the beginning of winter snow cover, respectively. ACO: Phase 0, forest canopy opening; I, snow cover; II, the growing season. WSC: Phase I, snow cover; II, the growing season

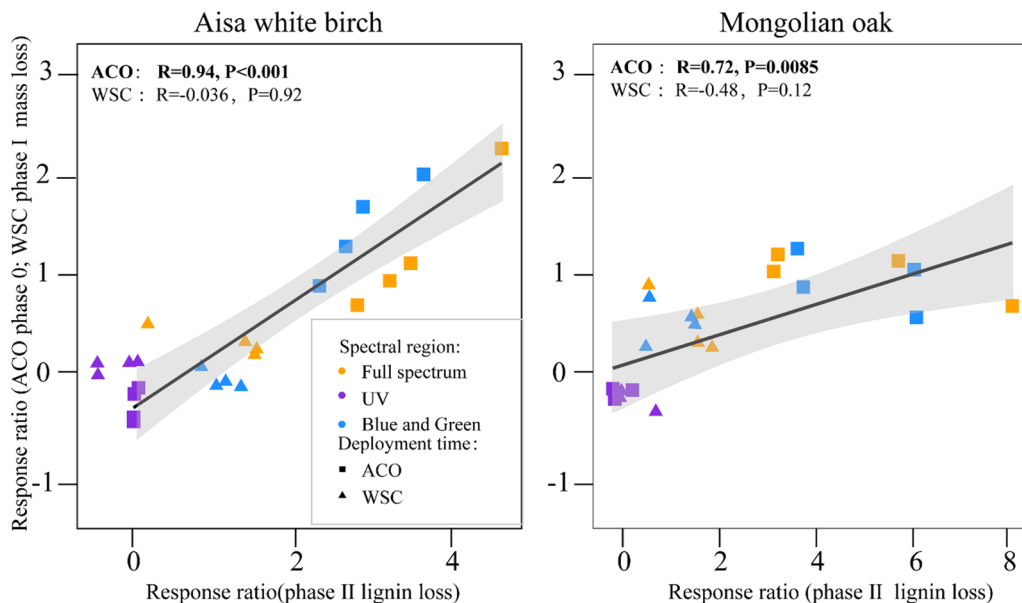


Fig. 8 Relationship between response ratios of ACO phase 0 and WSC phase I lignin and phase II mass loss to spectral regions. ACO and WSC represents that litterboxes were placed at the beginning of autumn canopy opening and at the beginning of winter snow cover, respectively. ACO: Phase 0, forest canopy opening; I, snow cover; II, the growing season. WSC: Phase I, snow cover; II, the growing season

and ecosystem function in response to changing climate.

Pre-exposure to autumn solar radiation modifies N dynamic during litter decomposition

N loss was faster in litter exposed for two months to autumn solar radiation than in litter placed just before snow cover (Figs. 2D, 4D). This indicates that N was mineralized with or without effects of photodegradation driven by blue-green light on the initial decomposition, and immobilized without sufficient exposure to solar radiation, as we hypothesized (H3). The results are consistent with previous studies showing that higher solar irradiance promotes nutrient release during the initial decomposition (Méndez et al. 2022; Wang et al. 2022b, 2023). The finding is contrary to traditional viewpoints that N tends to be initially immobilized because of bacterial action during the early stages of decomposition (Pei et al. 2019), but this perspective does not account for the effect of solar radiation. Here, N immobilization occurred in litter which started to decompose under the snowpack (Fig. 2D), where the ambient temperature and humidity benefit microbial activity (Gao et al. 2018) but not in litter that had been subject to pre-treatment over autumn in solar radiation. Given that pre-exposure to autumn solar radiation alleviates the bottleneck for N dynamic in litter decomposition, a change in autumn tree phenology would be expected to alter N cycling in the understorey.

N was released in both litter groups during the growing season in later decomposition (Figs. 5D, 6D). However, the magnitude of N release was greater in the forest gap than that in the understorey, suggesting that canopy structure may modulate the effect of solar radiation on N dynamics during litter decomposition. Similar results have been detected in various litter types, such as leaves, twigs, and logs (Wang et al. 2023, 2022b; Wu et al. 2023).

It is generally accepted that climate change will extend the autumn growing season and delay leaf-fall in temperate forest systems. Interspecific differences in phenological responses will largely determine litter decomposition processes and ecosystem carbon cycling, interacting with snow cover which may occur later in a warmer climate. Furthermore, the interplay between stratospheric ozone, climate factors (i.e. cloud cover), and land use practices (i.e. deforestation) can alter the exposure of litter to sunlight (Calinger and Curtis 2023; Li et al. 2021; Barnes et al. 2022). Future research should aim to provide quantification of how solar radiation affects greenhouse gas emissions and nutrient cycling in temperate forest ecosystems in the context of climate change.

Conclusion

The influence of autumn solar radiation on photodegradation significantly accelerates the initial mass loss rates of litter from two deciduous tree species, both in forest gap and the understorey, prior to the formation of the snowpack in a temperate forest in northeast Asia. Lignin was the primary target of photomineralization, mainly driven by blue-green light during the initial decomposition. Importantly, short-term photodegradation by autumn solar radiation has a legacy effect that accelerates mass loss through litter decomposition during the next growing season by 16% and 19% for Asian white birch and Mongolia oak, respectively, in the forest gap. N dynamics were dominated by N mineralization when litter was exposed to autumn solar radiation, N in the late fallen leaves is predominantly immobilization due to snow cover, but during the following growing season N was released from both litter groups subject to autumn solar radiation and those that started to decompose later. This suggests that changes in deciduous phenology and snow cover timing will affect C and N cycling in temperate forest ecosystems interacting with canopy structure and climate change, which alter plant organic matter exposure to solar radiation.

Abbreviations

ACO Autumn canopy opening
WSC Winter snow cover

Supplementary Information

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Supplementary Material 1.

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Not applicable.

Author contributions

QWW and JJD conceived and designed the experiment. XZL and YNW were responsible for project management, including leaf litter collection and the construction of the field decomposition experiment. They managed and retrieved litterboxes, and measured ash-free mass loss and nutrient losses. XZL curated the data, created visualizations, and wrote the original draft of the manuscript, with the remaining coauthors contributing to revisions.

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Availability of data and materials

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors agreed and approved the manuscript for publication in *Ecological Processes*.

Competing interests

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

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