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RESEARCH ARTICLE

The crucial role of blue light as a driver of litter photodegradation in terrestrial ecosystems

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Abstract

Background and aim Wherever sunlight reaches litter, there is potential for photodegradation to contribute to decomposition. Although recent studies have weighed the contribution of short wavelength visible and ultraviolet (UV) radiation as drivers of photodegradation, the relative importance of each spectral region across biomes and plant communities remains uncertain.

Methods We performed a systematic meta-analysis of studies that assessed photodegradation through spectrally selective attenuation of solar radiation, by synthesizing 30 published studies using field incubations of leaf litter from 110 plant species under ambient sunlight.

Results Globally, the full spectrum of sunlight significantly increased litter mass loss by 15.3% ± 1% across all studies compared to darkness. Blue light alone was responsible for most of this increase in mass loss (13.8% ± 1%), whereas neither UV

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radiation nor its individual constituents UV-B and UV-A radiation had significant effects at the global scale, being only important in specific environments. These waveband-dependent effects were modulated by climate and ecosystem type. Among initial litter traits, carbon content, lignin content, lignin to nitrogen ratio and SLA positively correlated with the rate of photodegradation. Global coverage of biomes and spectral regions was uneven across the meta-analysis potentially biasing the results, but also indicating where research in lacking.

Conclusions Across studies attenuating spectral regions of sunlight, our meta-analysis confirms that photodegradation is a significant driver of decomposition, but this effect is highly dependent on the spectral region considered. Blue light was the predominant driver of photodegradation across biomes rather than UV radiation.

Keywords Biogeochemical cycling · Carbon flux · Decomposition · Litter traits · Spectral composition · Photodegradation · Meta-analysis

Introduction

The capability of sunlight to impact litter decomposition in terrestrial ecosystems through the process of photodegradation is by now well established (Bais et al. 2018). Photodegradation involves three main mechanisms: photochemical mineralization, consisting of the direct breakdown of organic matter (Gallo et al. 2006), photofacilitation, meaning the facilitation of microbial decomposition following the photochemical mineralization of complex polymers (Baker and Allison 2015), and photoinhibition, referring to the inhibition of microbial decomposition (Barnes et al. 2015). Which of these processes is dominant depends not only on the spectral region considered, but also on other environmental factors, such as temperature and precipitation, interacting with photodegradation (King et al. 2012). In some cases, the positive (photochemical mineralization and consequent photofacilitation) and negative (photoinhibition) effects offset each other (Bais et al. 2018).

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Since the 1990s, research into litter photodegradation in terrestrial ecosystems has largely focused on the effects of UV radiation (280–400 nm), and more specifically UV-B radiation (280–315 nm), due to concern about their impact on litter decomposition after the formation of the stratospheric ozone hole (Caldwell and Flint 1994; Zepp et al. 1995). Only subsequently were the contributions of other spectral regions of sunlight to photodegradation considered (reviewed by King et al. 2012). This research has revealed that short-wavelength regions of the visible spectrum, blue (400–490 nm) and green (500–570 nm) light, are also drivers of photodegradation (Austin and Ballaré 2010) due to their ability to photochemically degrade lignin (Austin and Ballaré 2010; Austin et al. 2016). This process activates decomposer organisms by releasing breakdown products, potentially releasing a bottleneck in microbial decomposition (Austin et al. 2016). An additional step forward in our understanding of contribution of spectral regions to litter photodegradation was provided by Day and Bliss 2019 who devised a polychromatic spectral weighting function for carbon dioxide emission in sunlight from the litter of species from the Sonoran Desert, Arizona. Visible light was found to have 30% effectiveness and UV-A radiation (315–400 nm) to be 61% effective, making these two spectral regions much more important in photodegradation compared to UV-B radiation (9%) (Day and Bliss 2019).

Photodegradation has a role in litter decomposition in terrestrial ecosystems, not only in arid and semi-arid environments at low latitudes (Almagro et al. 2015; Day et al. 2007), as originally thought, but also at higher latitudes (Jones et al. 2016; Zaller et al. 2009) and in mesic environments (Brandt et al. 2010). Recently, forests have been added to the list of ecosystems where photodegradation affects biogeochemical cycling, extending the reach of this process to dynamic radiation environments where gap opening and forest management practices, as well as seasonal phenology, cause large fluctuations in received solar radiation (Méndez et al. 2019; Pieristè et al. 2019, 2020a, b; Wang et al. 2021).

By identifying global trends in the importance and drivers of photodegradation, we can aim to incorporate this knowledge into Earth System Models of the global carbon cycle. Currently, such models handle decomposition based on climatic factors, principally precipitation and temperature and initial litter quality which drive soil organism activities (García-Palacios et al. 2013). However, most studies have produced inconsistent and highly variable results across different environments (Parton et al. 2007). This could be explained by the interaction of photodegradation with other abiotic factors, such as temperature, precipitation and soil moisture, as the relative importance of photodegradation is reported to be enhanced in dryer conditions (Almagro et al. 2017; Brandt et al. 2007, 2010). Moreover, photodegradation rate increases with those factors that change the exposure of litter to sunlight, such as season, canopy structure and phenological stage, litter layer thickness or litter position (Almagro et al. 2015; Bravo-Oviedo et al. 2017; Henry et al. 2008; Mao et al. 2018; Moody et al. 2001; Rutledge et al. 2010). Additionally, the incident irradiance and spectral composition of solar radiation change with latitude, elevation and sun angle, meaning that underlying patterns of photodegradation should vary consistently across the globe (Aphalo 2018; Aphalo et al. 2012; Gallo et al. 2009).

Several litter traits were suggested to be good predictors of the photodegradation rate, such as initial lignin content (Austin and Ballaré 2010), initial hemicellulose and cellulose (Day et al. 2018; King et al. 2012; Pan et al. 2015). However, there are inconsistencies among studies in the identity of effect traits mediating photodegradation and their hierarchy of importance. This suggests that, while we understand the underlying mechanisms of photodegradation, we are not yet able to account for how it is moderated by plant morphological and biochemical traits, and interactions with biotic and abiotic environmental factors.

A quantitative assessment of the literature is required to test whether general trends in photodegradation globally, and the relative importance of different spectral regions, are consistent with expectations gleaned from the recent mechanistic advances identifying the processes underpinning photodegradation. Previously, the effects of UV-B-driven photodegradation were assessed in a meta-analysis by Song et al. 2013 finding UV-B radiation to have no significant, direct or indirect, effects on litter decomposition at the global scale. King et al. 2012 reviewed the effects of UV radiation and visible light below 450 nm, finding that exposure to these spectral regions can increase litter mass loss. However, these two studies (Song et al. 2013) and (King et al. 2012) included both experiments employing supplemental radiation treatments, were produced prior to the majority of studies into visible light, and did not analyse the effect of the separate spectral regions (e.g. UV-B, UV-A, blue light). To date the results from studies on the effects of photodegradation driven by different spectral regions under ambient sunlight, have not been comprehensively synthesised at the global scale. Knowledge of the impact of waveband-dependent photodegradation on litter mass loss across different biomes and plant communities could represent the first step towards quantifying the impact of sunlight on decomposition on a global scale. These estimates will be important because photodegradation is responsible for the release of greenhouse gases, such as methane (CH_4), carbon dioxide (CO_2) and carbon monoxide (CO), into the atmosphere (Brandt et al. 2009; Day et al. 2019; Schade et al. 1999).

Our objective was to synthesize published studies on the effect of photodegradation driven by UV radiation, its constituent UV-B and UV-A radiation, and blue light on mass loss from litter at the global scale. This would enable us to assess whether the relative importance of these spectral regions globally is consistent with the mechanistic advancements in our understanding of these processes. Moreover, we assess whether photodegradation rates are modulated by climate, ecosystem type, length of the experimental period and litter habit (evergreen or deciduous), as well as litter traits. We expect blue light- and UV-A radiation-driven photodegradation to enhance litter mass loss, due to the relatively great ability of these spectral regions to degrade lignin (Austin and Ballaré 2010). Moreover, we expect photodegradation to be more relevant (1) in arid than mesic conditions, where precipitation is likely to be the main driver of the decomposition process (Bais et al. 2018), as well as (2) in ecosystems with low canopy cover which allow most of the incident solar radiation to penetrate to the litter layer.

Material and methods

Data collection

Data for the meta-analysis were extracted from literature published between 1980 and January 2021, collected from Web of Science, Google Scholar, and

Scopus database. Details of the keywords used are shown in Online Resource 1. We selected only studies that spectrally selectively attenuated solar radiation to measure the photodegradation of surface leaf litter in terrestrial ecosystems. We excluded any studies that did not separate single wavebands or that did not allow the effect of single wavebands to be calculated due to the lack of a control treatment. Since one of our aims was to understand the effects of spectral composition on mass loss under ambient sunlight, all studies employing supplemental radiation were excluded. Moreover, as we aimed to examine the correlation between photodegradation rate and litter traits, we retained only studies employing leaf litter from a single species, while we excluded studies using litter mixtures. More details about study selection are found Online Resource 1. We considered dark treatments to be only treatments blocking more than 95% of the solar spectrum. We extracted data concerning litter mass loss and initial litter traits. Where data were not presented in tables, we extracted them directly from the figures using WebPlotDigitizer 4.2 (Rohatgi 2019). We retained a total of 30 articles which produced a total of 325 datapoints. The list of retained studies is shown in Online Resource 2. Several papers included comparisons of multiple plant species (A list of the 114 species included is shown in Online Resource 3), field sites and spectral treatments. The effects of five spectral regions were calculated: 1) UV radiation (280–400 nm); 2) UV-B radiation (280–315 nm); 3) UV-A radiation (315–400 nm); 4) blue light (400–490 nm) and 5) the full spectrum of visible light and UV radiation. The effect of each spectral region was obtained by comparison of pairs of spectral treatments applied in the original studies: the effects of excluding UV radiation, UV-B radiation and the full-spectrum were obtained by comparison of the control treatment with the no-UV, no-UVB and dark respectively; while the effect of UV-A radiation was obtained by comparison between the no-UV and the no-UVB treatment and the effect of blue light by contrasting the no-UV/blue and no-UV treatments as conducted in a study by Wang et al. (2020). There were too few studies to be able to test the effects of green light.

Additionally, we extracted complementary information from each study: ecosystem (grassland, shrubland, woodland and open area); length of the decay period (the duration of the experiment in months); habit (evergreen or deciduous); litter form (herbaceous; shrub, tree); latitude. Details about the categorisation of these data and complementary information are shown in Online Resource 4 and in the dataset (Pieristè et al. 2021). The climate at each study site was defined according to the updated Koppen-Geiger climate classification using the map provided by Beck et al. 2018, which divides the globe into five major climatic zones further separated into subdivisions based on temperature and precipitation. Details of the climate classification are shown in Online Resource 5.

In order to estimate global-scale quantities of C released from surface litter by photodegradation, we extracted data from the Soil Respiration Data Base (SRDB) (Bond-Lamberty and Thomson 2010) on the annual litter carbon flux from each of the biomes corresponding to the location of studies in the meta-analysis. These data allowed us to roughly estimate the carbon flux in each of these biomes attributable to litter mass loss due to photodegradation. Identification of the biomes was based on the World Wildlife Fund (WWF) biomes classification (Olson et al. 2001).

Statistical analysis

The effect sizes, expressed as log response ratio (lnRR) of mass loss, were computed with the function ‘escalc’ from the package ‘metafor’ (ver. 2.1–0) (Viechtbauer 2019), which uses sample sizes, standard deviations and means of the original studies and presents bias correction for small sampling. For each study, we selected only the final collection date to avoid the potential issue of time-dependent effect sizes. We used a three-level mixed effect model using study ID and effect size ID as random factors as described in (Assink and Wibbelink 2016), with categorical variables “Ecosystem”, “Decay”, “Climate”, “Habit”, “Life form” and “Latitude” as fixed factors. The use of multilevel modelling in meta-analyses is a robust method for dealing with the problem of dependent effect sizes (Assink and Wibbelink 2016; Cheung 2014; Noortgate et al. 2013). We used this method to test the overall effect of exclusion of each spectral region and the effect of the categorical variables with the function rma.mv() from the package ‘metafor’ (ver. 2.1–0) (Viechtbauer 2019), employing the Knapp and Hartung correction method for random meta-analyses (Assink and Wibbelink 2016; Knapp and Hartung 2003). From these models we obtained the estimated average lnRR which we used to calculate the percentage change to better interpret the magnitude effect with the formula from Pustejovsky 2018.

Following the same multi-level approach, we analysed the correlation between the rate of photodegradation (effect size = lnRR) and the initial litter traits, climatic variables during the study period and absolute latitude, using them as continuous moderators in the model. The litter traits considered were those initial traits reported in each study: carbon content (C); nitrogen content (N); carbon to nitrogen ratio (C:N); lignin content; lignin to nitrogen ratio (Lig:N) and specific leaf area (SLA). The climatic variables used were average (Tmean), minimum (Tmin) and maximum temperature (Tmax), and cumulative precipitation (PP), over the study period. These data were obtained from the NASA Langley Research Center POWER Project funded through the NASA Earth Science Directorate Applied Science Program (Sparks 2018) using the "nasapower" R package version 3.0.1 (Sparks 2020).

The paucity of published studies from certain climates, ecosystems, latitude, etc. has the potential to introduce bias into the meta-analysis. To assess the risk of bias, we explored the dataset of retained studies to identify over- and under-represented categories. To evaluate literature bias we employed an Egger's test (Egger et al. 1997) which uses the variance of the effect size as a moderator of a multi-level meta-analysis (Viechtbauer 2010), this allowed us to account for dependency among the effect sizes.

Results

Bias analysis and bias exploration

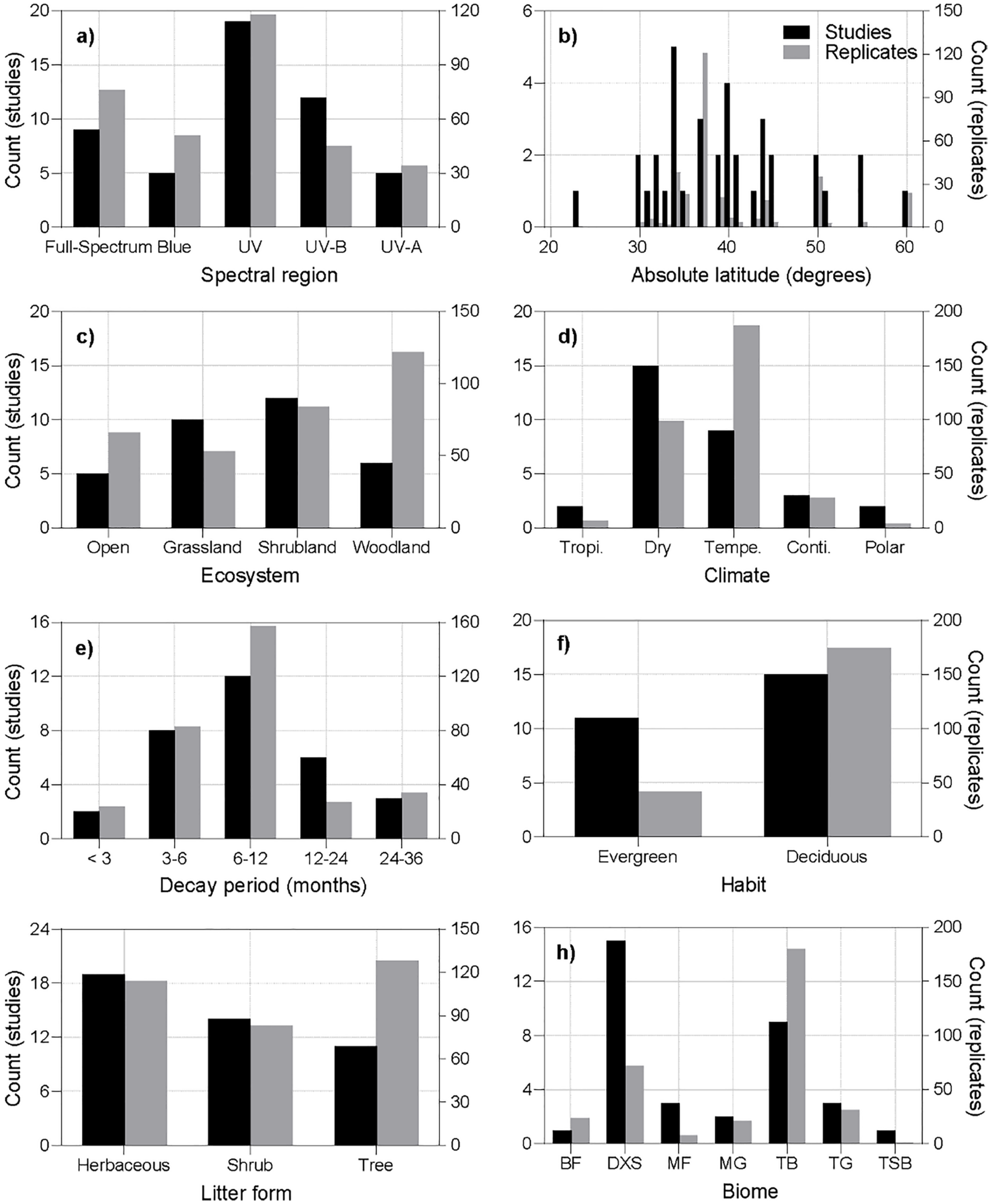
We did not find bias in any of the datasets used to calculate the effect of each spectral region: full-spectrum ($F_{1,74}=0.265$, p-value $=0.608$); blue light ($F_{1,49}=0.336$, p-value $=0.565$); UV-A radiation ($F_{1,32}=0.226$, p-value $=0.638$); UV-B radiation ($F_{1,43}=0.03$, p-value $=0.857$) and UV radiation ($F_{1,116}=0.345$, p-value $=0.558$). UV radiation was the most studied spectral region (20 studies, $n=118$), while blue light (5 studies, $n=51$) and UV-A radiation (5 studies, $n=34$) were under-represented in our dataset (Fig. 1a). Most studies were carried out at latitudes between 30° and 50°North and South, while data from high latitudes were lacking (Fig. 1b). Grassland and shrubland ecosystems were more studied than woodlands and open areas (Fig. 1c). Dry climates were the most studied, while polar and tropical climates were the least studied (Fig. 1d). In terms of the decay period, the first 12 months of decomposition were the most studied (Fig. 1e). The studies were located in seven biomes: "boreal forests/taiga", "deserts and xeric shrublands", "Mediterranean forests, woodlands and scrub", "montane grasslands and shrublands", "temperate broadleaf and mixed forests", "temperate grasslands, savannas and shrublands" and "tropical and subtropical moist broadleaf forests" (Fig. 2; Online Resource 6).

Effect of full-spectrum-driven photodegradation on litter mass loss

The full-spectrum of sunlight compared to a control in darkness significantly increased litter mass loss overall (+15.3% ± 1%, $p=0.040$, $n=76$, Fig. 3a, Table 1), however, this effect varied significantly depending on climate ($p=0.001$, Table 2), ecosystem type ($p<0.001$, Table 2), decay period ($p<0.001$, Table 2) and life form of the litter ($p=0.020$, Table 2). Specifically, only in dry (+36.3%, $p<0.001$, Fig. 3a) and temperate climates (+18.6%, $p=0.026$, Fig. 3a) did the full spectrum significantly increase mass loss. In terms of ecosystem type, the full-spectrum of sunlight increased mass loss only in open areas (+40.8%, $p=0.026$, Fig. 3a) and shrublands (+36.3%, $p<0.001$, Fig. 3a), while it had no significant effect in grasslands ($p=0.191$, Fig. 3a) or woodlands ($p=0.131$, Fig. 3a). Furthermore, the full spectrum of sunlight significantly increased litter mass loss in studies that lasted six to twelve months (+34%, $p<0.001$, Fig. 3a), but it had no significant effect across studies that lasted less than six months ($p=0.219$, Fig. 3a) nor more than twelve months ($p=0.420$, Fig. 3a). In terms of life form, the full-spectrum of sunlight increased mass loss only of shrub litter (+20.1%, $p=0.014$, Fig. 3a).

Effect of blue light-driven photodegradation on litter mass loss

Blue light caused an increase in mass loss overall (+13.8% ± 1%, $p=0.035$, $n=51$, Fig. 3b, Table 1) and this effect was dependent on climate ($p=0.013$, Table 2) and ecosystem type ($p<0.001$, Table 2). Blue light significantly increased litter mass loss only in dry climates (+9%, $p<0.001$, Fig. 3b)



but had a marginally non-significant effect on litter mass loss in temperate climates ($p = 0.052$, Fig. 3b) and no significant effect in continental climates ($p = 0.782$, Fig. 3b). Moreover, blue light significantly increased litter mass loss in open areas (+64%, $p < 0.001$, Fig. 3b) and shrublands (+9%,

◂**Fig. 1** Bias representation: number of studies and replicates by **a**) each spectral region, **b**) absolute latitude of the field sites of the studies, **c**) ecosystem type; **d**) climatic zone (see ESM Appendix-5 for more details about the climate classification); **e**) decay period (months), **f**) litter habit, **g**) litter form and **h**) biome type. The climate are: Tropical climate (Tropi.); Dry climate; Temperate climate (Tempe.); Continental climate (Conti.); Polar climate. The biomes are: Boreal forests / Taiga (BF); Deserts and xeric shrublands (DXS); Mediterranean Forests, Woodlands and Scrub (MF); Montane grasslands and shrublands (MG); Temperate broadleaf and mixed forests (TB); Temperate grasslands, savannas and shrublands (TG); Tropical and subtropical moist broadleaf forests (TSB). The repilcates are not repeated measures, but represent the number of independent treatments (e.g. field sites) of one species

$p<0.001$, Fig. 3b), but not in woodlands ($p=0.254$, Fig. 3b).

Effect of UV-driven photodegradation on litter mass loss

UV radiation had no significant effect on mass loss overall ($p=0.397$, $n=118$, Fig. 3e, Table 1). However, there was a significant interactive effect of UV radiation modulated by the decay period ($p=0.031$, Table 2), whereby in studies shorter than 3 months and longer than 24 months UV radiation increased mass loss by 43.7% ($p<0.001$, Fig. 3c) and 33.2% respectively ($p=0.031$, Fig. 3c). The UV-B spectral region within UV radiation, likewise did not have a significant overall effect on litter mass loss ($p=0.770$, $n=45$, Fig. 3d, Table 1). However, the effect of UV-B radiation changed according to climate ($p<0.001$, Table 2) and habit ($p=0.044$, Table 2). UV-B radiation significantly increased mass loss in dry (+13.1%, $p=0.007$, Fig. 3d) and temperate climates (+6.4%, $p=0.006$, Fig. 3d), while it reduced mass loss in polar climates (-20.9%, $p=0.020$, Fig. 3d). Moreover, UV-B radiation increased mass loss from the litter of both deciduous (+6.3%, $p=0.018$, Fig. 3d) and evergreen (+20.6%, $p=0.012$, Fig. 3d) shrubs and trees. We did not find a significant effect of UV-A radiation on mass loss overall ($p=0.606$, $n=34$, Fig. 3e, Table 1).

The relationship between photodegradation and abiotic factors

Photodegradation driven by the full-spectrum of sunlight was moderated by Tmax (0.011; $t_{(74)}=-2.524$, $p=0.014$, Table 3). Photodegradation attributable to blue light was significantly moderated by: precipitation (0.001; $t_{(51)}=2.887$, $p=0.006$, Table 3) and Tmin (0.014; $t_{(51)}=3.392$, $p=0.001$, Table 3). On the other hand, photodegradation attributable to the UV-B radiation was significantly moderated by: Tmean (0.017; $t_{(44)}=4.461$, $p<0.001$, Table 3), Tmax (0.013; $t_{(44)}=4.582$, $p<0.001$, Table 3) and absolute latitude (-0.006; $t_{(44)}=-2.313$, $p=0.006$, Table 3).

The relationship between Initial litter traits and photodegradation

Photodegradation driven by the full-spectrum of sunlight was moderated by initial C content (0.025; $t_{(67)}=3.964$, $p<0.001$, Table 3). The same was true for photodegradation driven by UV-B radiation (0.017; $t_{(36)}=3.527$, $p=0.001$, Table 3) and UV radiation (0.017; $t_{(76)}=2.386$, $p=0.020$, Table 3). In addition, photodegradation driven by UV-B was moderated by Lig:N (0.008; $t_{(29)}=2.156$, $p=0.040$, Table 3). Photodegradation attributable to blue light was significantly moderated by: initial lignin content (0.017; $t_{(36)}=2.455$, $p=0.019$, Table 3); Lig:N (0.016; $t_{(36)}=2.666$, $p=0.012$, Table 3) and SLA (0.001; $t_{(51)}=2.726$, $p=0.009$, Table 3).

Discussion

The relative importance of blue light and UV radiation in global photodegradation

Exposure to the full-spectrum of sunlight increased litter mass loss by 15.3% ± 1% overall (Table 1, Fig. 3a), confirming that sunlight is among the suite of abiotic factors driving decomposition across the globe. This result is in agreement with previous findings analysing the effect of the full-spectrum of sunlight on litter mass loss (Day et al. 2015; Ma et al. 2017; Pan et al. 2015). However, the magnitude of the effect is smaller than that found in an earlier meta-analysis (King et al. 2012), which calculated an increase in mass loss of 23% due to sunlight. Our meta-analysis includes studies that were carried out in temperate and hemi-boreal forest environments (Pieristè et al. 2019, 2020a, b; Wang et al. 2021); ecosystems that were not represented in the meta-analysis by King et al. 2012. In temperate and

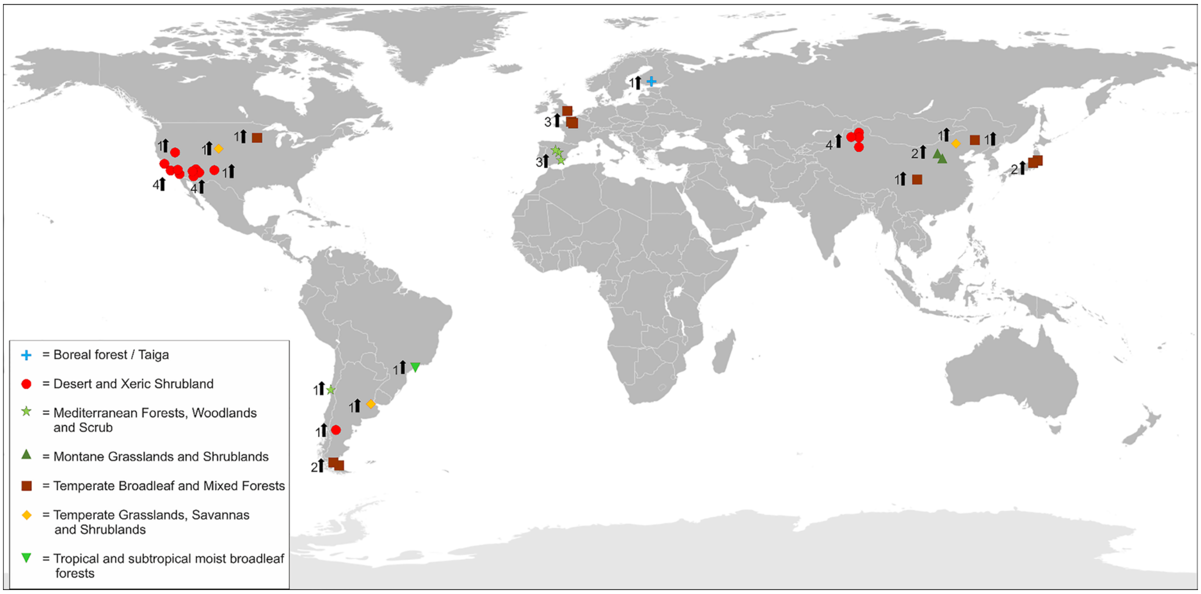


Fig. 2 Locations of the experimental sites of the studies considered in the meta-analysis divided according to the World Wildlife Fund (WWF) biome classification (see Online Resource 6)

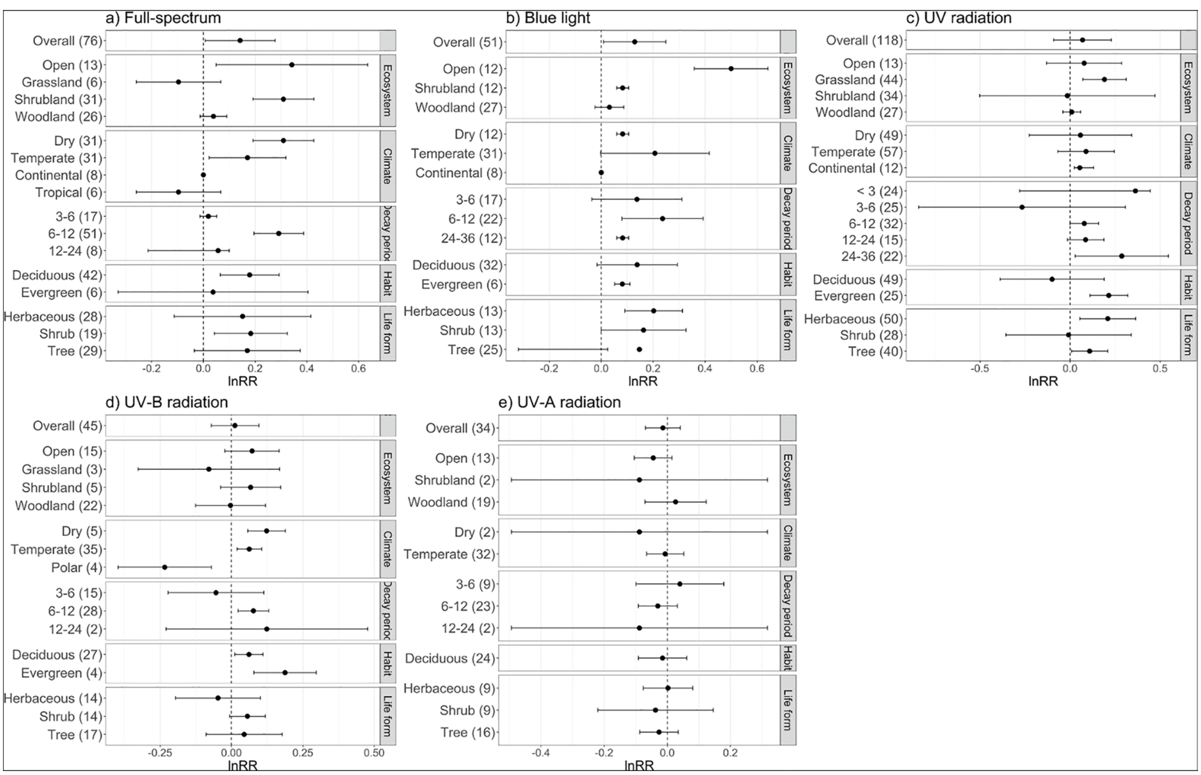


Fig. 3 Effects of exclusion of **a**) the full spectrum, **b**) blue light, **c**) UV-A radiation, **d**) UV-B radiation and **e**) UV radiation on litter mass loss according to categories of climate, ecosystem, decay period, habit and litter form. Average effect size (log response ratio) and 95% CI are shown. Numbers in parenthesis represent the number of replicates

Table 1 Overall estimated log response ratio (lnRR) of mass loss, 95% confidence interval and *p*-value for each spectral region. Values in bold indicate statistical-significance. n indicates the number of replicates

Spectral region	n	Estimate	95% CI		*p*-value	*% change*
Full-spectrum	**76**	**0.142**	**0.007**	**0.2768**	**0.040**	**15.26**
Blue light	**51**	**0.129**	**0.009**	**0.249**	**0.035**	**13.77**
UV-A radiation	34	- 0.014	-0.070	0.041	0.606	- 1.39
UV-B radiation	44	0.012	-0.071	0.096	0.770	1.21
UV radiation	118	0.069	- 0.091	0.228	0.397	7.14

Table 2 Heterogeneity between groups (Qb) and *p*-values of the moderators for each spectral region. Values in bold indicate statistical-significance

Spectral region	Variable	Qb	*p*-value
Full-spectrum	Climate	**5.82**	**0.001**
	Decay period	**8.72**	**< 0.001**
	Ecosystem	**9.70**	**< 0.001**
	Habit	0.71	0.405
	Life form	**4.14**	**0.020**
Blue	Climate	**4.73**	**0.013**
	Decay period	0.54	0.586
	Ecosystem	**38.51**	**< 0.001**
	Habit	0.06	0.801
	Life form	0.34	0.711
UV- A	Climate	1.05	0.312
	Decay period	1.25	0.301
	Ecosystem	1.44	0.252
	Habit	0.96	0.338
	Life form	0.13	0.879
UV- B	Climate	**8.77**	**< 0.001**
	Decay period	2.19	0.124
	Ecosystem	2.19	0.103
	Habit	**4.43**	**0.044**
	Life form	2.03	0.145
UV	Climate	0.02	0.979
	Decay period	**2.76**	**0.031**
	Ecosystem	2.31	0.080
	Habit	0.44	0.510
	Life form	1.87	0.158

boreal forests, sunlight tends to have the opposite net effect on photodegradation compared with forests at lower latitudes (Ma et al. 2017), actually decreasing litter mass loss in some litter species (Pieristè et al. 2019, 2020a, b). Hence, the inclusion of studies from these biomes may explain the lower net contribution of photodegradation to decomposition on the global scale that we report.

Comparing spectral regions, blue light explained most of the mass loss attributable to solar radiation globally (a 13.8% ± 1% increase in decomposition due to blue light; Table 1, Fig. 3b); while UV, UV-A and UV-B radiation had no significant effect on litter mass loss globally. This is in agreement with a previous meta-analysis showing no overall effect of UV-B radiation (Song et al. 2013). The high energetic capacity of UV radiation to cause oxidative stress in living organisms has the potential to slow down microbial decomposition, as reported in several studies (Moody et al. 1999, 2001; Verhoef et al. 2000), although this photoinhibition may sometimes be offset by direct photochemical mineralization (Gallo et al. 2009). These two antagonistic processes can lead the effects of UV and UV-B radiation to differ across biomes with climate according to the importance of microbial decomposition: for example, decomposition is increased by UV and UV-B radiation in arid and semiarid climates but this effect does not extend to temperate and continental climates (Gallo et al. 2006, 2009; Pieristè et al. 2019, 2020a, b). On the other hand, blue light is effective in causing photochemical mineralization, but appears not to produce photoinhibition (Austin et al. 2016); this is likely to be the reason why the global positive effect of blue light on litter decomposition is distinct from the inconsistent effect of UV radiation globally. Although the composition of spectral irradiance changes with latitude, elevation, canopy cover and structure (Wang et al. 2022), the energetic contribution of blue light always remains greater than that of UV radiation (Aphalo et al. 2012). The recent spectral weighting function for the emission of CO_2 through photodegradation illustrates the action of sunlight on decomposing litter (Day and Bliss 2019) and its consistency with the results of this global meta-analysis for sunlight and blue light supports the use of this action spectrum when up-scaling across ecosystems. However, unlike Day and Bliss (2019),

Table 3 Number of replicates (n), regression coefficient (β), *t*-value and *p*-value obtained from the three-level meta-analysis including initial litter traits, climatic variables and absolute latitude as continuous moderators. Initial litter traits are: carbon content (C), nitrogen content (N), carbon to nitrogen ratio (C:N), lignin content, lignin to nitrogen ratio (Lig:N) and specific leaf area (SLA). Climatic variables are: cumulative precipitation in mm (PP), average temperature in °C (Tmean), minimum temperature in °C (Tmin) and maximum temperature in °C (Tmax). The latitude represents absolute latitude. Values in bold indicate statistical-significance

Spectral region	Variable	n	β	*t*-value	*p*-value
Full-spectrum	C	**67**	**0.025 ± 0.006**	**3.964**	**< 0.001**
	N	67	- 0.020 ± 0.078	- 0.251	0.803
	C:N	67	0.004 ± 0.003	1.179	0.243
	Lignin	47	0.007 ± 0.005	1.527	0.134
	Lig:N	47	0.008 ± 0.006	1.298	0.201
	SLA	67	- 0.001 ± 0.001	- 0.659	0.512
	Latitude	76	0.003 ± 0.008	0.443	0.659
	PP	76	- 0.001 ± 0.000	- 1.139	0.258
	Tmean	76	0.001 ± 0.010	0.109	0.914
	Tmin	76	- 0.011 ± 0.007	1.686	0.096
	Tmax	**76**	**0.011 ± 0.004**	**2.524**	**0.014**
Blue	C	43	0.023 ± 0.013	1.835	0.074
	N	43	- 0.097 ± 0.056	- 1.650	0.107
	C:N	43	0.004 ± 0.004	1.714	0.094
	Lignin	**36**	**0.017 ± 0.007**	**2.455**	**0.019**
	Lig:N	**36**	**0.016 ± 0.006**	**2.666**	**0.012**
	SLA	**51**	**0.001 ± 0.000**	**2.726**	**0.009**
	Latitude	51	- 0.007 ± 0.004	- 1.656	0.104
	PP	**51**	**0.001 ± 0.000**	**2.887**	**0.006**
	Tmean	51	0.009 ± 0.005	1.746	0.087
	Tmin	**51**	**0.014 ± 0.004**	**3.392**	**0.001**
	Tmax	51	0.004 ± 0.004	0.849	0.400
UV-A	C	33	- 0.001 ± 0.010	- 0.118	0.907
	N	33	- 0.053 ± 0.059	- 0.901	0.374
	C:N	33	0.002 ± 0.002	1.352	0.186
	Lignin	26	- 0.007 ± 0.008	- 0.788	0.439
	Lig:N	26	0.003 ± 0.006	0.546	0.590
	SLA	31	0.001 ± 0.001	0.372	0.713
	Latitude	34	0.002 ± 0.005	0.376	0.709
	PP	34	- 0.000 ± 0.000	- 0.060	0.953
	Tmean	34	0.002 ± 0.009	0.159	0.875
	Tmin	34	0.004 ± 0.006	0.677	0.503
	Tmax	34	- 0.007 ± 0.009	- 0.755	0.456

Table 3 (continued)

Spectral region	Variable	n	β	*t*-value	*p*-value
UV-B	C	**36**	**0.017 ± 0.005**	**3.527**	**0.001**
	N	36	- 0.035 ± 0.041	- 0.847	0.403
	C:N	40	0.002 ± 0.001	1.663	0.105
	Lignin	31	0.006 ± 0.004	1.695	0.101
	Lig:N	**29**	**0.008 ± 0.004**	**2.156**	**0.040**
	SLA	31	- 0.000 ± 0.000	0.610	0.547
	Latitude	**44**	**- 0.006 ± 0.003**	**- 2.313**	**0.026**
	PP	44	0.000 ± 0.000	1.759	0.086
	Tmean	**44**	**0.017 ± 0.004**	**4.461**	**< 0.001**
	Tmin	44	0.002 ± 0.007	0.259	0.797
	Tmax	**44**	**0.013 ± 0.003**	**4.582**	**< 0.001**
UV	C	**76**	**0.017 ± 0.007**	**2.386**	**0.020**
	N	78	- 0.048 ± 0.047	- 1.021	0.311
	C:N	78	0.001 ± 0.001	1.087	0.281
	Lignin	84	- 0.002 ± 0.005	- 0.375	0.709
	Lig:N	61	0.001 ± 0.003	0.344	0.732
	SLA	82	- 0.001 ± 0.000	- 1.906	0.060
	Latitude	118	0.003 ± 0.008	0.356	0.723
	PP	118	0.001 ± 0.000	1.035	0.303
	Tmean	118	- 0.010 ± 0.012	- 0.874	0.384
	Tmin	118	- 0.007 ± 0.005	-1.231	0.221
	Tmax	118	0.016 ± 0.008	1.946	0.054

we did not identify UV-A radiation as the most effective spectral region driving carbon emission through photodegradation across all studies in our meta-analysis. This could be due to the fact that most studies testing the effect of UV-A radiation were located in cool moist temperate broadleaf forest biomes at high latitudes characterised by low UV-A radiation (Aphalo et al. 2012; Grifoni et al. 2008).

We estimated annual carbon flux from litter attributable to photodegradation driven by different spectral regions, applying the percentage contributed by photodegradation to the gross annual carbon flux lost from litter in each biome obtained from the SRDB dataset (Bond-Lamberty and Thomson 2010). This produced an estimate of photodegradation driven by the full spectrum of sunlight of up to 5–61 g C m^{-2} per year according to biome type (Table 4), while blue light would potentially be responsible for 4–55 g C m^{-2} per year according to biome type (Table 4).

Scaling up these estimates to a global scale, photodegradation due to the full spectrum of sunlight would contribute 1.95 Pg to the annual global terrestrial carbon flux over the seven biomes studied, with each biome responsible for carbon emissions of between 0.02 – 0.92 Pg. We would like to remind the reader that this estimate is indicative of the magnitude of the potential impact of photodegradation at the global scale based on upscaling the carbon flux data from studies of those biomes included in our meta-analysis and does not constitute a comprehensive global estimate. These estimates are greater than those from an existing modelling study (Foereid et al. 2011) which found photodegradation not to have a significant impact on the global C budget. However, at the time of that modelling study, no data were available for high latitudes and forest ecosystems. There is the need for updated global modelling studies that incorporate the recent conceptual advances in our knowledge of photodegradation at the mechanistic level and cover a broader diversity of environments.

Climate moderated photodegradation driven by blue light, UV-B radiation and the full-spectrum of sunlight, with the highest photodegradation rates occurring in dry climates. These results support the hypothesis that dry climatic conditions tend to promote photodegradation, where it is often the most important driver of decomposition when microbial activity is strongly reduced (Brandt et al. 2007; Gallo et al. 2006). On the contrary, in temperate and continental climates decomposition is likely to be driven by factors promoting biotic processes, such as precipitation and temperature cycles (Adair et al. 2008; Aerts 1997; Meentemeyer 1978). Nevertheless, we did not find a global correlation between cumulative precipitation and photodegradation driven by the full-spectrum of sunlight and UV radiation. This could be due to the fact that precipitation does not include other forms of moisture (e.g. fog and dew) known to be involved in photofacilitation (Gliksman et al. 2017). On the other hand, the precipitation was positively correlated with blue light photodegradation globally. This may suggest that blue light is involved in facilitating microbial decomposition (photofacilitation) in moist ecosystems, as previously proposed by Gliksman et al. (2017) and Pieristè et al. (2020a, b).

In addition, we found that full-spectrum and UV-B photodegradation, were positively correlated with both the maximum and average temperature. This is in agreement with the trend reported for a Mediterranean grassland (Almagro et al. 2015). This relationship suggests that under warmer conditions, which increase evaporative demand and may consequently reduce in litter moisture (Maestre et al. 2013), the relative importance of photodegradation may increase due to slower microbial decomposition (Almagro et al. 2015, 2017; Bais et al. 2018).

Initial litter traits as predictors of photodegradation rate at the global scale

In our meta-analysis, initial lignin content and initial Lig:N positively correlated with the rates of blue-light and UV-B photodegradation (Table 3). This result reaffirms the primary role of lignin in the process of photodegradation as a primary target of photochemical mineralization due to its capacity to absorb blue light and UV radiation (Austin and Ballaré 2010). The importance of this process has been well established for dry climates, but the meta-analysis extends this pattern to temperate and continental climates as well as ecosystems characterised by high canopy cover, where litter typically receives low irradiance depleted in blue light (Pieristè 2020). Moreover, these results

Table 4 Average carbon flux in g C m^{-2} and corresponding standard error (SE) attributable to photodegradation in each biome divided according to spectral regions. Contribution to carbon emission (+) and retention (-). However, data for the tropical and subtropical biome were not available (“na”)

Biome	Full-spectrum		Blue light	
	Average	SE	Average	SE
Boreal forests / Taiga	61.05	23.52	55.09	21.23
Deserts and xeric shrublands	14.13	3.92	12.75	3.54
Mediterranean forests, woodlands and scrub	7.32	0.00	6.61	0.00
Montane grasslands and shrublands	20.20	10.94	18.23	9.87
Temperate broadleaf and mixed forests	35.07	2.39	31.65	2.15
Temperate grasslands, savannas and shrublands	5.46	3.36	4.93	3.03
Tropical and subtropical moist broadleaf forests	na	na	na	na

highlight the greater importance of photodegradation in the decomposition of recalcitrant litter compared to labile litter (King et al. 2012; Pieristè et al. 2019). Recalcitrant litter is characterised by high Lig:N and high lignin content. This complex carbon macromolecule is not directly available to microbial decomposers before photofacilitation (Austin et al. 2016). Initial hemicellulose and cellulose content have also been proposed as potential targets of photodegradation (Day et al. 2018; Lin et al. 2015). Unfortunately, few studies have measured these traits, so we could not test this hypothesis in our meta-analysis.

Potential bias and further considerations

Every meta-analysis is subjected to bias, for this reason results must be interpreted with care. Exploring the literature published about photodegradation under ambient sunlight, we identified some over- and under-represented categories that could potentially affect our results. For instance, UV-driven photodegradation is the most studied, while relatively little attention has focused on blue and green light, as their importance in driving photodegradation was revealed relatively recently (Austin et al. 2016). We might expect that as more studies focus on these under-represented spectral regions, our results would change. Moreover, studies of photodegradation were mainly located at latitudes between 30° and 50° North and South (Fig. 1b), with equatorial and high latitudes being under-represented. As photodegradation has even proved relevant even under relatively low irradiances (Pieristè et al. 2019, 2020a, b), the study of photodegradation in biomes at high latitudes and with a dynamic vegetation structure will be necessary to understand the real impact of photodegradation at the global scale. Furthermore, woodlands are by far less studied than shrublands and grasslands and these studies are located at higher latitudes in temperate and continental climates, while grasslands have mainly been studied in arid and semiarid climates at lower latitudes. This segregation might partially explain the higher importance attributed to photodegradation in arid conditions.

A particularly contentious subject in photobiology is how best to manipulate the solar spectrum (Online Resource 7). In photodegradation studies, there is no standard method of filtering solar radiation and this makes it hard to compare multiple studies using different methods which create different micro-environments and exclude different classes of decomposers from reaching the litter, consequently altering the decomposition rates (King et al. 2012). Agreement on a standard method for the manipulation of solar radiation in photodegradation studies would allow a better comparison between them. Of course, the employment of attenuating filters to selectively exclude spectral wavebands and shading treatments also cause a difference in the microclimate to which litter is exposed. Unfortunately, filters almost inevitably modify moisture and temperature, and affect diurnal environmental fluctuations, which are even harder to control in field experiments than in laboratory conditions. Changes in moisture may lead to photofacilitation effects on litter decomposition diurnally (Gliksman et al. 2017) or seasonally (Berenstecheret al. 2020). Thus, attention should be paid to influence of moisture in photodegradation studies, especially those in mesic ecosystems where there is a strong interaction between solar radiation and moisture affecting litter decomposition. A recent assessment found C loss through thermal emission to be a relatively minor loss pathway compared to photolysis (Day et al. 2019), although the interaction of temperature with biotic processes may still significantly impact our results.

In our analysis, we did not consider potential interactive effects of wavebands combinations, as our aim was to evaluate the impact of specific wavebands on decomposition across different ecosystems and climates. However, when interpreting the results of this meta-analysis, the reader should keep in mind that in a natural environment there is not a clear separation between spectral regions and interactive effects can occur. In addition, the dosage of solar radiation could be more explicative of the results than the length of the decay period, since the amount of solar radiation incident on the litter greatly depends on the timing of the experiment, the weather conditions, and vegetation cover during the study period. Nevertheless, there are impediments to collecting the cumulative irradiance of specific spectral regions because many studies did not measure or give the data. The spectral measurement of experimental locations in the future studies will be essential to estimate the significance of photodegradation globally.

Conclusion

The present study confirmed the importance of sunlight as an abiotic driver of litter decomposition through the process of photodegradation at the global scale. The full spectrum of sunlight increased litter mass loss by 15.3% ± 1% at the global scale. This implies that photodegradation is an important contributor to the global terrestrial carbon flux. Our meta-analysis scales-up findings from dry and Mediterranean ecosystems that describe the mechanism of photodegradation, to affirm the important role of blue light in litter decomposition globally. This spectral region alone is responsible for an increase in mass loss of 13.8% ± 1%. On the other hand, UV radiation, and its constituents UV-B and UV-A radiation, had no significant effects overall only at a local scale: i.e., these waveband-dependent effects were modulated by climate and ecosystem type. Of covarying abiotic factors, average and maximum temperature positively correlated to photodegradation rate. Among initial litter traits, carbon content, lignin content, lignin to nitrogen ratio and SLA all positively correlated with the rate of photodegradation. However, we did not find one common trait that correlated with photodegradation across all the wavebands considered. The role of photodegradation at high latitudes and under tree canopies is at present understudied; more research in these areas will allow us to better define the role of photodegradation across the globe and would represent progress towards estimating its contribution to the global carbon budget.

Author contributions QWW and MP formulated the initial idea and designed the study, MP collected the data, QWW and MP analyzed the data. MP wrote the draft of the manuscript and the remaining co-authors revised the manuscript. QWW formatted the manuscript materials and prepared the submission.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding authors on reasonable request.

Declarations

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