



Review

# Photodegradation and Its Effect on Plant Litter Decomposition in Terrestrial Ecosystems: A Systematic Review

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**Abstract:** Photodegradation is an important mechanism that affects carbon and nutrient cycling; a significant amount of data has been reported previously. The present review includes the effect of a wider spectrum of solar radiation (sun light, UV, and visible light) on plant litter decay in terrestrial ecosystems. Although the positive effect of photodegradation on decomposition is most common, a substantial number of studies reports contrasting results. Litter from 148 plant species, from 41 families, have been used in photodegradation studies, representing functional groups of trees (33%), graminoids (30%), shrubs (23%), forbs (11%), and peat (1%). Although the majority of studies focused on mass loss, a growing number focuses on nutrient release. Positive effects on mass loss are most common across different climate regions and laboratory studies, whereas “positive” influence and “no effect” on nitrogen and lignin release are equally common in temperate and sub-tropical environments. This may potentially be due to other decomposition processes which increase in relevance with increasing moisture and can facilitate microbial activity, leaching, and fractioning by soil fauna. In addition to climate region, initial litter quality influences photodegradation. Field-based and laboratory experiments frequently obtain contrasting results, suggesting that the mechanisms controlling the responses are unclear and might be dependent on several interactions, and/or the differences in experimental approaches (such as UV filters), or coverage by particles. Future research should focus on interactions between different factors, and on conducting experiments that test specific relationships such as the potential interaction between photodegradation, soil moisture, microbial communities, soil fauna, and their effects on litter decomposition (both mass loss and nutrient release). Furthermore, the topic would benefit from international studies applying the same experimental approach, as has successfully been conducted in other fields.

**Keywords:** litter decomposition; photodegradation; solar UV radiation; nutrient release; nutrient breakdown; carbon loss; PRISMA guidelines



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## 1. Introduction

Plant litter decomposition plays a key role in the carbon cycling and nutrient cycling of terrestrial ecosystems [1,2]. Litter from different plant species undergoes decomposition at different rates [3–6]. The decomposition process is affected by both abiotic factors (such as solar UV radiation, temperature, and moisture) and biotic factors (such as litter species and decomposer communities) [7–9]. There are three major drivers affecting litter decomposition: climate, the quality of litter, and soil microbial and faunal communities [10–15]. Regarding abiotic factors, precipitation and temperature are important drivers of decomposition across ecosystems [16], whereas regarding biotic factors, litter quality plays a

significant role in decomposition. Litter with less structural tissue or a larger leaf area, high nutrient content, and lower secondary compounds is typically more easily decomposed [17]. In addition, low-quality litter species, in which C:N and lignin:N ratios are high, commonly exhibit lower mass loss than high-quality species [9,18–20].

Sunlight or artificial radiation source exposure can cause up to 60% mass loss of above-ground litter [19,21–23]. Photodegradation is a litter decay process where organic matter breaks down through the photochemical mineralization of complex macromolecules (such as lignin) that can absorb solar radiation (either UV radiation or short-wavelength visible light) [24], producing smaller organic components [25]. Solar radiation can influence pools and fluxes associated with plant litter decomposition [8]. It can indirectly influence microbial activity (photofacilitation) by producing labile organic matter from recalcitrant compounds [26]. Photodegradation, including both photochemical mineralization and photofacilitation [27], is an important driver partially controlling the decomposition of litter in deserts, semi-arid areas, shrublands, grasslands, and savannahs [8,21,25,28,29]. It has been reported that UV-B increases decomposition (due to photodegradation) in dry conditions, whereas in wet conditions, decomposition rates can decrease due to UV-B inhibiting microbial activities [19,30,31]. However, the effect of solar radiation on plant litter decay is less well understood than microbial degradation [32–34]. Depending on the source of DOM, solar radiation can have contrasting effects on recalcitrance and the microbial uptake of DOM [35]. Furthermore, CO<sub>2</sub> fluxes from microbial respiration can vary depending on whether solar radiation reduces microbial growth or increases labile carbon [36,37]. Thus, better understanding of the mechanism behind the effect of solar radiation on decomposition is needed.

A number of literature reviews have been carried out on forest litter decomposition [38–45]. In addition, there have been reviews on the effect of environmental factors on decomposition processes in arid and semi-arid regions [46], on litter decomposition, climate, and litter quality [11,47], on the rates of litter decomposition in terrestrial ecosystems [48], and on the role of invertebrates on leaf litter decomposition [12,49–51]. Two previous review studies related to photodegradation focused on UV radiation [8,52]. Four meta-analyses on litter decomposition [53–56] focused on nitrogen addition and litter decomposition [54], the effects of nutrient enrichment on litter decomposition in streams [53], the impact of UV-B exposure on litter decomposition [55], and the interaction between photodegradation and microbial decomposition under UV radiation [56]. A significant amount of data has accumulated to date (more than ten years old). In addition, the present review includes the effect of a broader spectrum of solar radiation (sunlight, UV, and visible light) on plant litter decay in terrestrial ecosystems. We summarize the role of photodegradation in the litter decomposition of terrestrial ecosystems and the effect of photodegradation on carbon loss and nutrient breakdown. In addition, we discuss the importance of photodegradation in different ecosystems (arid, semi-arid, temperate, and tropical) and compare the results of field experiments with those of laboratory experiments. Furthermore, we identify the plant species and functional groups of litter and discuss the role of interactions between photodegradation and litter quality in litter carbon and nutrient release.

## 2. Methods

### *Literature Review*

A literature search was conducted following the PRISMA guidelines for systematic reviews [57]. Google Scholar was used in June 2021 with the keywords “photodegradation”, “plant litter”, and “decomposition”. The words “aquatic” and “marine” were excluded from the search. The search included the full text of articles, their abstracts, and keywords. Only experimental studies written in English were included in the current review. In total, 1310 records were identified. After initial screening, 97 articles were analyzed in depth for the inclusion and exclusion criteria, resulting in a final selection of 68 papers to be included in the review (Figure S1). Articles were excluded for one of the following two reasons:

language (not being in English), or articles not being experimental (review or modeling papers) (Figure S1).

We only included experimental studies in our review in field or laboratory conditions. Our inclusion parameters were (1) the effect of photodegradation on mass loss and (2) the effect of photodegradation on carbon and nutrient breakdown (loss). Each study was assigned positive (+), negative (−), or no effect (0). A positive score indicated that litter mass, carbon, and nutrient breakdown (carbon, nitrogen, phosphorus, and lignin) had significantly increased, whereas a negative score showed that litter mass, carbon, and nutrient breakdown had significantly decreased. A (0) score was given when photodegradation was found to have no effect on litter mass loss and nutrient breakdown. Negative scores were also given to increases in phenol components. In contrast, positive scores were given to decreases in phenol components because high levels of phenol in plant litter bring about a decline in microbial activity, which causes the decomposition rate to decrease [23,58].

From these studies, we extracted data on the country, habitat (e.g., arid, semi-arid, temperate, sub-tropical, or laboratory conditions), numbers and names of plant species used, study duration, the effect of photodegradation on mass loss, and carbon and nutrient loss (release). The extracted data mainly concerned (1) photodegradation and (2) identifying how litter from different plant species was affected by photodegradation in various climate types. Not all articles reported the exact numbers and represented their results in graphs; therefore, we created a table to show whether the effect of photodegradation on mass loss, carbon, and nutrient loss (release) of plant litter had positive or negative effects or no effect scores.

### 3. Results and Discussion

#### 3.1. Synthesis of Results

UV radiation (UV-B (280–315 nm) and UV-A (315–400 nm)) and regions with short-wavelength visible light (420–570 nm) influence the decomposition of plant litter [32]. Photodegradation occurs by both direct (photomineralization and microbial photoinhibition) and indirect (photoprimering) processes [8,59,60]; several studies have discussed factors that enhance the photodegradation of plant litter [7,8]. Litter mass loss has been recorded as being between 14% and 60%, depending on the period of exposure, the amount of radiation, and the species of plant litter [19,61,62]. The majority of studies originate from two countries (USA and China); other regions, such as Africa, Australia, India, and South America, require more attention for future studies. Climate regions and the initial litter quality of the different plant species have a major influence on photodegradation. Positive effects of photodegradation were frequently reported among all climate regions. Although not as frequent (as positive effects), “no effect” is reported more often in temperate and sub-tropical regions (and laboratory conditions). This may potentially be due to higher moisture levels which boost the relative importance of other factors for decomposition processes. Furthermore, the frequent discrepancy between field and laboratory studies has not been explained, suggesting that there are unidentified mechanisms influencing the responses. The fact that studies have reported contrasting results from all climate regions might be due to interactions between different factors and different experimental approaches (such as different radiation filters). Thus, future research needs experiments that test specific relationships, such as the potential interaction between photodegradation, soil moisture, microbial communities, soil fauna, and their effects on litter decomposition (both mass loss and nutrient release). Furthermore, the topic would benefit from international studies applying the same experimental approach used in other fields (such as ITEX for climate change studies) [63].

#### 3.2. Distribution (Country and Habitat), Duration, Plant Species, and Functional Groups Included in Photodegradation Studies

Out of the 69 experimental sites, 12 were situated in arid, 19 in semi-arid, 10 in temperate, nine in sub-tropical habitats, and 19 in in vitro conditions, across 20 countries. These included the USA (26 studies), China (13), Argentina (7), the UK (4), France (2), New

Zealand (2), Spain (2), and one study for each other country (Tables 1 and S1). Two studies included two countries, bringing the total country count to 20. The average experiment duration was 506 days, with a minimum of 14 and a maximum of 3650 days. Most studies (15) were performed for 300–400 days, followed by 0–100, 100–200, 200–300, 400–500, and 700–800 days (in decreasing order, Table S2). The different effects (positive, negative, no effect) were found irrespective of study length (Table 1). Leaves and senescent leaf litter were the most common (78.5%) litter type used in experiments, followed by woody debris, needles, straw, pine, seeds, and peat (Table 1). Most studies used only one litter species (35.4%), although some used two or three species (Table S3). Two studies included 12 litter species [25,64], and one had 23 species [32]. In studies with multiple species, the species were placed in separate litter bags.

**Table 1.** Effects of photodegradation on nutrient breakdown (loss) for different litter types and plant species in arid climates. For full scientific names, see Table S5.

Climate Types	Country	Experiment Duration (Days)	Litter Types	Number of Species	Litter (Plant) Species	Effect of Photodegradation (EP)					Methods			References	
						1. Litter Mass Loss	2. Effect on Nutrient Breakdown (ENB)					Evaluating Litter Decomposition	Evaluating Radiation Effect		Nutrient Analyses (C, N, P, Lignin, and Phenolic)
							C% Loss	N% Loss	P% Loss	Lignin Loss	Phenolic Content				
Arid	USA	280	Leaves	1	<i>A. deltoidea</i>	+	NA	+	+	NA	NA	Litter bag technique.	UV transparent plastic film, UV opaque blocking plastic film. Ash-free dry mass ANOVA.	Elemental analyzer	[65]
	USA	730	Grass	2	<i>A. gerardi</i> , <i>B. gracilis</i>	(+,0) *	NA	(+,0) *	NA	(+,0) *	NA	Litter bag technique.	UV transparent acrylic plastic screen, UV blocking polycarbonate plastic screen. Ash-free dry mass ANOVA.	Elemental analyzer, fiber analyzer, spectroscopy	[66]
	USA	120–150	Leaves, twigs, seeds	1	<i>L. tridentata</i>	+	0	0	NA	+	NA	Litter bag technique.	Aclar UV transparent plastic film and mylar UV block plastic film ANOVA.	Elemental analyzer	[61]
	USA	757	Senescent leaf	2	<i>A. fatua</i> , <i>S. mellifera</i>	(+,0) *	NA	NA	NA	+	NA	Litter bag technique. Ash-free dry mass.	UV pass, UV block. Ash-free dry mass ANOVA.	Fiber analyzer	[67]
	USA	486–639	senescent	3	<i>J. monosperma</i> , <i>P. edulis</i> , <i>P. deltoidea</i>	+	+	0	0	NA	NA	Litter bag technique ash-free dry mass. Decay rate coefficients, K: $Mt = M_0e^{-kt}$ using linear regression.	Sunlight exposure (shade or ambient) ANOVA.	Elemental analyzer	[68]
	USA	731	Honey mesquite leaflets	1	<i>P. glandulosa</i>	0	0	0	NA	NA	NA	Litter bag technique modification with litter cages. Ash-free dry mass. Decay rate coefficients, K: $Mt = M_0e^{-kt}$ using a 1) split-plot generalized linear model (GLM) and 2) ANCOVA model.	Step-wise multiple regression and Akaike information criterion corrected (AICc) model.	Elemental analyzer	[69]

Table 1. Cont.

USA	365	Filter paper, thick sheets of basswood, leaves	3	Cellulosic filter paper, <i>Tilia sp.</i> , <i>P. glandulosa</i>	0	0	0	NA	NA	NA	Litter bag technique. Ash-free dry mass. Decay rate coefficients, K: Mt = $M_0e^{-kt}$ .	ANOVA	Elemental analyzer	[70]
China	913	Leaves, stem	3	<i>H. ammodendron</i> , <i>P. australis</i> , <i>T. aestivum</i>	+	+	(+)*	NA	(+)*	NA	Litter bag technique. Ash-free dry mass.	UV-transparent aclar fluoropolymer films, UV filtering acrylic sheets. ANOVA and ANCOVA.	Elemental analyzer, colorimetric analysis, fiber analysis	[71]
China	875	Leaves, stem	5	<i>S. arabicus</i> , <i>E. oxyrrhynchum</i> , <i>S. passerine</i> , <i>S. santolinum</i> , <i>H. ammodendron</i>	+	NA	NA	NA	+	NA	Litter bag technique.	UV block acrylic film, solar radiation transparent frame without film. Paired Student's <i>t</i> -test was used to test UV treatment effects on those parameters across the entire dataset. The UV photodegradation effect (UVE) was calculated as the ratio of ((sunlight—UV block)/sunlight) decomposition rate (k), with data based on subplot.	Elemental analyzer, colorimetric analysis, fiber analysis	[72]
USA	365 * 10	Senescent leaves, grass	5	<i>B. eriopoda</i> , <i>O. hymenoides</i> , <i>J. monosperma</i> , <i>L. tridentata</i> , <i>B. gracilis</i> ,	+	+	+	NA	+	NA	Litter bag technique. Ash-free dry mass.	NA	Elemental analyzer	[73]

Table 1. Cont.

Habitat	Country	Experiment Duration (Days)	Litter Types	Number of Litter Species	Litter (Plant) Species	Effect of Photodegradation (EP)					Methods			References	
						1. Litter Mass Loss	2. Effect on Nutrient Break Down (ENB)				Evaluating Litter Decomposition	Evaluating Radiation Effect	Nutrient Analyses (C, N, P, Lignin and Phenolic)		
							C% Loss	N% Loss	P% Loss	Lignin Loss					Phenolic Content
Semi-Arid	Spain	457	Senescent leaves	1	<i>S. tenacissima</i>	+	NA	NA	NA	+	NA	Litter bag technique. A single exponential decay model ([74] was used for the decomposition constant $k$ ( $yr-1$ ))	ANOVA	Elemental analyzer, Fiber Analyzer	[30]
	Spain	457	Senescent leaves	2	<i>S. tenacissima</i> , <i>R. sphaerocarpa</i>	+	NA	(0,+)	NA	+		Litter bag technique.	Ash-free dry mass basis at the end of the experiment. ANOVA	Elemental analyzer, fiber analyzer	[75]
	Argentina	540	Senescent leaves	3	<i>S. speciosa</i> , <i>P. ligularis</i> , <i>S. humilis</i>	+	+	NA	NA	NA	NA	Litter bag technique. ANOVA	NA	NA	[21]
	USA	224	Senesced leaflets	2	<i>P. glandulosa</i> , <i>Prosopis velutina</i>	+	+	±	NA	NA	NA	Leaflets. Ash content was statically compared. Decomposition decay constants were estimated using linear regressions of intrans formed mass loss data and compared statically with Student's $t$ -test	Film ANOVA	Elemental analyzer	[76]
	Argentina	420	Leaves and fine woody stems	2	<i>L. divaricata</i> , <i>N. tenuis</i>	+	NA	0	NA	0	+	Litter bag technique	2 mm nylon mesh blocked approximately 7%, 13%, and 10% of the PAR, UVB and UVA, respectively.	C concentration: dry digestion at 550 °C, total N: semi-micro Kjeldahl	[77]
	USA	1095	Senesced tissue	3	<i>B. gracilis</i> , <i>S. comata</i> , <i>A. longiseta</i>	+	NA	(0,+)	NA	0	NA	Litter bag technique	Polycarbonate plastic (UV block) and acrylic (UV pass)	Elemental analyzer, fiber analyzer	[19]

Table 1. Cont.

USA	3650	Leaves, conifer, graminoid	6	A. <i>saccharum</i> , D. <i>Glauca</i> , P. <i>resinosa</i> , Q. <i>prinus</i> , T. <i>plicata</i> , T. <i>aestivum</i>	+	+	+	NA	-	NA	DayCent-UV model Litter bag technique	The LIDET mass and nitrogen remaining data from the six different surface litter decay results from CPER site were used to parameterize UV litter decay parameters. We used a model optimization program to calculate the optimal values of the parameters.	NA	[78]
USA	2190	Grass	6	B. <i>distachyon</i> , H. <i>glabra</i> , T. <i>dubium</i> , T. <i>hirtum</i> , D. <i>volubile</i> , E. <i>botrys</i>	0	+	+	NA	NA	NA	DayCent-UV model using a simplified Farquhar model of SIPNET	Modified model	NA	[79]
China	365	Senescent leaves	8	P. <i>villosa</i> , P. <i>centrasiaticum</i> , C. <i>pseudophragmites</i> , S. <i>psammophila</i> , C. <i>korshinskii</i> , A. <i>pungens</i> , C. <i>chinganicum</i> , A. <i>bracteata</i>	+	+	(0,+,-) *	NA	NA	NA	Litter bag technique	UV transparent acrylic plastic, UV blocking polycarbonate plastic. ANOVA	Element analyzer	[80]
China	1020	Senesced (stem, branches and twigs) finer woody	4	A. <i>ordosica</i> , C. <i>korshinskii</i> , H. <i>laeve</i> , S. <i>psammophila</i>	0 *	NA	NA	NA	NA	NA	Litter bag technique the Archimedes' principle of water displacement were used to measure. Initial and decomposed litter volumes were measured using	UV transparent acrylic plastic, UV blocking polycarbonate plastic. ANOVA	NA	[81]



Table 1. Cont.

Chile	150	Green leaves	2	<i>P. chilensis</i> , <i>P. pungens</i>	+	(+, 0) *	0	NA	+	NA	Litter bag technique Biomass loss % = ((initial weight—final weight) /initial weight)*100.	Plexiglas UV transmitting film, Mylar- type UV blocking film ANOVA	Elemental analyzer	[82]
Israel, Italy, Spain	276	Fresh, standing dead material	3	<i>A. sterilis</i> , <i>S. prolifera</i> , <i>C. villosa</i>	0	NA	NA	NA	NA	NA	No litter bags were used	Multiple linear regression model	NA	[83]
Israel	NA	Standing dead plant material, freshly fallen litter	6	<i>A. sterilis</i> , <i>S. prolifera</i> , <i>S. officinale</i> , <i>D. pentaphyllum</i> , <i>H. italicum</i> , <i>C. monspeliensis</i>	+	NA	0	NA	+	NA	Litter bag technique	No screens or frames (control), transparent polyethylene screens, solar UV and PAR blocked by 179 chrome or orange filter ANOVA	NA	[84]
China	180	Senescent leaves	2	<i>P. sylvestris</i> var. <i>mongolica</i> , <i>P. Xi-aozhuanica</i>	+	NA	± *	NA	± *	NA	Litter boxes	Acrylic UV pass boxes, polycarbonate UV block boxes ANOVA	Continuous-flow auto analyzer	[85]
Argentina	365	Senesced	1	<i>P. nigra</i>	+	NA	0	–	+	NA	Litter bag technique	Polyethylene transparent film filter, orange block filter	Elemental analyzer and fiber analyzer	[86]
USA	320	Leaves	1	<i>P. velutina</i>	0	0	+	NA	NA	NA	Litter bag technique. Ash-free dry mass	UV transparent acrylic plastic, UV blocking polycarbonate plastic. ANOVA	Elemental analyzer	[60]
USA	363	Senescent leaves	2	<i>Tamarix Sp.</i> , <i>L. latifolium</i>	0	NA	0 *	+	NA	NA	Litter bag technique	No cover plastic (control), aclar UV transparent plastic film and mylar UV block plastic film. Slopes of the linear regressions. ANOVA	CN analyzer	[87]
USA	157	Grass	1	<i>E. glaucus</i>	NA	+	+	NA	+	NA	Litter bag technique	Clear plastic film, aluminum foil.	Gas chromatograph	[88]

Table 1. Cont.

Habitat	Country	Experiment Duration (Days)	Litter Types	Number of Litter Species	Litter (Plant) Species	Effect of Photodegradation (EP)					Methods			References	
						1. Litter Mass Loss	2. Effect on Nutrient Consumption (ENC)					Evaluating Litter Decomposition	Evaluating Radiation Effect		Nutrient Analyses (C, N, P, Lignin and Phenolic)
							C% Loss	N% Loss	P% Loss	lignin Loss	Phenolic Content				
Temperate	Argentina	100	Senescent leaves	23	<i>A. auracana</i> , <i>B. pictus</i> , <i>C. acanthoides</i> , <i>C. culeou</i> , <i>D. glomerata</i> , <i>F. americana</i> , <i>G. max</i> , <i>H. annuus</i> , <i>L. multiflorum</i> , <i>M. boaria</i> , <i>M. spinosum</i> , <i>N. obliqua</i> , <i>N. dombeyi</i> , <i>N. nervosa</i> , <i>N. antarctica</i> , <i>P. quadrifarium</i> , <i>P. ponderosa</i> , <i>P. ligularis</i> , <i>P. nigra</i> , <i>S. scoparium</i> , <i>S. speciosa</i> , <i>T. aestivum</i> , <i>Z. mays</i>	+	+	NA	NA	+	NA	Ash-free dry mass.	Three light treatments [(i) >290 nm; (ii) >400 nm; (iii) >550 nm] meta analyses.	Spectrophotometer, fiber analyzer	[32]
	Sweden	300–365	Senescent leaves	1	<i>V. myrtillus</i>	+	NA	NA	NA	NA	NA	Litter cups.	Direct and indirect effect of UVB. ANOVA.	NA	[23]
	USA	72	Leaf, stem of grass, forb	2	<i>C. vesicaria</i> , <i>L. multiflorum</i>	+	+	(0, +) *	NA	+	NA	Polyester mesh pulled tight across the top of 10 cm diameter PVC rings.	NA	Elemental analyzer	[89]
	The Netherlands	730	senesced leaf	2	<i>C. arenaria</i> , <i>C. epigejos</i>	0	0	0	0	0	0	Litter bag technique. Student's <i>t</i> -test,	Bivariate statistical tests. A Hotelling test.	Elemental analyzer, calorimetrically	[90]
	USA	300	Senescent leaves	2	<i>Q. rubra</i> L., <i>A. rubrum</i> L.	0	+	± *	NA	± *	+	Mesh	UVB-transmit acetate film, UVB-block polyester film a linear mixed effects (LME) model.	Elemental analyzer, gas chromatography–mass spectrometry, thermochemical analysis	[91]
	Norway, Sweden, the Netherlands, Greece	420	Leaves	1	<i>B. pubescens</i>	(+, 0) *	NA	(+, 0) *	NA	0	NA	Mesh ANOVA	ANOVA.	Elemental analyzer	[92]

Table 1. Cont.

Argentina	306	Senescent leaves	1	<i>G. magellanica</i>	(−)*	NA	0	0	0	NA	Litter bag technique.	Aclar UV transparent plastic film and mylar UV block plastic film. UV-B-absorbing compounds were expressed as absorbance units (UA) per milligram of dry mass diluted in 1 mL of extract.	Chemical analysis	[33]
France	300	Leaves	3	<i>F. excelsior</i> , <i>F. sylvatica</i> , <i>Q. robur</i>	(+)*	+	-	NA	NA	NA	Litter bag technique.	Five different filters. NA	Elemental analyzer	[93]
France	180	Senescent leaves	1	<i>Fagus sylvatica</i> L.	(−)*	0	+	NA	NA	NA	Litter bag technique.	Six different UV treatments were used.	Elemental analyzer	[94]
UK	365	Leaves	1	<i>F. excelsior</i>	+	−	−	NA	0	NA	Litter bag technique.	Four treatments: all UV, UVA only, no UV and ambient UV (control). ANOVA.	Elemental analyzer	[95]
Finland	186	Senescent leaves	2	<i>B. pendula</i> , <i>F. sylvatica</i>	+	−	0	NA	NA	0	NA.	Four filter types: dark, no-UVA/Blue, no-UVA, full-spectrum). A split-plot mixed-model ANOVA.	Element analyzer, HPLC	[96]
Japan	230	Senescent leaves	12	<i>F. camtschatica</i> , <i>P. trilobata</i> , <i>L. obtusiloba</i> Blume, <i>S. chinensis</i> , <i>H. sieboldiana</i> , <i>F. japonica</i> , <i>V. coignetiae</i> , <i>L. bicolor</i> Turcz. <i>var. bicolor</i> , <i>A. carpini-folium</i> , <i>F. crenata</i> Blume, <i>B. platyphylla</i> , <i>Q. crispula</i> Blume	+	+	NA	NA	NA	NA	Litter bag technique.	Six treatments: full-spectrum, no UVB, no UV, no UV/blue, no UV/blue-green and dark treatment. ANOVA. Benjamini–Hochberg (BH) method used to calculate the <i>p</i> -value.	Elemental analyzer	[25]

Table 1. Cont.

Habitat	Country	Experiment Duration (Days)	Litter Types	Number of Litter Species	Litter (Plant) Species	Effect of Photodegradation (EP)					Methods			References	
						1. litter Mass Loss	2. Effect on Nutrient Consumption (ENC)				Evaluating Litter Decomposition	Evaluating Radiation Effect	Nutrient Analyses (C, N, P, Lignin and Phenolic)		
							C% Loss	N% Loss	P% Loss	Lignin Loss					Phenolic Content
Subtropical	Australia	180	Leaves	3	<i>E. camaldulensis subsp. refulgens</i> , <i>A. coriacea</i> , <i>M. argentea</i>	NA	+	+	NA	NA	NA	Litter bag technique	NA	Elemental analyzer	[97]
	China	730	Needle and broadleaf foliar litter	6	<i>P. massoniana</i> , <i>C. iliate</i> , <i>C. lanceolata</i> , <i>C. camphora</i> , <i>T. iliate</i> , <i>Q. acutissima</i>	+	NA	NA	NA	NA	NA	Litter bag technique. Mass loss calculated as follows: $C = (M_{t-1} - M_t) / (M_0 - M_t) 100$	NA	NA	[98]
	Brazil	300	Senescent leaves	1	<i>T. sellowiana</i>	+	+	0	NA	0	NA	Litter bag technique. Ash-free dry mass. Three decomposition models were evaluated: the single evaluation model, the double exponential, and the exponential deceleration.	Three treatments using plastic film: a clear transparent films, Mylar-type blocking film, and Maylar type blocking film under shade.	Elemental analyzer	[59]
	China	365	Needles	2	<i>C. lanceolata</i> , <i>P. massoniana</i>	+	NA	0/+	+	0	NA	Litter bag technique. Exponential decay model.	Two treatments: ambient and elevated UV-B exposure. ANOVA.	CN analyzer, photometric	[99]
	China	600	leaves	1	<i>P. pubescens</i>	0	+	-	0	0	NA	Litter bag technique. Differences between mass at the start of the experiment and mass at each sampling time were used to calculate the rate of leaf litter decomposition.	Elevated UV-B radiation, elevated UV-B radiation, and elevated N deposition (UV-B + N) and control group. ANOVA.	Analysis	[100]
	China	720	Coarse woody debris	2	<i>C. lanceolata</i> , <i>C. camphora</i>	+	NA	NA	NA	NA	NA	24 segments of coarse woody debris.	NA	Elemental analyzer	[101]

Table 1. Cont.

Habitat	Country	Experiment Duration (Days)	Litter Types	Number of Litter Species	Litter (Plant) Species	Effect of Photodegradation (EP)					Methods			References	
						1. Litter Mass Loss	2. Effect on Nutrient Consumption (ENC)				Evaluating Litter Decomposition	Evaluating Radiation Effect	Nutrient Analyses (C, N, P, Lignin and Phenolic)		
							C% Loss	N% Loss	P% Loss	Lignin Loss					
Laboratory Conditions	India	90	Stem, seed, grass	3	<i>A. calamus</i> , <i>Q. tenuiflorum</i> , <i>C. citratus</i>	(+ / 0 *)	(−, 0 *)	(−, 0 *)	NA	NA	(−, 0 *)	Litter bag technique.	Three treatments: one ambient UVB (control); two supplemental UV-B exposure at sUV1 (±1.8 kJ m <sup>−2</sup> d <sup>−1</sup> ) and 3- at sUV2 (±3.6 kJ m <sup>−2</sup> d <sup>−1</sup> ). ANOVA.	Different chemical analysis methods	[102]
	USA	70	Leaf and stem of dead litter, freshly fallen oak litter, grass litter	5	<i>A. gerardii</i> , <i>B. eriopoda</i> , <i>B. gracilis</i> , <i>Q. ellipsoidalis</i> , <i>Q. macrocarpa</i>	0	0	0	NA	NA	NA	Microcosms.	UV lamp. ANOVA.	Elemental analyzer, fiber analyzer	[28]
	USA	426	Senescent leaves	3	<i>P. velutina</i> , <i>C. dactylon</i> , <i>A. deltoidea</i>	+	+	NA	NA	NA	NA	Incubation tube.	Polychromatic solar radiation broadband radiation sensors were used to monitor irradiance. Nonlinear least-squares regression.	Spectral weighting functions (WFs) for the photochemical emission of CO <sub>2</sub>	[103]
	UK	289	Senescent leaves	1	<i>M. giganteus</i>	+	0	0	NA	NA	NA	Dry plant material was placed in foil trays.	The growth chamber light was supplemented with 4 Arcadia 3D reptile lamp, 90 cm. Student's <i>t</i> -test. ANOVA.	NA	[36]
	Siberia	14	Peat	3	<i>Scheuchzeria peat</i> , <i>Sph. Fuscum peat</i> , <i>Sph. Papillosum peat</i>	+	+	NA	NA	0	NA	Bags with cotton on one side for heat exchange followed by drying and storage in jar.	UV transparent Alcal plastic film. Student's <i>t</i> -test.	Elemental analyzer	[104]
	USA	180	Senescent leaf	2	<i>P. edulis</i> , <i>J. monosperma</i>	0	0	0	NA	NA	± *	Microcosms.	Beneath fluorescent lamps containing UV-A and UV-B tubes. ANOVA.	Elemental analyzer	[22]

Table 1. Cont.

Sweden	62	Senescent leaves	1	<i>V. uliginosum</i>	0	+	+	+	–	+	Before and after the experiment, the litter in each microcosm was air-dried at room temperature and weighed. The relative mass loss (%) was calculated.	UVB indirect effect: CO <sub>2</sub> release using microcosms. ANOVA.	Allen 1989 methods	[23]
New Zealand	60	Pine and ryegrass	2	<i>P. radiata</i> , <i>L. perenne</i> cv <i>Nui</i>	0	NA	NA	NA	–	NA	Petri dishes.	Fluorescent UV lamps direct weight loss.	Acid detergent fiber sulfuric acid procedure followed by gravimetric determination of the residues	[105]
New Zealand	59	Senescent, fresh foliage leaves, grass, needles, humus	3	<i>P. radiata</i> , <i>L. scoparium</i> , <i>H. lanatus</i> L	–	NA	NA	NA	NA	NA	Polystyrene Petri dishes.	Six UV-emitting fluorescent lights. Litter materials were exposed to five levels (0, 30, 56, 75, and 100%) of incident UV-B radiation using metal mesh screens that allowed different levels of radiation transmission. ANOVA.	NA	[106]
USA	365	Senescent litter lying	1	<i>B. diandrus</i>	+	–	+	NA	0	NA	NA.	Steel frames with plastic louvers that either pass or block UV radiation. Student's <i>t</i> -test.	Elemental analyzer	[107]
USA	128	Senescent leaves	3	<i>A. fatua</i> , <i>B. diandrus</i> , <i>Q. douglasii</i>	+	NA	NA	NA	0	NA	Mass loss.	Envelops made of UV transparent polychlorotrifluoroethylene film. Student's <i>t</i> -test.	Elemental analyzer	[27]
China	228	Straw	1	<i>O. sativa</i> (rice)	0*	0*	NA	NA	NA	0*	Litter bag technique (aluminum mesh bags).	Four treatments: an ambient UVB under dry and wet condition and reduced UVB under dry and wet conditions. A general linear model.	Elemental analyzer	[108]

Table 1. Cont.

UK	448	Leaves	1	<i>Q. robur</i>	0	(−*)	0*	0*	(+*)	NA	Mass loss.	UV lamp. Two-way generalized linear model and a Tukey's multiple comparisons test multiple comparisons test a split-plot. ANOVA.	Flow colorimetry (for N and P), elemental analyzer (for carbon)	[109]
UK	244	Leaves	1	<i>Q. robur L.</i>	+	+	+	+	+	+	Litter bag technique.	UV lamp. ANOVA and a Tukey's multiple comparisons test.	NA	[110]
Argentina	883	Straw, leaves	1	<i>H. vulgare L. (barley)</i>	+	+	+	−	−	NA	Litter bag technique. Ash-free dry mass.	Two treatments: under near-ambient UV-B and under reduced UV-B conditions. ANOVA.	NA	[62]
USA	200	Leaves, stems, re-productive	2	<i>2 Sorghum bicolor cultivars</i>	+	+	±*	NA	−	NA	Litter bag technique.	Aclar UV transparent plastic film. ANOVA.	Elemental analyzer, fiber analyzer	[111]
USA	24	Leaves	1	<i>P. tremuloides</i>	±*	NA	−	NA	NA	NA	Container was used in a greenhouse.	Microcosms under three UVB treatments: no UVB, ambient UVB and elevated UVB. A biological spectral weighting function (BSWF) was used.	Elemental analyzer	[31]
China	365	Leaves	2	<i>C. camphora, C. glauca</i>	+	NA	+	NA	NA	NA	Litter bag technique. Exponential decay model.	ANOVA.	NA	[112]
China	450	Straw	1	<i>O. sativa (rice)</i>	+	+	+	NA	−	+	Pots were placed in a greenhouse.	Two UVB treatments: enhanced UVB radiation and ambient UV radiation using aclar UV transparent plastic film and fluorescent UV-B lamps. ANOVA.	Elemental analyzer	[113]

(\*) more detail in Section 3.

Litter from 148 different plant species has been used to examine the effect of solar or UV radiation on decomposition. These 148 different plant species belonged to 41 families (Table S4). Litter sources were from different functional groups, including trees (33%), graminoids (30%), shrubs (23%), forbs (11%) and peat (1%) (Table S4 and Figure S2). The most common tree family was Fabaceae (8.2%), followed by Fagaceae (7.7%) and Pinaceae (5.1%). With the exception of one graminoid species, which belonged to the Cyperaceae family, all species that were used belonged to the family Poaceae. The most dominant shrub family was Fabaceae, followed by Asteraceae, Cupressaceae, Salicaceae, and Amaranthaceae. Peat was found to belong to the Scheuchzeriaceae family.

### 3.3. Litter Quality and Photodegradation

From our extracted data, we found that the surface area of litter, litter pigment, plant species, litter layer thickness, litter type, and initial litter chemistry affected litter decomposition rates and could enhance the photodegradation process. Litter with a larger surface area [28] and thicker litter layer tended to degrade faster [85]. Green leaves had greater mass loss than yellow leaves [96,114]. Furthermore, litter type and species significantly affected decay constants across habitats [115]. The litter's origin (plant species) played a significant role in litter mass loss, likely due to initial litter chemistry [22]. However, some studies showed no relationship between litter's nitrogen release and its initial nitrogen content. Photopriming, in contrast, was not found to have any effect on decay constants for any of the studied litter species [70].

The potential influence of photodegradation, which includes the interaction between sunlight and leaves at different senescent stages, has not been studied extensively [94]. UV radiation is absorbed by phenolic compounds in the leaf, potentially interfering with the photodegradation [116]. Green leaf litter has been observed to have greater mass loss, has higher chlorophyll, photosynthetic enzymes, and nitrogen content [96,114]. In addition, although global nitrogen release is mainly driven by the initial nitrogen content in the litter, arid areas which are exposed to high levels of UV radiation are an exception, where nitrogen release appears to be independent of the initial nitrogen content [16].

### 3.4. Climate and Photodegradation

The majority of the studies (54 out of 67) were field experiments carried out in different habitats, including arid, semi-arid, temperate, and sub-tropical conditions. Nineteen studies were conducted in laboratory conditions (Tables 1 and 2). Fifty-four studies showed that climate zone, season, conditions (dry or wet), precipitation (rainfall), and latitude all interacted with photodegradation by increasing or decreasing mass loss and the rate of decomposition. The effect of photodegradation varies both among and within climate types. However, positive effects on mass loss are more common in dry environments, such as arid or semi-arid climates (Table 2) [19,22,61,115,117]. In semi-arid regions, the rate of litter decomposition ( $k$ ) can be highly variable [48], varying from 0.1 to 1.2 g g<sup>-1</sup> yr<sup>-1</sup> for the same amount of rainfall, which suggests that decomposition does not depend solely on precipitation [118]. Moreover, the effect of photodegradation has also been found in temperate and sub-tropical climates [23,89,98]. In addition, the seasonal influence on litter decomposition with photodegradation was more important in summer than in winter due to higher levels of sunlight and UV radiation [119]. Photodegradation increased decomposition levels in dry weather in semi-arid areas [21,66], but not in wet conditions [19]. Decay constants of the litter, on the other hand, were lower under drought conditions than under the two other precipitation treatments (50% precipitation reduction, 150% precipitation addition; precipitation = rainfall manipulation) [70]. In addition, litter mass loss has been found to increase during summer periods, with no difference in decomposition rates among litter species [80] or in forest gaps that receive more sunlight compared with surrounding denser forest [25]. Although photodegradation does play a role in peat litter decomposition at high latitudes, it plays a more significant role at lower latitudes in semi-arid areas [104]. Climate manipulations (warming, rainfall reduction, and a combination of the two) had a



significant effect on *Stipa* litter mass loss, with higher decay rates in litter that had been exposed to UV radiation than litter that had not [30].

**Table 2.** Effect of photodegradation on mass loss in different climate types and laboratory conditions. Positive effect = mass loss increases. \* Note that the total number of studies is 67, but some studies included more than one response; thus,  $n = 75$  for responses (see Table 1).

Effect on Mass Loss/Climate	Positive (n)	Positive (%)	Negative (n)	Negative (%)	No Effect (n)	No Effect (%)
Arid ( $n = 15$ )	12	80	0	0	3	20
Semi-arid ( $n = 19$ )	15	79	0	0	3	16
Temperate ( $n = 11$ )	6	55	2	18	3	27
Subtropical ( $n = 9$ )	6	67	0	0	2	22
Laboratory conditions ( $n = 21$ )	12	57	2	10	7	33
* Total ( $n = 75$ )	51	68	4	5	18	24

Litter decomposition rates are controlled by three main factors, climate is the dominant factor in areas that experience unfavorable weather conditions, whereas under favorable conditions litter quality is the prevailing factor [11]. Due to the effect that climate variability has on total incoming radiation, it is difficult to analyze the overall impact that photodegradation has on nutrient fluxes [80,120–122]. The impact of photodegradation increases in arid areas due to high levels of UV radiation [92,107,123,124] and low levels of microbial activity [125–128]. However, several studies have reported that photodegradation can enhance microbial litter decomposition in dry regions by photoprimering [56,129–131]. Furthermore, the rate of mass loss is higher in dry seasons, with significant interactions between climate (temperate, tropical, etc.) and sampling season.

### 3.5. Effect of Photodegradation on Litter Mass Loss

Photodegradation by UV radiation exposure has been shown to be important in several studies across different climatic settings [21,22,132,133]. The majority (67%) of the examined studies found that litter mass loss increased under exposure to solar or UV radiation. However, 5% reported a negative effect, 25% found no effect, whereas 3% had no available data (Tables 1 and 2). In addition, a few studies did not mention the impact of photodegradation on mass loss (Table 1). Effects varied both among species and locations. The positive effects of photodegradation on mass loss are more common in arid and semi-arid climates, followed by sub-tropical climates, laboratory conditions, and temperate climates (Table 2).

Photodegradation by UV radiation exposure has been shown to accelerate the decomposition rate [134]. Multiple studies have concluded that UV-B has the effect of accelerating litter decomposition [19,21,25,61,65,66,89,95,110,112], as can UV-A [93,110] (Table 1). For example, UV had a positive effect on the decomposition rates of *Bouteloua gracilis* and *Andropogon gerardi* (two species with contrasting lignin content) across a precipitation gradient [66]. Similarly, mass loss was greater for litter from 12 species under full sunlight compared with litter that did not receive UV/blue sunlight, or did not receive UV sunlight in the Sonoran Desert [64]. In addition, UV-B exposure increased the mass loss of litter from *Larrea tridentata* in the Sonoran desert [61]. In laboratory conditions, the annual fractional weight loss of litter from UV-B treatment arrays was greater than that of litter from UV-A controls and ambient arrays [110], and elevated UV-B was found to have a significant impact on the decomposition rates of *Cinnamomum camphora* and *Cyclobalanopsis glauca* leaf litter [112]. Elevated UV-B radiation was found to accelerate the decomposition of coarse woody debris (*Cinnamomum camphora* and *Cunninghamia lanceolata*) in subtropical Chinese forests [101]. Similarly, in a study conducted over 12 months in China, UV-B treatment was not found to have an effect on mass loss (Table 1) [99]. Furthermore, radiation intensity was not found to increase weight loss in pine and grass litter [105].

Other studies have reported that UV-B radiation had a negative effect on litter decomposition [33,109]. The mass loss of *Gunnera magellanica* litter, for example, was higher when the litter had been exposed to reduced UV-B treatment than under near-ambient UV radiation in temperate Argentina [33]. Within the inland dune ecosystems of China, however, woody litter on the surface (and suspended above the surface) exposed to UV radiation exhibited significantly lower mass loss than buried wood litter [80]. It is therefore reasonable to assume that microbial decomposition is more important for the decomposition of woody material than photodegradation [80].

Studies have also reported that UV-B radiation has no effect [22,28,87,90,94,105,108,109] (Tables 1 and 3). The lack of response to photodegradation likely correlates with a lack of response to UV exposure [87,124]. For example, the decay rate of *Stipa tenacissima* litter which had been exposed to UV did not differ from litter which had not been exposed [30], and although UV treatment had no effect on mass loss, it had a significant effect on dissolved organic carbon in Juniper and Pinon litter in arid ecosystems [22]. Indeed, it is possible that the positive and negative effects found in different studies may even each other out, on the understanding that UV-B and UV-A radiation differ in their effect on decomposition according to environmental conditions and litter chemistry [32].

**Table 3.** Effect of photodegradation on nutrient breakdown in plant litter.

Effect on Mass Loss/Climate	C Loss Positive (n)	C Loss Positive (%)	C Loss Negative (n)	C Loss Negative (%)	C Loss No Effect (n)	C Loss No Effect (%)	C Loss NA
Arid	5	45	1	9	1	9	4
Semi-arid	6	33	0	0	2	11	10
Temperate	5	50	0	0	2	20	3
Subtropical	4	44	2	22	0	0	3
Laboratory conditions	7	35	3	15	5	25	5
Total	27	40	6	9	10	15	25
Effect on Mass Loss/Climate	N Loss Positive (n)	N Loss Positive (%)	N Loss Negative (n)	N Loss Negative (%)	N Loss no Effect (n)	N Loss no Effect (%)	N Loss NA
Arid	6	50	1	8	3	25	2
Semi-arid	8	35	3	13	8	35	4
Temperate	4	31	2	15	4	31	3
Subtropical	3	30	2	20	3	30	2
Laboratory conditions	7	33	3	14	5	24	6
Total	28	35	11	14	23	29	17
Effect on Mass Loss/Climate	Lignin Loss Positive (n)	Lignin Loss Positive (%)	Lignin Loss Negative (n)	Lignin Loss Negative (%)	Lignin Loss no Effect (n)	Lignin Loss no Effect (%)	Lignin Loss NA
Arid	6	55	0	0	1	9	4
Semi-arid	7	39	2	11	2	11	7
Temperate	3	27	1	9	3	27	4
Subtropical	0	0	0	0	4	44	5
Laboratory conditions	2	11	5	26	3	16	9
Total	18	26	8	12	13	19	29

The effect of photodegradation on mass loss has been found to vary among species in several studies. UV radiation significantly increases mass loss in *Avena fatua* litter, but not in *Salvia mellifera* litter, which has been attributed to differences in litter chemistry [67]. The UV exposure level was reported to have a negative effect on the weight of pine and manuka litter (exhibiting increases of about 0.5% and 1%, respectively), no significant effect was reported for grass or humus samples [106]. Similarly, a laboratory study with enhanced UV-B increased the decomposition of two species, although it had no effect on leaf litter of a third species (Table 1) [102]. The effect can also vary among locations. UV-B was found to have a significantly negative effect on mass loss in Patras (Greece) and Abisko (Subarctic Sweden), but no significant effect on mass loss in Amsterdam (the Netherlands) or Adventdalen (High Arctic Svalbard) [92].

Attempts to understand the role of UV in litter decomposition rates by replicating weight losses observed in field studies under laboratory conditions have produced mixed results [96,106]. Although most field and laboratory studies found significant weight losses due to photodegradation [19,21,61,62,135], positive effects were less frequent in laboratory conditions compared with field studies [22,23,28,105,108,109]. (Tables 1 and 3). In contrast, one study found that UV radiation decreased mass loss in a temperate forest, whereas it increased mass loss under a controlled laboratory environment [96]. However, studies have been unable to explain the cause behind the differences, suggesting that some unidentified aspects or mechanisms lead to the discrepancy [106].

For decades, litter decomposition rates of plant species have been reported, especially in field studies [4,47]. Factors that regulate decomposition rates (K values) involve (1) climatic factors such as temperature, precipitation, and actual evaporation [47,136–138]; (2) litter quality, which includes nitrogen content, carbon:nitrogen ratios, lignin content, and lignin:nitrogen ratios [47,139–142]; (3) vegetation and litter types [4,140,143] and (4) geographic variables, for example altitude [47,144]. In recent years, many studies have shown that sunlight and its UV-driven radiation may be a significant driver of leaf litter decomposition in dryland ecosystems through the process of photodegradation [21,22,66]. However, not all studies have observed a significant effect of solar UV-B photodegradation on litter decomposition [105] and others found that the UV-driven photodegradation could vary with litter quality [87]. Furthermore, decomposition was strongly correlated with the soil coverage of litter, either as an adhering soil film or as loose soil in the soil litter matrix, or fully shielding litter from UV radiation and negating the photodegradation effect [76].

### 3.6. Soil Biota and Photodegradation

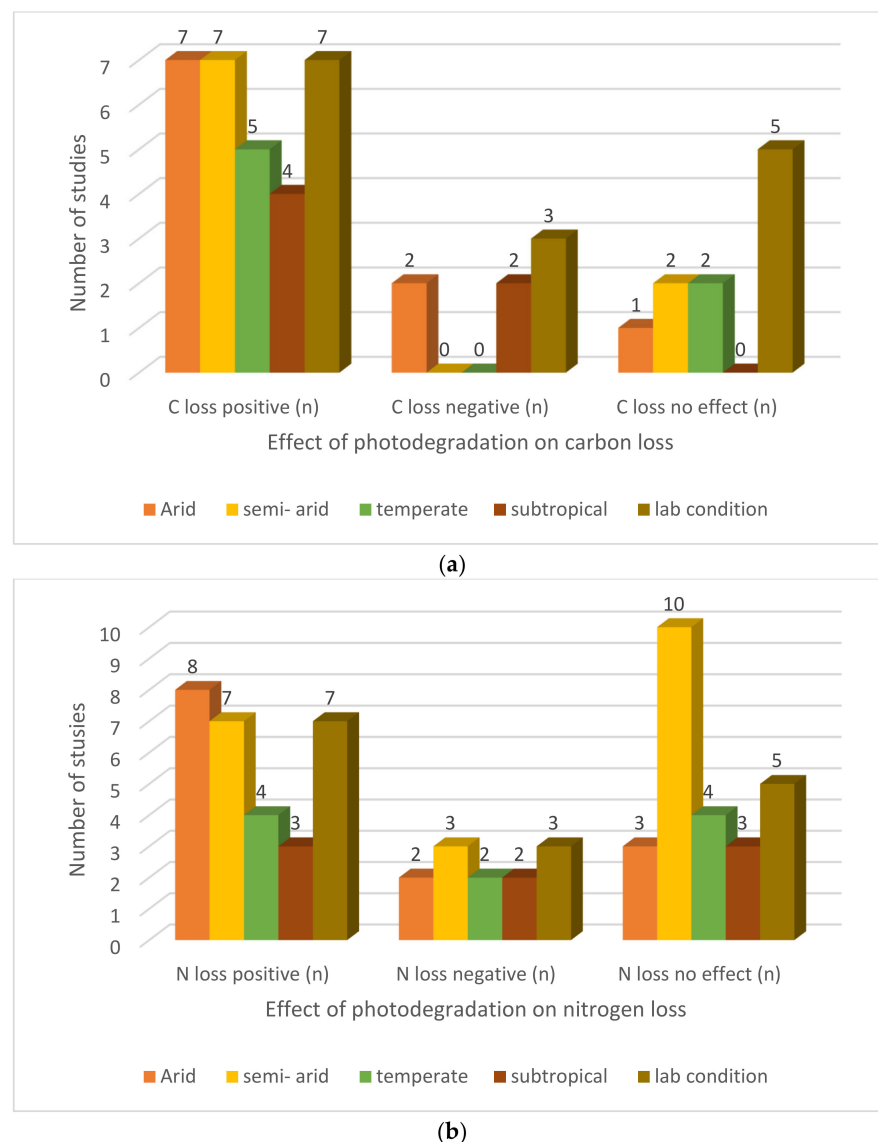
Soil organisms are long known to play a crucial role in nutrient cycling and decomposition processes [13,15]. The majority of soil carbon on Earth is found in high-latitude soils; following this, the highest abundances of bacteria, fungi, nematodes, and springtails are found in sub-Arctic and Arctic regions [145–149]. Bacteria tend to be more dominant in grasslands, whereas fungi are more abundant in forest ecosystems; however, bacteria and fungi can show high diversity in hot desert ecosystems as well [146,150–152]. In addition, invertebrates are important decomposers in several systems [148,153]. The microbial communities interact with the abiotic environment, the moisture levels being especially crucial [56,83]. Thus, microbial decomposition is higher during the night when moisture levels are higher, while photodegradation can play a more important role during the day [83]. The way photodegradation interacts with microbial decomposition is complex. For example, a meta-analysis suggests that UV radiation can increase the biodegradability of litter, increasing the access to lignin and labile carbon for microbes; at the same time, UV radiation caused changes in the microbial communities. Furthermore, the results suggested that UV negatively affected microbial activity, because there was no difference in remaining litter mass between abiotic and biotic conditions [56]. The microbial activity can be influenced by UV radiation in several ways, thus affecting litter decomposition. Similar to other molecules, DNA can absorb photons. This can result in cells of microorganisms being damaged by free radicals and active oxygen species [37]. Microorganisms with pigments such as melanin are more resistant to UV radiation than those without protective pigments [33,123]. Thus, this alters the dynamics and compositions of microbial communities. The quantity and quality of the carbon supply, plant photosynthate allocation, root exudation [154], and litter chemistry [23] can also be indirectly affected by UV, leading to an indirect impact on the microbial communities.

Although there is an increasing number of studies on the interaction between microbial and photodegradation, these have mainly focused on bacterial and fungal communities. Studies including protists are lacking, and invertebrates are rare. The role of protists in decomposition processes and nutrient cycling in aquatic ecosystems has been thoroughly studied [155]; however, they are under-represented in studies on soils [156]. A global meta-analysis on the impact of climate and litter quality on decomposition by soil fauna using proxy estimates (using soil fauna litter bag exclusions experiments) found that soil fauna increased decomposition across biomes [12]. However, it should be noted that the

meta-analysis did not explicitly test the effect of photodegradation. In contrast, a study in semi-arid Argentina, aiming to estimate the impact of soil organisms on decomposition in the absence of photodegradation, found no decomposition effect on surface litter from soil fauna. At the same time, inhibiting fungi decreased the decomposition [157].

### 3.7. Effect of Photodegradation on Carbon and Nutrient Release

Modeling studies suggest that photodegradation accelerates carbon and nitrogen cycling in the system by reducing the amount of C and N in the litter and soil [79]. The initial quality and chemistry of the litter have been suggested to affect the photodegradation rate [8]. However, only a few photodegradation studies have focused on changes in litter chemistry during the decomposition process [55,61]. The ratios of C:N [158] and lignin:N [159–161], as well as nitrogen [158] and lignin concentrations (concentrations [162,163], are considered to be key regulators of litter degradation rates [136,161,164]). The most common findings suggest the positive effect of photodegradation on nutrient release; however, this is not always the case, with arid and semi-arid areas reporting higher percentages of positive effects from photodegradation when compared with temperate and sub-tropical areas (Figure 1 and Table S5).



**Figure 1.** The number of studies reporting positive, negative, or no effect of photodegradation on (a) carbon and (b) nitrogen breakdown in different climate types and under laboratory conditions.

In terms of the effect of photodegradation on carbon loss, different studies have reached contrasting conclusions, with the most common findings suggesting a positive effect [69,80,110], and fewer studies finding no, negative [109], or contrasting results [82] (Figure 1 and Table 3). With regard to climate types, a positive effect was the most frequent finding (50%) in arid and temperate conditions, followed by sub-tropical (44%), semi-arid (38%), and laboratory conditions (35%) (Figure 1 and Table 3). Moreover, various studies have reported that UV treatments can have variable effects on C loss [66,82,89]. One study concluded that the positive effect of photodegradation on C loss was caused by indirect effects and that UV radiation did not affect any abiotic pathways apart from CO<sub>2</sub> release [28]. Other studies, however, have reported that the complex relationship between the effect of solar radiation on litter decay and C turnover is yet to be fully understood [7,8,21,104].

The effects of photodegradation on lignin loss in litter vary from positive [24,30,32,61,64,67,71,86,88] to negative [111,113], no effect [19,23,27,92,95,99,100,105,109,165], and variable effects (Table 1). Positive effects are the most common (29%), followed by no effects (21%) and negative effects (11%), (Table 3). The majority (57%) of field studies conducted in arid regions found positive effects, followed by 40% of field studies conducted in semi-arid regions, 27% in temperate regions, and 11% in laboratory conditions (Table 3). The effects on lignin loss may vary among plant species [66,82,89]. For example, lignin loss showed no significant difference between UV treatment in *Andropogon gerardi* litter, whereas in *Bouteloua gracilis* litter, loss was twice as high under UV pass treatment as opposed to UV block treatment [66]. Similarly, UV radiation significantly decreased the lignin content in *Proustia* litter, whereas *Porlieria* did not exhibit a significant decrease [82]. The effects of photodegradation on lignin loss may also vary over time. For example, the total lignin yield or total extractable lignin phenol structures decreased after the first 5 months, but then increased again after 10 months [91]. Furthermore, elevated UV-B radiation had a negative effect on plant growth and was found to produce more recalcitrant substrates (lignin) which reacted with N to produce more resistant components, as well as impacting the decomposition rate of rice straw [113].

A number of experiments have evaluated the effects of sunlight on mass loss and lignin degradation [30,58,60,61,65,75,76,89,129,165] (Table 1). Lignin contents have been shown to decrease without detecting the same effect on cellulose [24,32]. Others observed a decrease in litter cellulose, but not in lignin [19,66,129].

C loss has been shown to be affected by incubation period, species, UV treatment, position, and interactions of all these factors, except for the interaction between incubation period and UV [80]. Photochemical mineralization causes litter mass loss and carbon loss rates to increase; this process leads to the release of volatile carbon compounds such as carbon monoxide (CO), carbon dioxide (CO<sub>2</sub>), and methane (CH<sub>4</sub>) into the atmosphere [20,28,32,103]. The photochemical process is an important vector of C loss in arid ecosystems, due to its ability to transform organic matter inside senescent litter [21,28,135]. In contrast, many models are based only on litter quality and climate [166]; however, including the effect of photodegradation improves the predictions of such modules. Furthermore, several studies have reported indirect effects on C turnover of litter exposure to solar radiation or UV, leading to changes in litter chemistry [36,68,89].

Lignin is a photosensitive complex polymer compound [167] which consists of aromatic phenolic subunits [111]. All phenolic subunits can absorb UV-B and UV-A wavebands [168]. For this reason, the influence of photodegradation has been assumed to be stronger for litter with a high lignin concentration [24,86,169]. However, one meta-analysis found no effect of the initial lignin content when ambient conditions were compared with reduced UV radiation, and found a negative relationship when enhanced UV radiation was compared with ambient or reduced UV radiation [8]. A further meta-analysis found that UV alone had no significant effect on lignin decay, although it increased lignin decay when coinciding with microbial activity [56]. Under sand burial conditions, it was not proven whether there was relationship between the highest initial lignin content and lowest mass losses [170].



Photo-exposure can break down carbon chains, which mainly affects lignin; photo-exposure is a process that facilitates microbial degradation [24,56,75,83,131,171]. Although photo-exposure may not directly reduce lignin content, it may indirectly contribute to changes in the litter, making it more susceptible to microbial decomposition [104]. These changes might include the formation of reactive oxygen species (ROS), caused by indirect photolysis interacting with lignin [8].

In terms of the effect of photodegradation on nitrogen loss, different studies have reached contrasting conclusions, with the most common findings being positive effects, with fewer studies finding no effects, or negative effects (Table 3). Moreover, UV-B has also been reported to increase the N content of litter [95], whereas other studies have shown that photodegradation has no effect on N release from litter [28,69,82,86,109]. In addition, other studies have suggested that the effect of photodegradation on N loss may vary with time and location (Tables 1 and 3). In addition, many studies have reported reduced N immobilization in photodegradation [31,66,99,165], and that N immobilization is more significantly affected by UV in the summer [37,172] (Tables 1 and 3).

When the C:N ratio decreases, the rate of decomposition usually increases, because the N content is generally considered to be an important factor in regulating the rate of decomposition [161]. Litter decay is heavily influenced by N dynamics, and microbial N mineralization or immobilization is determined by the stoichiometric balance between soil microbes and litter [173]. N immobilization was observed in humid regions during decomposition, as a result of high C:N ratios in the litter [16,68,173–175]. Furthermore, a higher initial N content was found to promote litter decomposition rates [73,176]. Except for arid regions, N immobilization is rare in other climate regions, suggesting high levels of photodegradation and carbon-use efficiency, and low microbial activity in arid regions [16,19,56,88,107,177]. Therefore, N release patterns reflect the role of photodegradation in litter decomposition and its photopriming effects on microbial decomposition.

Only a few studies have measured litter phosphorus (P) [86,99,110] and phenolic compounds [96], both in the initial chemical litter and during decomposition. Studies have found varying responses of P release to photodegradation, such as positive effects from UV-B treatment [110], although negative effects from full exposure to the sun [86]; however, another study found contrasting responses of P release from needles of two conifers, positive on *Cunninghamia lanceolata* and no effect on *Pinus massoniana* [99]. No causes for the different responses have been suggested. Thus, the mechanism behind the varying responses remains unclear.

An experiment in four different temperate forest stands in Finland found a very small effect of photodegradation of surface litter in temperate forests [96]. Specifically, there was no major effect of UV on phenolic compounds or phenolic profiles in the decomposing litter from tree leaves. Different field UV treatments only affected a few individual phenolic compounds [96].

#### 4. Conclusions

Increasing attention is being paid to the importance of photodegradation in decomposition processes, not only in arid regions. However, the majority of studies originate from two countries (USA and China); thus, other regions such as Africa, Australia, India, and South America require more attention for future studies. Arid regions report positive effects with greater frequency. Similarly, the initial litter quality from different plant species influences the extent of photodegradation. “No effect” of photodegradation is widespread in temperate and sub-tropical regions (and laboratory experiments), potentially due to increased moisture levels which boost the relative importance of other factors for decomposition processes. Field-based and laboratory experiments frequently obtain contrasting results, suggesting that the mechanisms controlling the responses are unclear and might depend on several interactions. Soil coverage is another mechanism that could cause different responses, by shielding litter from UV radiation. Although the number of studies including bacterial and fungal communities is increasing, there is a need for targeted studies on the

interaction between protists, invertebrates, and photodegradation. Especially, there is a gap in knowledge on the interaction between protist decomposers, invertebrate decomposers, microbial decomposition, and photodegradation, and how these evolve over time in the decomposition process. The change in decomposers over time can be tracked using environmental DNA in multi-year experiments. Thus, future research should focus on interactions between different factors, with experiments that test specific relationships, such as the potential interactions between photodegradation, soil moisture, microbial communities, soil fauna, and their effects on litter decomposition (both mass loss and nutrient release). This would benefit from interdisciplinary cooperation between taxonomic and ecological experts covering plant and entomological fields, microbiological experts (covering bacteria, fungi, and protists), and environmental chemistry. Furthermore, the topic would benefit from international studies applying the same experimental multi-year approach successfully used in other fields (such as ITEX for climate change studies) [63].

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/soilsystems7010006/s1>, Figure S1: Flowchart detailing the procedure implemented in this systematic review, Figure S2: Percentage of litter from different plant functional groups used in photodegradation studies; Table S1: Number of study sites on photodegradation in different countries. Note that two studies\* includes studies from more than one country; Table S2: Number of experimental photodegradation studies with different durations (number of days); Table S3: Number of litter (plant) species used in photodegradation studies; Table S4: List of litter (plant) species used in studies (number of studies and percentage), plant functional group, and plant family; Table S5: Effect of photodegradation on Carbon & nutrient breakdown in plant litter.

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