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Sunlight promotes aboveground carbon loss by producing polysaccharides from litter decomposition in a temperate forest

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Abstract Photodegradation is considered as a universal contributing factor to litter decomposition and carbon (C) cycling within the Earth's biomes. Identifying how solar radiation modifies the molecular structure of litter is essential to understand the mechanism controlling its decomposition and reaction to shifts in climatic conditions and land-use. In this study, we performed a spectral-attenuation experiment following litter decomposition in an understory and gap of a temperate deciduous forest. We found that short-wavelength visible light, especially blue light, was the main factor driving variation in litter molecular structure of *Fagus crenata* Blume, *Quercus crispula* Blume, *Acer*

carpinifolium Siebold & Zuccarini and *Betula platyphylla* Sukaczew, explaining respectively 56.5%, 19.4%, 66.3%, and 16.7% of variation in its chemical composition. However, the variation also depended on canopy openness: Only in the forest gap was lignin aromatic C negatively associated with C-oxygen (C–O) bonding in polysaccharides receiving treatments containing blue light of the full spectrum of solar radiation. Regardless of species, the decomposition index of litter that explained changes in mass and lignin loss was driven by the relative content of C–O stretching in polysaccharides and lignin aromatic C. The results suggest that the availability of readily degradable polysaccharides produced by the reduction in lignin aromatic C most plausibly explains the rate of litter photodegradation. Photo-products of photodegradation might augment the C pool destabilized by the input of readily degradable organic compounds (i.e., polysaccharides).

Lu Chang and Jiaojiao Deng made equal contributions to this paper.

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Introduction

Litter decomposition is a crucial ecological process for carbon (C) and nutrient conversion within ecosystems, driving plant productivity and the C balance of the soil organic matter pool across terrestrial ecosystems (Bradford et al. 2016; Li et al. 2023a; Zhang et al. 2024). Photodegradation driven

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by solar radiation has been considered to be a universal contributor to litter decomposition and C cycling in terrestrial ecosystems (Erdenebileg et al. 2018; Barnes et al. 2023; Wang et al. 2023). The relative importance of solar radiation to decomposition and C turnover depends on abiotic and biotic factors, especially initial litter traits, solar spectral compositions, vegetation cover, and seasonal changes (Deng et al. 2023; Li et al. 2023a, 2023b; Wang et al. 2023). Exploring the mechanism of how solar radiation drives litter decay is crucial to predict C cycling and its associated feedback to climate change.

Photodegradation directly breaks down organic matter and promotes greenhouse gas (e.g., CH₄ and CO₂) emissions through photochemical mineralization of complex macromolecular compounds which absorb ultraviolet (UV) radiation (290–400 nm) and short-wavelength visible light [blue and green light (BG), 400–600 nm] (Keiser et al. 2021; Austin and Ballaré 2024). Non-gaseous photoproducts such as polysaccharides, organic acids, aldehydes, alcohols, and phenols are soluble or readily decomposable (Day et al. 2018; Méndez et al. 2022). They can further accelerate microbial decay through photofacilitation (Berenstecher et al. 2020; Li et al. 2024) and leaching from litter (Day et al. 2022). In addition, the leachate transported belowground may regulate the stability of soil organic carbon (SOC) through soil priming effects. These processes suggest that litter chemical composition influences photodegradation of litter organic C and decomposition.

Litter chemical composition (i.e., lignin, hemicellulose, and cellulose) differs in light absorption coefficients, bond energy, as well as resistance to microbial decomposition (Austin and Vivanco 2006; Ranade and García-Gil 2024; Zhao et al. 2024). Lignin, as a complex group of aromatic polymers, exists in cell walls and is a photo-receptive compound which is preferentially degraded due to photodegradation (Austin and Ballaré 2010, 2024). Solar radiation, particularly UV radiation and BG light, accelerates lignin degradation (Wang et al. 2021). In general, a higher lignin

concentration in the litter tends to correlate with a stronger photodegradation effect (Wang et al. 2021). However, litter chemical compounds are large and complex polymers. Quantifying how solar radiation modifies characteristics of the C molecular structure is essential to evaluate and predict litter photodegradation and its subsequent effects on SOC.

The molecular structure and abundance of organic C in plant litter have been explored to investigate the possible mechanisms of photodegradation through Fourier Transform Infrared (FTIR) analysis (Soong et al. 2014). This has found aromatics and alkyl signals assigned to lignin to be less intense after two months exposure to solar radiation (Farnet Da Silva et al. 2023). UV radiation can reduce the relative abundance of aromatic C, methoxyl C, and N-alkyl (Yao et al. 2022). Furthermore, a change in environmental conditions, particularly increased moisture, means polysaccharides from lignocellulose may further facilitate litter conversion (Farnet Da Silva et al. 2023) and promote subsequent microbial decomposition (Yao et al. 2022). However, these findings have only been derived from experiments in microcosms. The general response of organic C molecular structure to solar radiation and its contribution to *in-situ* decomposition (i.e., in forest ecosystems) remains unclear.

In forest ecosystems, canopy structure and phenology determine spectral composition and irradiance intensity reaching the ground throughout the year (Hartikainen et al. 2020; Tang et al. 2024; Xie et al. 2024). Research has found that, even in the understory with comparatively low solar radiation, photodegradation can facilitate C turnover (Pieristè et al. 2019). Our recent study indicated that exposure to the full radiation spectrum and its blue light fraction can increase litter decay rates by nearly 120% and 90%, respectively (Wang et al. 2023). However, the transformations within C molecular structure attributable to photodegradation through litter decomposition remain unknown. This information gap limits our understanding of the interactive effects of solar radiation, land-use change and climate change on litter decomposition and forest C cycling.

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To address this issue, we evaluated the response of the C molecular structure of litter to solar radiation during litter decomposition by a factorial experiment with spectral-attenuation treatments in the understory and gap in a temperate deciduous forest. Our hypotheses were: (1) solar radiation would significantly modify the molecular structure of C in litter in the forest gap, where irradiance intensity is higher than in the understory; (2) short-wavelength visible light, especially blue light, would accelerate litter decomposition by reducing lignin aromatic C and increasing carbon–oxygen (C–O) stretching in polysaccharides.

Materials and methods

2.1 Study description

The study area was located in the Ogawa Forest Reserve (OFR, c. 100 ha) (36°56′ N, 140°35′ E) in northern Ibaraki Prefecture, central Japan, which is characterized by severe winters and summer monsoons with average annual precipitation and temperatures of 1750 mm and 12.4 °C. The mature and old-growth forests are mainly dominated by *Fagus crenata* Blume. Detailed site information is found in a previous study (Wang et al. 2022). A 50 m × 50 m plot was established in the understory of the OFR, and four blocks in the plot where the light environment was naturally influenced by seasonal canopy changes. A similar-sized plot with four blocks in the gap outside the OFR approximately 5-km away was created less than a year before the experiment, which provided an ambient light environment and comparable soil conditions with the understory plot. Topographical factors, including gradient (20°), aspect (south, 180°), and slope, were also similar in the two plots. Plots were protected against wild mammals (mainly boars) by fences.

2.2 Litter collection

Freshly fallen leaves of *F. crenata* Blume, *Quercus crispula* Blume, *Acer carpinifolium* Siebold & Zuccarini, and *Betula platyphylla* Sukaczew were collected in October, 2017. Leaf litter samples, without petioles, were pressed in newspapers with wooden frames and air-dried in a dark room at 25 °C before transferring them to litter-boxes.

2.3 Experimental design and measurement

Litter-boxes were prepared according to our previous design (Wang et al. 2022). Litter-box frames were made of sterile plastic straws (1.3 cm diameter, 21 cm long and 18 cm wide; Bihin, Japan). The tops were equipped with various spectral filters, including Full-spectrum (transmitting solar radiation > 280 nm), No-UV-B (> 315 nm), No-UV (> 400 nm),

No-UV/Blue (> 500 nm), No-UV/Blue-Green (No-UV/BG) (> 580 nm), and Dark (no light) treatments, according to Wang et al. (2022). We drilled 2-mm holes into the filters to allow air, moisture, and microbes to interact with the litter. A sterile 2-mm polyethylene fiber mesh was placed on the bottom of the litter-boxes to allow only mesofauna access to the litter. Leaves (2–8 per species, 1.0 g) were fixed on the bottom mesh with stainless steel staples.

Litter boxes were randomly laid out on the soil in four blocks in each plot on April 18, 2018 (before canopy flushing). Plots were checked every two weeks and any debris on the litter-boxes were removed. Four replicate litter-boxes were randomly collected at 50, 110, 170 and 230 days of the experiment (June 7, August 6, October 5, and December 4, 2018), corresponding to the canopy phenology from canopy flush, completely closed canopy, leaf senescence, and autumn canopy opening, respectively.

Retrieval litter-boxes were cleaned and air-dried at 25 °C in a dark room to a constant weight. The experiment included a total of 768 litter-boxes (2 plots × 4 litter species × 6 filter-treatments × 4 replicates × 4 collection times). The ash-free mass was determined with a muffle oven (550 °C for 5 h). Lignin content was measured by an improved acetyl-bromide procedure (Fukushima and Hatfield 2001). Lignin content of *F. crenata* and *A. carpinifolium* were 21.3% and 23.0%, respectively, significantly higher than those of *Q. crispula* (16.4%) and *B. platyphylla* (15.7%).

2.4 Fourier Transform Infrared (FTIR) spectroscopy

FTIR spectroscopy was used to detect the vibration characteristics of chemical functional groups within a sample by measuring the absorbance versus wave number. We ground 2.0 mg of litter in 200 mg of potassium bromide (KBr) and pressed the mixture into a pellet for analysis by transmission FTIR. FTIR spectra were measured using a Nicolet 6700 FTIR spectrometer in absorbance mode at 4 cm⁻¹ resolution and 4000–400 cm⁻¹ wave number. The spectra consisted of 64 scans and were corrected against the spectrum of the KBr pellet in ambient conditions (Lei et al. 2023).

2.5 Statistical analyses

Based on Omnic software baseline correction and normalization, the characteristic peaks in FTIR spectra in different samples were analyzed (Lei et al. 2023). A principal component analysis (PCA) was conducted to detect variations in the FTIR spectral dataset in relation to litter molecular structure and spectral treatments (Jolliffe 2009). Redundancy analysis (RAD) was assessed the comparative impacts of spectral irradiance (measured below filters) on chemical functional groups, mass loss and lignin loss using the vegan package with RStudio. Statistical significance was analyzed

through the Monte Carlo permutation methods and Bonferroni's test (permutations = 999 times, $P < 0.05$).

The effect of solar spectrum on lignin aromatic C and C–O stretching in polysaccharides was estimated as a change between spectral contrasts, transmitting solar radiation: > 280 nm versus > Dark treatment, > 280 nm versus > 315 nm, > 315 nm versus > 400 nm, > 400 nm versus > 500 nm, > 500 nm versus > 580 nm, and > 580 nm versus Dark treatment, gave the Full spectrum from UV-B to Red light, UV-B, UV-A, Blue, Green, and Red light, respectively. The change in each factor was estimated as the \ln (Napierian logarithm) ratio of 280 nm divided by Dark treatment, $\ln(> 280 \text{ nm/Dark treatment})$. As the RR value (i.e., RR_{Blue}) increased above zero, more chemical functional groups were accumulating, attributed to a specific spectral region such as blue light compared with litter that did not receive blue light. Litter mass loss and lignin loss were calculated as: $T_0 - T_i$, where T_0 is the initial litter mass or lignin mass and T_i the remaining litter mass or lignin mass. The relationships between the mass loss/lignin loss and PC1 were examined by linear regressions. The effect of the different solar spectrum (i.e., blue) on the changes of lignin aromatic C and C–O stretching in polysaccharides was calculated by subtracting the measured variable under 400 nm from the measured variable under 500 nm. The correlation between polysaccharides and lignin degradation was analyzed using linear regression. All analysis and figures were done using R version 4.2.3 software with ggplot2.

Results

3.1 Molecular structures of litter

Litter spectra displayed a range of distinct peaks between 2000 and 800 cm^{-1} in fingerprint region. Overall, FTIR spectra of different filter-treatments obtained at 230 days showed a degree of similarity between *F. crenata*, *Q. crispula*, *A. carpinifolium* and *B. platyphylla* (Fig. 1). The fingerprint region contained eight bands representing functional groups associated with the different compounds in litter, with bands from 1660 to 1630 cm^{-1} and from 1170 to 950 cm^{-1} (Fig. 1). The peak at 1050 cm^{-1} could be assigned to C–O stretching in polysaccharides or polysaccharide-like substances (Madari et al. 2006). It could also be assigned to C=O (carbonyl groups) at 1660–1630 cm^{-1} , adsorbed O–H, conjugated C=O, and I-amide (Madari et al. 2006). Bands in the region of 1430–1422 cm^{-1} , 1470–1450 cm^{-1} and 1515–1505 cm^{-1} could be assigned to aromatic skeletal vibrations combined with C–H in-plane deform, C–H deformation (methyl and methylene) in monolignols aliphatic C–H, and aromatic skeletal vibration of lignin, respectively; these bands may reflect lignin content (Faix 1991; Saparrat

et al. 2010) (Table S1). The results of our analysis are based on FTIR wave numbers associated with polysaccharides and lignin functions listed in Table S1.

3.2 Response of litter molecular structure to spectral attenuation treatments during decomposition

The initial litter molecular structure from *F. crenata*, *Q. crispula*, *A. carpinifolium* and *B. platyphylla* was significantly different along PC1 (explaining 70.71% of the variation) ($R = 0.71$, $P = 0.001$) (Fig. S1a). The separations on PC1 were principally driven by C–O stretching in polysaccharides, aromatic skeletal vibrations combined with C–H, aromatic skeletal vibrations plus C=O stretching, and C=O stretching in unconjugated ketone carbonyl group. Compared to *Q. crispula* and *B. platyphylla*, *F. crenata* and *A. carpinifolium* litter had more C–O stretching in polysaccharides and aromatic skeletal vibrations combined with C–H, and less aromatic skeletal vibrations plus C=O stretching and C=O stretching in unconjugated ketone carbonyl (Fig. S1b; Table S1). When comparing the FTIR spectra of the four different litter from the different filter-treatments, the degradation level under No-UV/BG, No-UV/Blue and Dark treatments (that attenuated blue light) segregated along PC1 (explained 44.09%–77.61% of the variation) from the other groups in the forest gap (*F. crenata*: $R = 0.35$, $P < 0.001$; *Q. crispula*: $R = 0.21$, $P < 0.001$; *A. carpinifolium*: $R = 0.43$, $P < 0.001$; *B. platyphylla*: $R = 0.24$, $P < 0.001$) (Fig. 2). For all species, wave numbers with the highest eigenvector loading among Full-spectrum, No-UV-B, and No-UV treatments (left end of PC axis 1; Fig. 2) were 1119–1011 cm^{-1} , suggesting the dominance of C–O stretching in polysaccharides. In contrast, wave numbers with the highest eigenvector loadings among No-UV/BG, No-UV/Blue and Dark treatments (right end of PC axis 1; Fig. 2) were 1610–1601, 1515–1508, 1457–1450, and 1430–1427 cm^{-1} , suggesting the dominance of lignin aromatic C, whereas no similar patterns were found among different litter treatments in the understory (Fig. S2).

In addition, how solar radiation affected the molecular structure of litter during the decomposition process in the forest gap was investigated. After 50 days decomposition, different patterns along PC1 were observed between No-UV/BG, No-UV/Blue, plus Dark treatments and Full-spectrum, No-UV-B, plus No-UV treatments for both *F. crenata* and *A. carpinifolium* (Figs. S3, S4). PC1 was explained mainly by C–O stretching in polysaccharides and lignin aromatic C. For litter of both *Q. crispula* and *B. platyphylla*, No-UV/BG, No-UV/Blue, and Dark treatments were differentiated from others according to PC1 at 50 days, 110 days, and 230 days in the forest gap (Figs. S5, S6). PC1 was explained mainly by C–O stretching in polysaccharides, C=O stretching in unconjugated ketone carbonyl and lignin aromatic C at 50 days and 110 days, while PC1 was explained mainly by

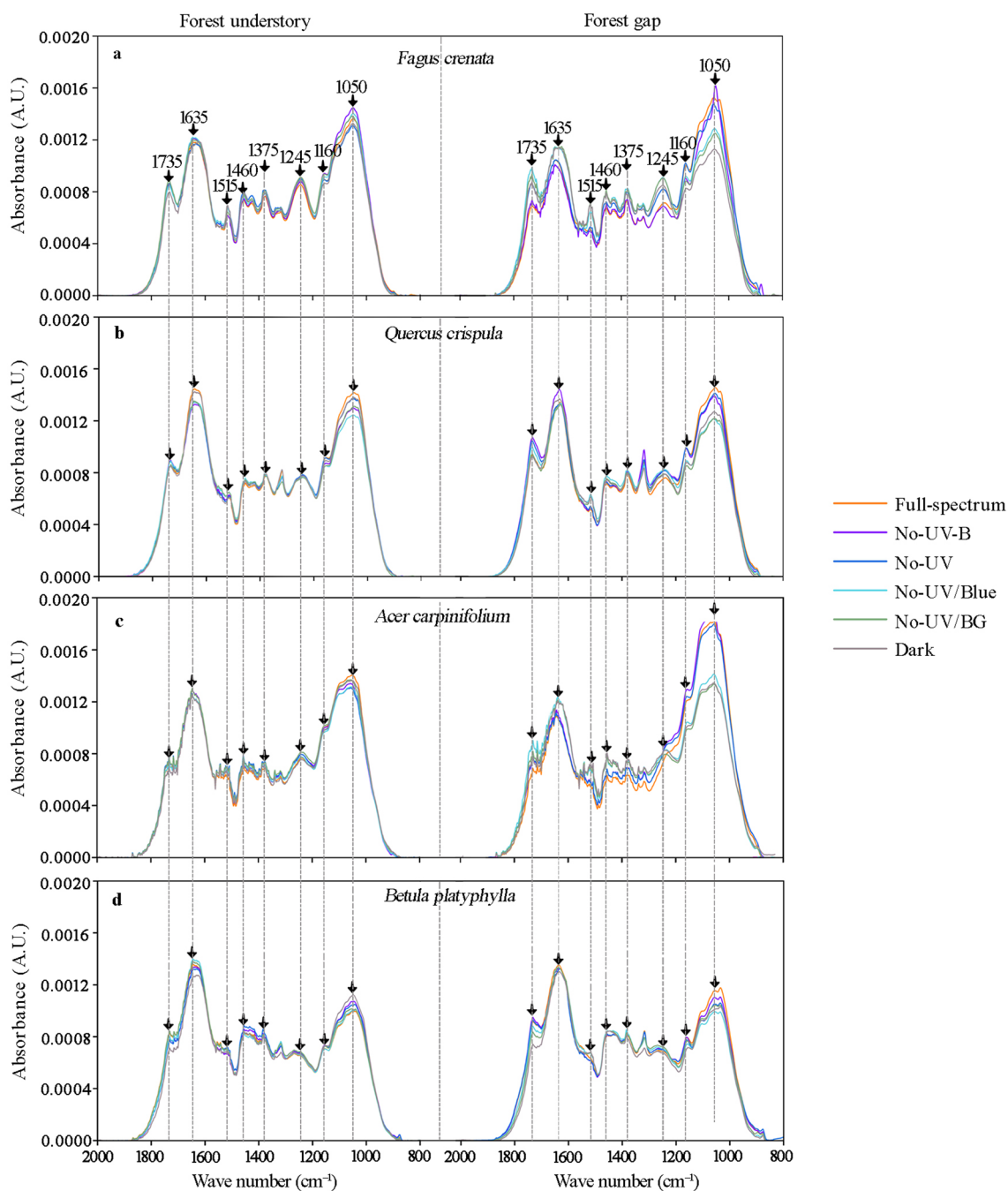


Fig. 1 Fourier Transform Infrared (FTIR) spectra of litter in the gap and understory under spectral-attenuation treatments; **a** *Fagus crenata*, **b** *Quercus crispula*, **c** *Acer carpinifolium*, and **d** *Betula platyphylla*. Peak labels indicate similarities among species

C–O stretching in polysaccharides and lignin aromatic C at 230 days.

3.3 Effects of spectral regions on litter molecular structure

Variation in the litter molecular structure of C–O stretching of polysaccharides and lignin aromatic C was significantly

driven by spectral regions. For *F. crenata*, *Q. crispula*, *A. carpinifolium* and *B. platyphylla*, blue light was the main factor driving variations in litter molecular structure, explaining 56.5%, 19.4%, 66.3%, and 16.7% of the chemical composition variations, respectively (Fig. 3; Fig. S7; Table S2; Table S3). In addition, blue light had a positive effect on C–O stretching of polysaccharides and a negative one on lignin mass, mass loss and lignin aromatic C

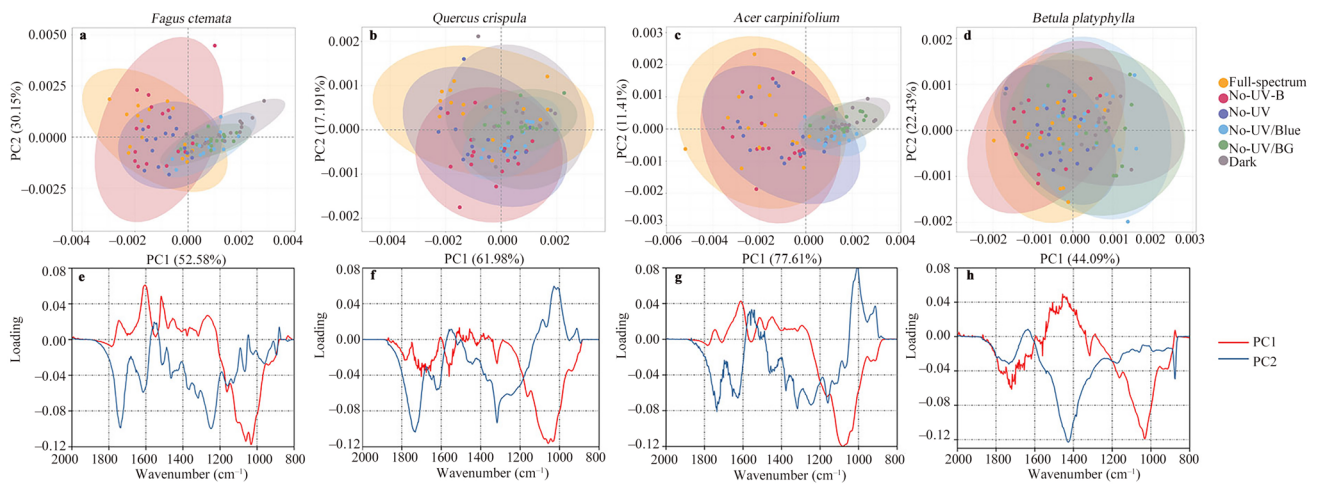


Fig. 2 Principal component analysis (PCA) of FTIR spectra of litter in the forest gap under spectral-attenuation treatments. Biplot resulting from PCA of **a** *Fagus crenata*, **b** *Quercus crispula*, **c** *Acer carpinifolium*, and **d** *Betula platyphylla*. **e–h** Line charts for loadings, the largest are at polysaccharides characteristics and lignin regions, being mainly responsible for the variation in PC1

(Fig. 3; Fig. S7). The relative impact of spectral regions on polysaccharides and lignin aromatic C at the last collection was also quantified. For all species, $RR_{Full\ spectrum}$ and RR_{Blue} consistently produced a positive response on the C–O stretching of polysaccharides and a negative one on lignin aromatic C (Fig. 4), indicating that blue light mainly promoted lignin aromatic C decomposition and the accumulation of polysaccharides.

3.4 Photodegradation effects on litter mass loss

Mass loss and lignin loss were compared to FTIR-PC1 scores. For all species, FTIR-PC1 was significantly and negatively correlated with mass and lignin loss (Fig. 5), indicating that higher relative content of lignin aromatic C resulted in less lignin and mass loss. In contrast, with higher relative C–O stretching in polysaccharides, lignin and mass loss were greater. In addition, there was highly negative relationship between lignin aromatic C and C–O stretching in polysaccharides under full spectrum and blue light, but not under UV-A, UV-B, green, and red light (Fig. 6). Our results suggest that blue light may accelerate litter decomposition by decreasing lignin aromatic C to increase the availability of C–O stretching in polysaccharides when litter is exposed to solar radiation.

Discussion

Overall, there was evidence supporting our hypothesis that solar radiation promoted litter decomposition by altering litter molecular structure in temperate forests, based on our *in-situ* spectral-attenuation experiment, especially for *F.*

ifolium, and **d** *Betula platyphylla*. **e–h** Line charts for loadings, the largest are at polysaccharides characteristics and lignin regions, being mainly responsible for the variation in PC1

crenata and *A. carpinifolium*. Photodegradation, driven by blue light, significantly modified litter molecular structure, especially lignin aromatic C and C–O stretching in polysaccharides. Litter photodegradation is likely due to the degradation of lignin aromatic C, which results in more readily degradable polysaccharides. The increase of photo-oxidized compounds derived from lignin aromatic C degradation might regulate soil C stability.

4.1 Photodegradation and litter molecular structure based on spectral composition and litter species

Solar radiation had a critical impact on the degradation and breakdown of litter; this process operated in the forest gap to a greater extent than in the forest understory (Fig. 2; Fig. S2). This difference may be attributed to the stronger irradiance, particularly blue light, which reached the litter surface in forest gaps (Wang et al. 2022). It is consistent with previous findings that gap formation caused by forest regeneration accelerated C turnover and nutrient cycling by promoting litter decomposition (Ni et al. 2018). In addition, litter with high initial lignin (*F. crenata* and *A. carpinifolium*) was more prone to photodegradation by blue light than litter with low lignin content (*Q. crispula* and *B. platyphylla*) (Fig. 2). This suggests that photodegradation driven by blue light controls lignin decomposition, whereas canopy structure and phenology can modify patterns of litter C release during decomposition because of the changes in solar radiation reaching the forest floor when a gap is created. Therefore, including the dynamics of understory solar radiation influenced by canopy phenology and structure would improve estimates of C cycling in forests, responding to changes in climate and land-use (Wang et al. 2022).

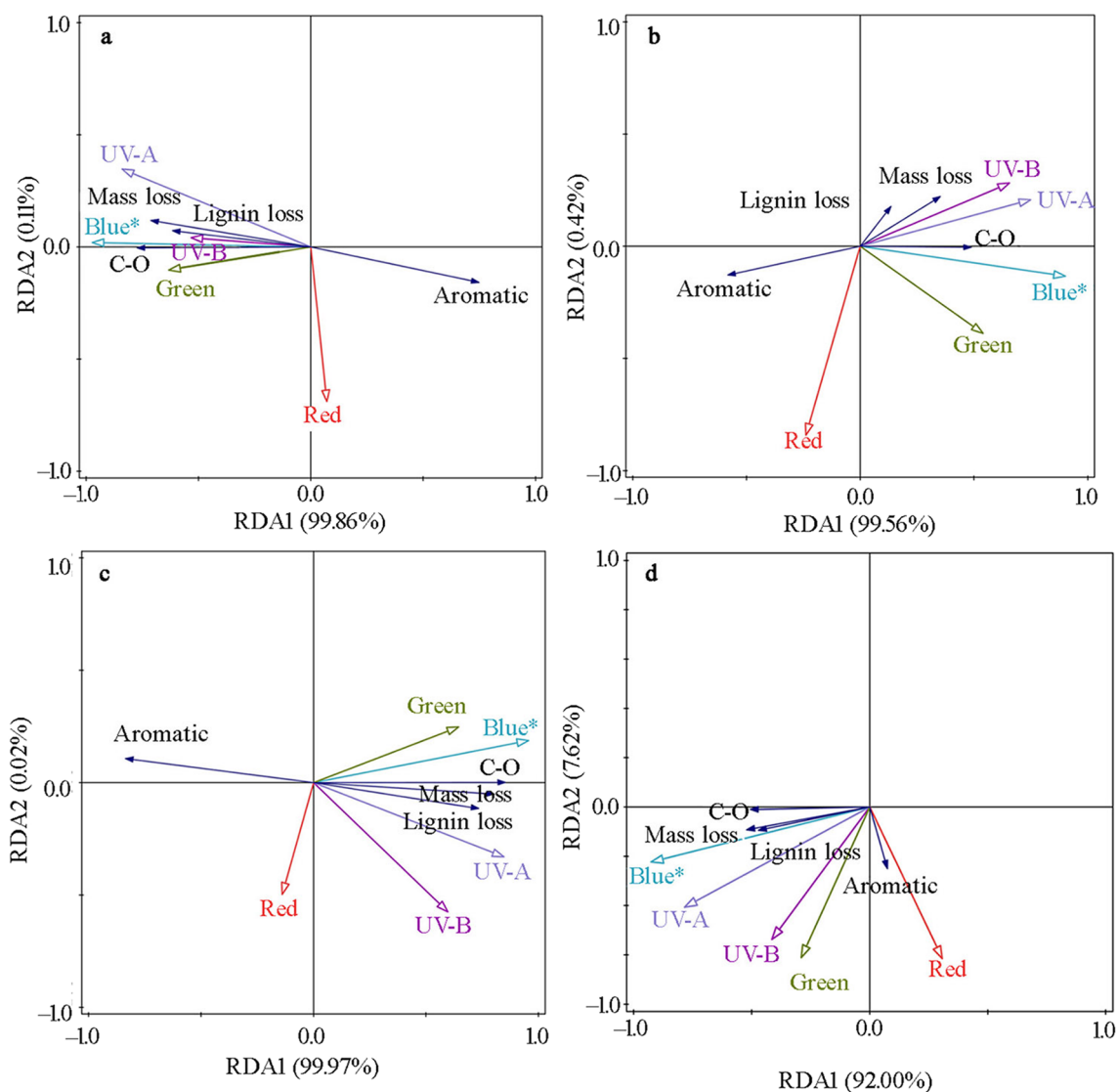


Fig. 3 Relationship between mass loss, lignin loss, molecular structure and spectral composition; **a** *Fagus crenata*, **b** *Quercus crispula*, **c** *Acer carpinifolium*, and **d** *Betula platyphylla* in the forest gap. For detailed RDA results, refer to Table S2 and S3

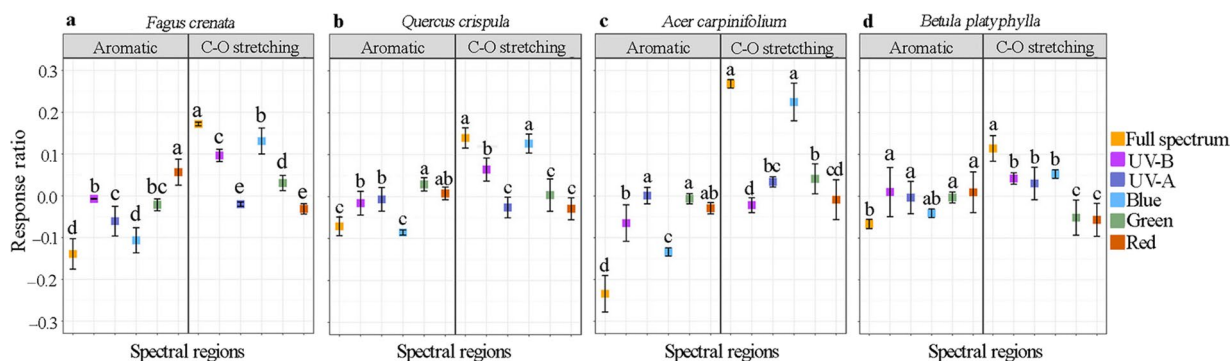


Fig. 4 Effect size of solar radiation on lignin aromatic C and C–O stretching in polysaccharides in the forest gap; **a** *Fagus crenata*, **b** *Quercus crispula*, **c** *Acer carpinifolium*, and **d** *Betula platyphylla*. Aromatic: lignin aromatic C; C–O stretching: C–O stretching in poly-

saccharides. The response ratio of solar spectrum on lignin aromatic C and C–O stretching in polysaccharides were estimated as a change between spectral contrasts. Lowercase letters denote significant differences among spectral regions ($P < 0.05$)

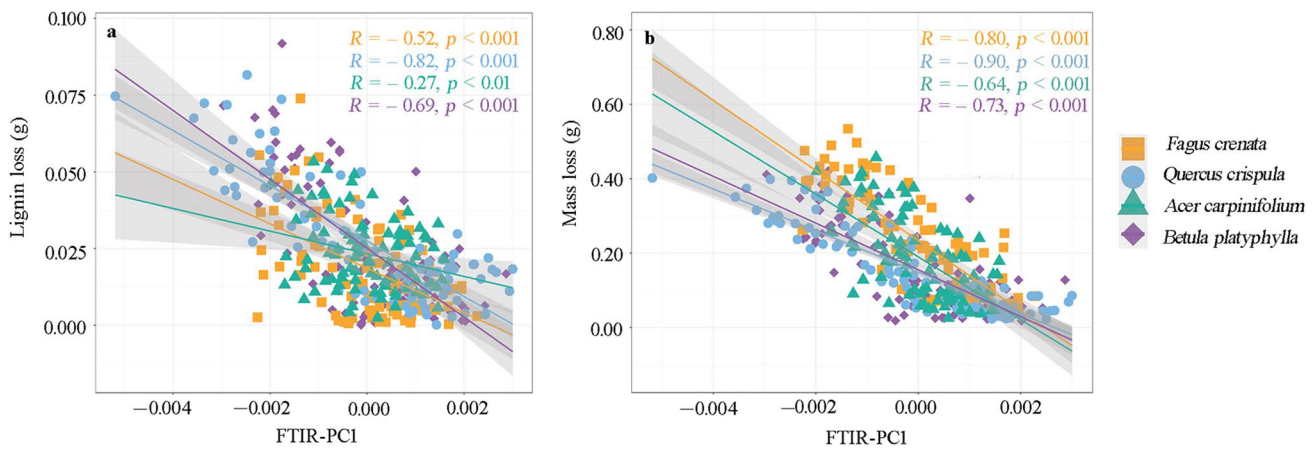


Fig. 5 Correlation between FTIR-PC1 and **a** Lignin loss and **b** Mass loss for different species in the forest gap. Solid coloured lines indicate significant relationships ($P < 0.05$). If the correlation is significant, colored shading shows the 95% confidence bands of the best-fit line

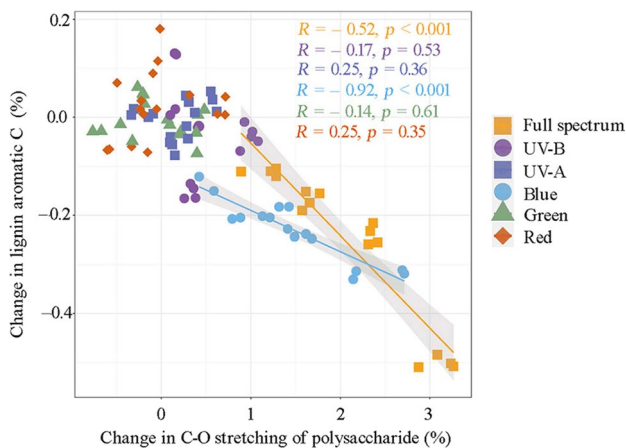


Fig. 6 Relationship between change in lignin aromatic C offlitter and change in C–O stretching of polysaccharides

FTIR data demonstrated that photodegradation generally altered litter molecular structure, including lignin aromatic C and C–O stretching in polysaccharides (Fig. 2). This result is in agreement with previous studies relevant to photochemical decomposition at the molecular level. After the two-month exposure in summer, lignin markers (both aromatic and phenol) significantly decreased, and the leaf chemical signature was characterized by polysaccharides (Farnet Da Silva et al. 2023). Previous research has found that the proportion of lignin guaiacyl (G), syringyl (S), phydroxyphenyl (H), and β -aryl ether linkages decreases due to photodegradation (Frouz et al. 2011; Lin et al. 2015). An important finding of our study was the significance of blue light in lignin aromatic C breakdown (Figs. 3, 4, S7), rather than UV radiation, which was until now generally considered to be the primary spectral region driving this process (Almagro et al. 2017). Aromatic C

breakdown occurs because lignin, as a complex phenolic polymer deposited in secondary cell walls, can effectively absorb blue light (Austin et al. 2016). In sunlight, the energetic contribution of blue light is greater than that of UV radiation (Aphalo et al. 2012), although the composition of spectral irradiance varies depending on density and configuration of the canopy (Wang et al. 2022). Thus, lignin molecular structure is greatly affected by solar radiation (especially blue light), which then mediates litter decomposition.

Nevertheless, the influence of sunlight on litter molecular structure varied considerably depending on species and seasons. For *F. crenata* and *A. carpinifolium*, lignin aromatic C and C–O stretching in polysaccharides changed significantly in response to blue light (Figs. S3, S4). However, beyond polysaccharides and lignin aromatic C, C=O stretching in unconjugated ketones and carbonyl meant both *Q. crispula* and *B. platyphylla* were also prone to photodegradation by blue light at the early stages of litter decomposition (Figs. S5, S6). The reason for this discrepancy may be that the initial molecular structure of the four species' litter differed significantly. *Q. crispula* and *B. platyphylla* had more C=O stretch in unconjugated ketone and carbonyl than *F. crenata* and *A. carpinifolium* (Fig. S1). However, the increasing in C=O stretch in unconjugated ketone carbonyl might be a result of lignin oxidation (Wang and Ren 2009). In addition, the polysaccharides content increased under photodegradation by blue light during lignin aromatic C degradation, confirming earlier reports that litter exposed to sunlight had higher polysaccharides or water-soluble fractions (Frouz et al. 2011; Jiang et al. 2022). Our results support findings that lignin aromatic C can be converted into polysaccharides, ketones, and aldehydes when litter is exposed to solar radiation (Day et al. 2018; Farnet Da Silva et al. 2023).

4.2 Effects of changes in litter molecules to the mass loss of litter

The dynamics of litter chemical composition at the molecular level provides a comprehensive approach to analyze plant-derived C loss (Lammers et al. 2009; Hu et al. 2023). In this present study, the full spectrum of solar radiation and its blue-light fraction both accelerated litter decomposition by decreasing lignin aromatic C and increasing the availability of polysaccharides (Figs. 5, 6) so that microbial enzymes could better access and degrade secondary cell wall carbohydrates (Austin et al. 2016). Our results provide *in-situ* evidence that photodegradation accelerates the breakdown of the litter molecular structure for C turnover in forest ecosystems (Wang et al. 2022). Moreover, considering that rainfall can also increase the leaching of small molecules or soluble organics generated by lignin photodegradation, thereby promoting mass loss (Day et al. 2022), helps to explain why most studies assessing the effects of canopy cover report more rapid litter turnover in forest gaps across various ecosystems, i.e., in tropical (Marinho et al. 2020), subtropical (Song et al. 2014; Jiang et al. 2023), and temperate forests (Pieristè et al. 2019; Wang et al. 2021). These findings not only have improved our understanding of the molecular mechanism of litter photodegradation, but have also provided rational suggestions for forest management based on litter and soil organic C.

According to traditional biodegradation models, lignin, as a recalcitrant compound, was considered resistant to microbial decomposition (Cornwell et al. 2008). Leaching of soluble compounds from newly fallen litter and preferential degradation of less chemically complex C compounds were believed to drive early mass loss (Adair et al. 2008). Intriguingly, our results provide evidence that photodegradation induces early loss of lignin aromatic C in litter in a mesic temperate forest (Figs. S3, S4, S5, S6). They suggest that photodegradation did not only release C from lignin, but also increased leaching loss and microbial degradation by altering the lignin C molecular structure of litter. This finding is supported by research in diverse ecosystems (Austin and Ballaré 2010; Barnes et al. 2023). In the context of climate change and land-use, it is essential to study the molecular mechanisms and litter photodegradation to enhance the prediction power of decomposition models (Gliksman et al. 2018).

4.3 Future research perspectives

This study provides an in-depth analysis of litter molecular structural changes during photodegradation, emphasizing their influence on the decomposition process. The transformations of molecular structure identified during litter photodegradation enhance our understanding of organic

matter degradation mechanisms in temperate forests. This alternative pathway explaining early lignin losses also has important implications for C loss and storage. If the products of lignin photo-mineralization are more readily assimilated by soil microorganisms during early decomposition, they may constitute an additional pool of C, destabilizing SOC pools (Lehmann and Kleber 2015). Hence, we should note the effects of litter photodegradation on SOC formation mechanisms.

The influence of solar radiation on litter degradation should be considered as a significant driver of organic matter turnover in terrestrial ecosystems in the context of climate change and land-use (Barnes et al. 2022). Extreme climate events, human activities, land-use changes, and natural disasters can significantly modify canopy structure and openness (Wan et al. 2019), which not only affects the amount of litter production, but more importantly changes the exposure of litter to sunlight (Yamada et al. 2014; Wan and He 2020), thereby significantly accelerating the C cycle. Therefore, from the perspective of minimizing C release, it is important to enhance the management of existing forest cover by reducing canopy disturbances through the implementation of continuous cover silvicultural systems. This approach is fundamental both to preserving existing C stores and enhancing forest capacity for C sequestration.

Conclusion

This study revealed how litter C decomposition was driven by solar radiation. Awareness of the mechanisms involved allowed for more accurate prediction of chemical changes in litter organic C and for modelling of nutrient cycling processes. Solar radiation significantly altered the litter molecular structure, especially in the forest gap. Blue light photodegraded complex macromolecules (lignin aromatic C) into soluble organic C or to small molecules (degradable polysaccharides), and potentially accelerated litter decomposition. This suggests that the ratios of C–O stretching in polysaccharides and lignin aromatic C would be robust decay indicators of decomposition rates in litter exposed to solar radiation, especially to blue light. Accordingly, such photo-products might comprise an additional C pool that affects the stability of soil C.

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