

Responses of litter decomposition and nutrient release to ultraviolet radiation: a meta-analysis

Weiming Yan^{1,2*}, Zhouping Shangguan¹, Yangquanwei Zhong^{3*}

5 ¹ State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A&F University, Yangling, Shaanxi 712100, P.R. China

² Institute of soil and water conservation, Chinese Academy of Sciences, Yangling, Shaanxi 712100, P.R. China

10 ³ Center for Ecological and Environmental Sciences, Key Laboratory for Space Bioscience & Biotechnology, Northwestern Polytechnical University, Xi'an, 710072, P.R. China

Correspondence to: zhongyqw@foxmail.com

Abstract. Ultraviolet (UV) radiation plays an important role in litter decomposition. Despite years of research, it is still not fully understood that the role of UV radiation in litter decomposition and carbon (C) and nutrient release, as well as the direct (litter decay directly exposed to UV) and indirect (plants received UV during growth) effects. In this study, a meta-analysis that comprised 54 published studies concerning UV radiation experiments, including 598 observations, was performed to quantify the responses of litter decomposition and C and nutrient release to UV radiation. UV enhancement and attenuation showed significant effects on weight loss and nitrogen (N) and phosphorus (P) release across all studies. The direct and indirect effects of UV-B enhancement showed different effect on the lignin release, whereas the direct effects of litter mass loss showed a larger response than the indirect effects under UV attenuation, and showed opposite effect on N release. Changes in UV radiation did not affect both litter mass loss and nutrients release under laboratory conditions, ~~but-and~~ litter type ~~only~~ affected only the magnitude of mass loss and nutrients release, not the directions. In addition, mass loss and nutrients release under UV radiation varied over the decomposition process: UV enhancement accelerated litter decomposition but required UV accumulation, whereas the UV attenuation effect decreased with time. The litter decomposition decay increased as precipitation ranged from 0 to 200 mm, and then decreased as precipitation increased to 500 mm, and the response of decomposition

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decay increased as the precipitation below 700 mm. Overall, changing in UV ~~attenuation showed~~had considerable effects on both litter mass loss and nutrient release, suggesting that changes in UV radiation may greatly impact C and nutrient cycling in terrestrial ecosystems.

Keywords: Ultraviolet radiation, direct/indirect effects, litter types, mass loss, nutrient release

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1 Introduction

Plant litter decomposition plays a key role in carbon (C) and nutrient cycling in terrestrial ecosystems (García-Palacios et al., 2016; Prescott, 2005; Xu et al., 2013; Zhang et al., 2013). Increasing numbers of studies have proven the importance of abiotic (e.g., warming and drought, solar ultraviolet (UV) radiation) and biotic (e.g., plant species and diversity, soil decomposer communities) drivers of litter decomposition (Almagro et al., 2017; King et al., 2012; Brandt et al., 2010). Previous studies have shown that UV radiation is an important driver of litter decomposition in ecosystems, although the magnitude and direction of decomposition differ among studies (Day et al., 2015; Brandt et al., 2009; Brandt et al., 2010). Due to the increase in human activity, the amount of UV radiation reaching the earth's surface has changed (Williamson et al., 2014), including increased UV radiation in the Southern Hemisphere (Herman, 2010) and reduced UV radiation in the Northern Hemisphere (Calbo and González, 2005). Research on the effects of UV radiation on litter decomposition and C and nutrient release could provide important information for predicting C and nutrient cycling in terrestrial ecosystems under changes in UV radiation.

In general, soil microbes plays key roles s in litter decomposition (Moorhead and Sinsabaugh, 2006). The effects s of UV radiation on litter decomposition can be divided into two main processes: the breakdown of organic matter directly into C-based gases (Brandt et al., 2009; Lee et al., 2012; Rutledge et al., 2010); and the conversion of large resistant compounds to smaller compounds that are more readily degradable by soil microbes (Lambie et al., 2014; Gallo et al., 2009). Litter decomposition may be affected by UV radiation directly or indirectly and involves both biotic and abiotic processes. The direct effects of UV radiation are manifested by altering the decomposition rate directly via the photochemical breakdown of litter or by altering the abundance and community composition of decomposers. The indirect effects of UV radiation are manifested as changes in the chemical composition and physical

properties of the litter during the growth and senescence of plants (Wang et al., 2015). Studies of the effects of UV radiation on litter decomposition have shown inconsistent responses (Pancotto et al., 2003). Experimental studies of the effects of UV enhancement on plants have shown increases, no change or even decreases in litter decomposition (Newsham et al., 2001; Hoorens et al., 2004; Song et al., 2013b), and studies of the UV enhancement of soils have similarly found inconsistent effects (Moody et al., 2001; Gehrke et al., 1995). In addition, the direction and magnitude of litter decomposition under changing UV conditions also depend on plant species, vegetation type, decay period length and experimental conditions (Song et al., 2013a; Kirschbaum et al., 2011). For example, Pancotto et al. (2005) reported that UV attenuation on the soil reduced litter decomposition but increased it when plants were grown under conditions of UV attenuation. The effects of UV radiation on litter decomposition can be inconsistent among studies due to study variation in exposure durations (Song et al., 2013b), but how litter decomposition varies over time remains unclear. Furthermore, and research under controlled laboratory conditions found no effect of UV enhancement on litter decomposition (Kirschbaum et al., 2011). These observations highlight that a generalized mechanism of the effects of UV radiation on litter decomposition does not exist. Thus, to better understand the role of UV radiation on litter decomposition, different factors such as vegetation type and experimental duration and incubation conditions should be considered.

~~However, in~~ some regions, litter decomposition is proportional to time and cannot be explained by exponential decomposition models (Parton et al., 2007). Thus, UV radiation has been recognized as one of the most important drivers of litter decomposition and as responsible for the unexpected rapid decomposition in arid ecosystems (Austin and Ballare, 2010; Brandt et al., 2009; Day et al., 2015). Positive effects of UV radiation on litter decomposition have been observed in areas with an annual precipitation ranging of 152–726 mm (Pancotto et al., 2003; Day et al., 2015; Huang and Li, 2017; Huang et al., 2017). In areas of lower precipitation, although UV radiation inhibits microbial decomposition, photodegradation, the breakdown of organic matter via solar radiation, is a dominant factor in litter decomposition because the sparse vegetation causes the litter to receive high level of solar radiation (Austin and Vivanco, 2006), which directly increases the rate of organic matter breakdown and can supply easily decomposable substrates to soil decomposers (Austin and Vivanco, 2006; Pancotto et al., 2003; Brandt et al., 2010; Huang et al., 2017). However, the effects of UV radiation on litter decomposition have frequently been inconsistent under dry and wet conditions. For example, greater

effects on litter decomposition have been reported under dry conditions than under wet conditions (Brandt et al., 2007); in contrast, other studies have reported that the effects of UV radiation on litter decomposition under dry conditions are negligible (Uselman et al., 2011). Litter decomposition under conditions of low precipitation is the result of the balance between positive photodecomposition and negative biodecomposition due to low amounts of available water. However, whether changes in UV radiation show similar effects on litter decomposition under different precipitation regimens remains unclear, which is important for understanding C and nutrient cycling.

Previous studies have concentrated mainly on the effects of UV radiation on the litter mass loss, and less attention has been paid to the release of C and nutrients from litter and on the correlation between litter mass loss and nutrient release in response to changes in UV radiation (Wang et al., 2015). Three meta-analyses addressing the effect of UV radiation on litter decomposition have been conducted (King et al., 2012; Song et al., 2013a; Wang et al., 2015). However, the results of these meta-analyses varied. One of these studies mainly focused on the litter weight remaining and litter chemistry under elevated UV radiation (Wang et al. 2015), whereas the others examined only the litter weight remaining under changes in UV-B radiation (King et al., 2012; Song et al., 2013a). In general, the loss of litter weight increases as decomposition time increases, whereas nutrient release exhibits different patterns. For example, the nitrogen (N) remaining in litter was shown to increase after fifteen months of photodegradation of litter decomposition in semiarid Mediterranean grasslands (Almagro et al., 2017). Thus, to better understand the C and nutrient release from litter, clarification of the correlation between mass loss and nutrient release during litter decomposition under changes in UV radiation is urgently needed.

To clarify the effects of UV radiation on litter decomposition, especially the effects of UV radiation on C and nutrient release in the litter decomposition process, we conducted a meta-analysis of studies based on litter decomposition worldwide using UV radiation. Our main goal was to resolve the conflicting results presented to date and to clarify the response of nutrient release to UV radiation, which may be different from the response of litter mass loss. A total of 598 paired observations were collected to address the following: (1) how litter decomposition and C and nutrient release respond to UV radiation under different experiment conditions (different UV radiation types, direct vs. indirect effects of UV radiation, experimental conditions, litter types and experiment duration); (2) how the sensitivity of litter decomposition rates changes in response to UV radiation in different climate areas; and (3) whether the

relationship between C and nutrient release and litter mass loss changes under changes in UV.

2 Materials and Methods

2.1 Data preparation

Published articles were identified using the Web of Science and online databases of the Chinese Academy of Sciences (prior to December 2017) by querying the following combinations of terms: (ultraviolet/UV/photodecomposition/UV-B) and (litter decomposition/litter quality/litter nutrients). To avoid bias in the selection of publications, articles were selected based on the following criteria: (1) the study included at least one paired data set (control and treatment) from experiments involving UV enhancement and attenuation as well as photodecomposition; (2) mass loss and remaining nutrients in litter measured after different durations were denoted separately; and (3) the mean, standard deviation/error and number of replicates in the control and treatment groups could be calculated or directly extracted from the text, tables or digitized graphs.

For each selected study, the experimental location and environmental variables, such as the mean annual temperature and mean annual precipitation, were obtained directly from published papers. In addition, UV radiation types, the indirect or direct effects of UV radiation, plant litter species, leaf sources (forest or grassland), initial litter weight, and litter chemical properties (C, N, P, and lignin remaining or released) were recorded. Each nutrient remaining during decomposition was calculated as the percentage of the original nutrient content remaining: $\text{nutrient remaining}\% = (N_t * \text{Mass}_t) / (N_0 * \text{Mass}_0)$, where N_t is the nutrient concentration at time t , Mass_t is the dry mass at time t , N_0 is the initial nutrient concentration, and Mass_0 is the initial dry mass. The cumulative nutrient release from the litter during incubation was calculated as follows: $\text{cumulative nutrient loss} = N_0 * \text{Mass}_0 - N_t * \text{Mass}_t$. In total, 54 published papers covering multiple sites worldwide (Fig. S1) that satisfied our selection criteria for this study were selected from more than 1000 published papers. A list of literature sources and data are shown in the Supporting Information. All original data were extracted from the text, tables, figures and or appendices of the publications. For those studies with data presented graphically, Get-Data Graph Digitizer (ver. 2.20, Russian Federation) was used to digitize and extract the numerical data.

2.2 Data analysis

The response ratios (RRs, the natural logs of the ratios of the mean values of the parameters in the treatment group to those in the control group) for the biomass loss and nutrient changes were evaluated using the following equation (Hedges et al., 1999):

$$RR = \ln(X_e / X_c) = \ln X_e - \ln X_c \quad \text{Eq. (1),}$$

5 where X_e and X_c are the response values of each individual observation in the experimental and control treatments, respectively. The corresponding sample variance for each RR was calculated as follows:

$$v_i = (S_e / X_e)^2 / n_e + (S_c / X_c)^2 / n_c \quad \text{Eq. (2),}$$

where n_e , S_e , and X_e represent the sample size, standard deviation and mean response values in the experimental group, respectively, and n_c , S_c , and X_c represent the sample size, standard deviation and

10 mean response values in the control group, respectively. The reciprocal of the variance ($w = 1 / v_i$) was considered the weight of each RR. The mean weighted response ratio (RR_{++}) was calculated from the RR for individual pairwise comparisons between the treatment and control groups as follows:

$$RR_{++} = \frac{\sum_{i=1}^m \sum_{j=1}^k w_{ij} RR_{ij}}{\sum_{i=1}^m \sum_{j=1}^k w_{ij}} \quad \text{Eq. (3),}$$

where m is the number of groups and k is the number of comparisons in the corresponding group. In

15 addition, the standard error of RR_{++} was estimated as follows:

$$(RR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^m \sum_{j=1}^k w_{ij}}} \quad \text{Eq. (4).}$$

When the decomposition time spanned more than one time category, we categorized it to the shorter decomposition period; for example, an experiment that lasted exactly 4 months was categorized as 2-4 months. A similar approach was used to categorize precipitation. In the UV enhancement dataset, only

20 UV-B enhancement was included, whereas the UV attenuation dataset included both UV-B and UV-(A+B)

attenuation. The sample size was calculated as the number of paired observations. The meta-analysis was performed using R software (version 3.1.1) (R Core Team, 2014). The natural logs of the RRs for the individual and combined treatments were determined by specifying study as a random factor in the model

with the “metafor” package. The effects of changes in UV radiation on the loss of biomass and nutrient

25 changes were considered significant if the 95% confidence interval (CI) of the RR did not overlap with

zero. The “maps” package was used to generate a map of the global site distribution (Fig. S1) (Becker and Wilks, 2005). The meta-analytic models were selected using the same approach used by Terrer et al.

(2016) and van Groenigen et al. (2017), in which all possible models that could be constructed using combinations of the experimental factors (changes in UV radiation, litter type, experiment type,

direct/indirect effects, incubation time) described above were considered main effects, using the “glmulti” package in R. The relative importance of each factor was then calculated as the sum of the Akaike weights derived for all the models in which the factor was included. A regression analysis was conducted to evaluate the relationship between nutrient release and loss of litter weight, and a general linear model was used to compare the slopes of the loss of litter weight and nutrient release between the UV treatment and control groups.

3 Results

3.1 UV radiation type

As expected, UV enhancement and attenuation showed opposite effects on mass loss and nutrient release. UV enhancement and attenuation showed significant effects on k decay, with RRs of 0.09 and -0.41 (Fig. 1), respectively; furthermore, UV-B enhancement and attenuation showed significant effects on mass loss, with RRs of 0.04 and -0.35, respectively. UV enhancement promoted N and phosphorus (P) release, with RRs of -0.16 and -0.08 of N and P remaining, respectively. UV attenuation showed the opposite effects on N and P remaining, with RRs of 0.08 and 0.10. The effects of changes in UV radiation on C and lignin release were not significant. Both UV-(A+B) and UV-B attenuation showed similar effects on mass loss and N and P release (Fig. S2). Across all studies, the RR of k decay was significantly correlated with the change in UV radiation (Fig. S3); it increased as the UV enhancement increased and decreased as the UV attenuation increased except when the UV attenuation was lower than the threshold, where it increased with increasing UV attenuation. These findings indicated different sensitivities of litter decomposition to changes in UV radiation and a shift from direct to indirect effects of UV radiation.

3.2 Direct and indirect effects

The sum of Akaike weights indicated that litter decomposition was affected by UV enhancement or attenuation, life forms (forest or grassland), experimental condition (field or laboratory), effect type (direct, via exposure of litter to UV, or indirect, via exposure of plants to UV during growth), and experimental duration (Fig. S4). The results were then used to calculate the treatment effects for the changes in each experimental condition. Due to the small differences between UV-B and UV-(A+B) attenuation on litter decomposition, we pooled the UV-B and UV-(A+B) findings into the category UV

attenuation. The direct and indirect effects differed (Figs. 2a and b). Litter decomposition increased when both the soil and plants were subjected to enhanced UV-B radiation (Fig. 2a), and UV-B enhancement significantly promoted N release when the plants were grown under UV-B enhancement. Furthermore, P and lignin contents increased when the soil was under UV enhancement, whereas C release was unaffected by UV-B enhancement. However, UV radiation significantly affected litter decomposition when the soil was subjected to UV attenuation, and positive litter decomposition effects were observed when plants were under UV attenuation (Fig. 2b). N release under UV attenuation showed the opposite pattern between the soil and plants.

3.3 Experimental conditions and ecosystem type

The results from field experiments showed that UV enhancement and attenuation increased and decreased litter decomposition, respectively (Figs. 3a and b). The samples size for laboratory conditions was small; however, based on the limited data, neither UV enhancement nor attenuation had an effect on litter decomposition or nutrient release, although mass loss occurred under UV attenuation. Litter decomposition and N and P release from litter in the field were significantly affected by changes in UV radiation. In addition, UV changes affected litter decomposition differently for different ecosystem types and leaf sources (Figs. 3c and d), but only the rate of decomposition, not the direction, was affected. In addition, UV enhancement significantly affected the mass loss and N and P release of broad-leaved plants, whereas UV attenuation significant decreased the litter mass loss of grasses, herbs, broad-leaved and needle-leaved plants (Fig. S5).

3.4 Experimental duration

The RRs of mass loss and nutrient release varied with incubation time (Fig. 4). UV enhancement had no significant effect on mass loss in the first four months of the experiment but ~~did~~promoted litter decomposition from 4 months to 18 months (Fig. 4a). As incubation time progressed, UV enhancement had no effect on litter C release (Fig. 4b) and promoted the release of N in 6 months to 12 months, but showed N enrichment of litter after 18 months decomposition (Fig. 4c), and promoted the release of both P and lignin after 18 months (Figs. 4d and e). The UV attenuation negatively affected mass loss, but the effect decreased as the incubation time increased (Fig. 4f). The direction and rate of nutrient loss under UV attenuation differed among C, N, P and lignin (Figs. 4g-j).

3.5 Precipitation

Precipitation showed a significant correlation with decomposition decay under control treatment (Fig. S6a), and k decay increased with the decline of precipitation below 450 mm. UV attenuation significant decreased k decay at precipitation ranges of 100 to 200 mm and of 1400 to 1500 mm (Fig. 5).

- 5 In addition, the RR of k decay under UV attenuation showed a significant relationship with mean annual precipitation (Fig. S6b), increasing with precipitation until 500 mm.

3.6 Relationships between litter mass loss and nutrient release

Various effects of changes in UV radiation on the RRs of remaining nutrients and weight remaining were found (Fig. 6). The slope of the RRs of remaining C and N and the weight remaining under UV attenuation were 1.31 and 1.23, respectively, however, the effects of both UV enhancement and UV attenuation on the relationship between each of C, N and P and mass loss relative to the ambient environment were not significant ($p>0.05$). Interestingly, UV enhancement significant promoted the lignin release compared with the ambient environment ($p<0.01$).

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4 Discussion

15 In the present study, a meta-analysis was performed to assess the effects of UV exposure on the dynamics of litter decomposition and nutrient release. We found that leaf sources (grassland or forest), experimental condition (field or laboratory), experimental duration, and exposure type (direct or indirect effects) affected litter decomposition and nutrient release under UV exposure.

4.1 Differential responses of litter mass loss and nutrient release

20 In the present study, UV enhancement positively affected litter mass loss, whereas UV attenuation reduced mass loss (Fig. 1). These findings are consistent with the results of those studies (Almagro et al., 2017; Gehrke et al., 1995; Song et al., 2013b; Pancotto et al., 2003) and are mainly due to larger effect of photodecomposition than of the abundance and community composition of microbial decomposers on litter decomposition (Austin and Vivanco, 2006; Smith et al., 2010; Song et al., 2014b). In addition,

25 changes of litter quality under also contributed to the decomposition (Fig. S6). However, interestingly,

changes in UV radiation did not affect the release of C, which was a focus of our concern, may be indicated that a different regulatory mechanism other than UV radiation may be controlling litter decomposition, although the small sample size may have contributed to the insignificant results. Therefore, more studies needed to determine the effects of UV changes on the release of C.

5 The decomposition process can be affected by UV radiation received either by plants during growth or by litter during decomposition. The direction and rate of litter decomposition and nutrient release differed due to the direct and indirect effects of changes in UV radiation (Fig. 2), as the direct effects were regulated mainly by the effects of the UV radiation on the soil microorganisms, whereas the indirect effects were regulated mainly by the change in litter chemical properties (Pancotto et al., 2003). UV
10 enhancement promoted litter decomposition, mainly due to the enhancement of photodecomposition as well as to the high initial litter N content because litter decomposition decay showed significant relationship with N concentration (Figs. S6 and S7). However, N release was not affected when the soil subjected to UV enhancement, reflecting the balance between increased photodecomposition and decreased activity of decomposer organisms (Pancotto et al., 2003). In addition, UV attenuation on the
15 soil reduced litter decomposition, possibly due to a reduced effect of photodecomposition (Pancotto et al., 2005; Song et al., 2013a). However, when plants were exposed to UV attenuation during growth exhibited no effect on the loss of litter mass but promoted the release of N, which needs further investigation.

 The effects of changes in UV radiation on litter decomposition varied with the experimental
20 conditions and litter type (Fig. 3). With the exception of mass loss under UV attenuation in laboratory conditions, changes in UV radiation did not affect litter decomposition or nutrient release. In contrast, a significant effect was observed in the field studies, indicating differences between laboratory and field experiments. These results are consistent with those of previous laboratory-based studies (Kirschbaum et al., 2011; Lambie et al., 2014) in which the limited observed effects of UV radiation may have been
25 due to differences in environmental conditions, such as soil moisture status from those in the field conditions. In addition, as expected, N and P release increased and decreased under UV enhancement and attenuation, respectively, but C release was not affected. Litter type affected only the magnitude of litter decomposition and not the direction in response to changes in UV radiation: this effect was due to the variation among species in litter quality, which affects decomposition rate (Day et al., 2015).

30 Litter decomposition is a temporal and dynamic process, and the sensitivity of litter decomposition

to changes in UV radiation varies with incubation time (Wang et al., 2017). The duration of the experiments often influenced the results. For example, neutral or even negative responses of litter decomposition to UV exposure were mostly recorded in short-term experiments (Kirschbaum et al., 2011; Lambie et al., 2014), whereas positive responses were frequently observed in long-term experiments (Austin and Vivanco, 2006; Brandt et al., 2010). In the present study, litter decomposition also varied with decomposition time under UV enhancement and attenuation; the effects of UV enhancement on decomposition exhibited three-stage temporal dynamics (Fig. 4). UV enhancement did not impact the mass loss during the early stage (0-4 months) but significantly promoted litter decomposition during the intermediate stage (4-18 months), indicating that the UV enhancement could accelerate litter decomposition, given a sufficient period of UV accumulation (Wang et al., 2017), as well as accelerate nutrient release. However, UV attenuation significantly reduced the litter decomposition during the early stage, and the effect diminished as the decomposition time increased.

4.2 Sensitivity of litter decomposition under UV change with precipitation

Climatic (precipitation, temperature) and litter-composition variables (C:N or lignin:N) are often used to predict mass loss rates (Gallo et al., 2009) because the activity of microorganisms that decompose litter is regulated mainly by these variables. However, an increasing numbers of studies indicated a key role of photodecomposition in arid ecosystems (Austin and Vivanco, 2006; Day et al., 2015; Gallo et al., 2009). In the present study, k decay remained large in areas of relatively low precipitation (Fig. 5), indicating that photodecomposition is an important factor in arid ecosystems (Gallo et al., 2009; Almagro et al., 2017; Day et al., 2015). Previous studies have shown that the attenuation of radiation can even reduce decomposition by as much as 60% (Austin and Vivanco, 2006). In the present study, k decay increased as precipitation decreased from 500 mm to 100 mm (Fig. S6a) due to the positive effect of photodecomposition on litter decomposition in areas where with low annual precipitation (Huang et al., 2017). In addition, the RR of k decay indicated that UV attenuation reduces litter decomposition. The effect of UV attenuation on litter decomposition was greater under 100 to 200 mm of precipitation than under high-precipitation conditions (Fig. 5), mainly because photodecomposition was the dominant driver of litter decomposition in the low precipitation areas (Brandt et al., 2010; Brandt et al., 2007). The results demonstrated that the effects of UV radiation on litter decomposition differ with climatic conditions (Ballare et al., 2011).

4.3 Relationship between mass loss and nutrient release under UV change

Across all studies, mass loss and nutrient release were significantly correlated but the relationship differed between UV enhancement and UV attenuation (Fig. 6). The change in UV radiation also affected the relationship between mass loss and nutrient release. The RRs of remaining C and N were significantly correlated with the RR of weight remaining under UV attenuation, and the slopes were greater than 1, but the relationships were not significantly different from those observed under control conditions ($p > 0.05$). However, the remaining lignin was negatively correlated with the weight remaining under UV attenuation, indicating that, relative to the decomposition of litter weight, the release of lignin occurred more quickly at the beginning of decomposition but became enriched during the later stages of decomposition (McClaugherty and Berg, 1987). However, the relationship between lignin and mass remaining under UV enhancement showed significant difference compared with ambient environment ($p < 0.01$).

4.4 Implications and uncertainties

Our study revealed that responses of nutrient release and mass loss in litter decomposition to UV change varied, depending on the direct or indirect effect of UV, experimental conditions and experiment duration. The results clarified how UV changes affect mass loss and nutrient release during litter decomposition. Several critical challenges remain for future studies. Most studies have concentrated on the effect of UV on litter mass loss, and less attention has been paid to the release and ultimate fate of litter C and N (i.e., storage in soil vs. emission to the atmosphere), which were the focus of concern here (Wang et al., 2015).

In addition, climate change usually involves changes in multiple environmental factors, such as temperature and precipitation pattern, which might simultaneously and interactively affect litter decomposition (Brandt et al., 2007; Zepp et al., 2007). However, few studies have focused on photodecomposition in the context of global changes. Therefore, to better understand the effects of UV in a changing global environment, future studies should investigate how climate change affects the balance between the positive and negative effects of changes in UV on litter decomposition.

5 Conclusions

The current study, which was based on global data, shows that UV radiation plays an important role in litter decomposition and that the effect of photodecomposition becomes stronger as precipitation decreases below 855 mm, at which point litter decomposition becomes sensitive to UV attenuation. The effects of changes in UV radiation on litter decomposition also differ depending on the direct and indirect effects of changes in UV radiation, as UV attenuation on plants does not affect the litter mass loss. In addition, except for an effect of UV attenuation on mass loss, changes in UV radiation under laboratory conditions do not affect litter decomposition or nutrient release, and the mass loss under UV radiation is characterized by three-stage temporal dynamics. Furthermore, the relationship between mass loss and nutrient release is altered under UV attenuation, this finding suggests that future studies should consider nutrient release instead of focusing mainly on the effects of UV radiation on litter mass loss.

Author contributions. W. Y conceived and led the study. All authors contributed to writing and editing the manuscript.

Competing interests. The authors declare that they have no conflict of interest.

Acknowledgments. The study was funded by the National Postdoctoral Program for Innovative Talents (BX201700200), the China Postdoctoral Science Foundation (2018M631200), the Fundamental Research Funds for the Central Universities (2452017233), the National Key Research and Development Program of China (2016YFC0501605) and the National Natural Science Foundation of China (41390463, 31370425).

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5

6 Figure legends

7 **Figure 1** Effects of UV treatment on litter mass loss and remaining nutrients. The black symbols indicate
8 significant differences ($p < 0.05$) between the response ratios (RRs) and zero. The vertical dotted line
9 represents a mean effect size of 0. The sample size for each variable is shown, with that for UV
10 enhancement and attenuation shown from left to right, respectively.

11 **Figure 2** The direct effects (litter decay directly exposed to UV) and indirect effects (plants received UV
12 during growth) of UV enhancement (a) and attenuation (b) on litter mass loss and remaining nutrients.
13 The black symbols indicate significant differences ($p < 0.05$) between the response ratios (RRs) and zero.
14 soil and plant denote direct and indirect effects, respectively; and the sample size for the indirect and
15 direct effects is shown from left to right.

16 **Figure 3** Effects of UV enhancement (a) and attenuation (b) on litter mass loss and remaining nutrients
17 in laboratory and field experiments and the effects of UV enhancement (c) and attenuation (d) on litter
18 decomposition and remaining nutrients in herb and wood litters. The black symbols indicate significant
19 differences ($p < 0.05$) between the response ratios (RRs) and zero. The sample size for each variable is
20 shown and represents laboratory and field experiments (a and b, respectively) and the grassland and
21 forest litters (c and d, respectively), from left to right.

22 **Figure 4** Effects of UV enhancement (a-e) and attenuation (f-j) on litter mass loss and remaining nutrients
23 during decomposition. The dashed line represents zero. The black symbols indicate significant
24 differences ($p < 0.05$) between the response ratios (RRs) and zero. The sample size for each variable is
25 shown above the symbol.

26 **Figure 5** The k decay under ambient environment (Control) and UV attenuation under different
27 precipitation, and * indicates significant differences ($p < 0.05$) between the control and UV attenuation
28 treatments.

29 **Figure 6** Relationships of the response ratios (RRs) of the remaining nutrients and litter weight remaining.
30 The slope values are based on all data, and p values of the relationships between remaining nutrients and
31 litter weight under UV enhancement (UV+) and attenuation (UV-) are shown. Black dashed lines
32 represent regression lines that show significant correlations between remaining nutrients and litter weight
33 remaining under UV+ or UV- conditions. $p < 0.05$ between ambient environment (CK) and UV+ or UV-
34 conditions indicates a significant difference between the relationship observed under CK and that
35 observed under with UV+ or UV-.

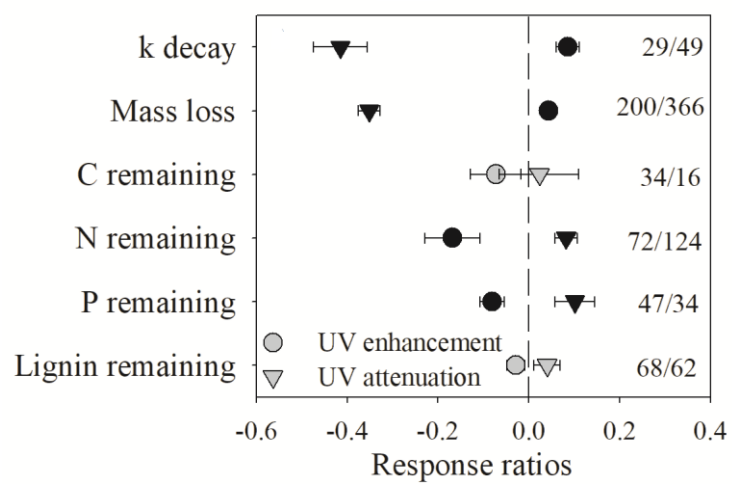


Figure 1

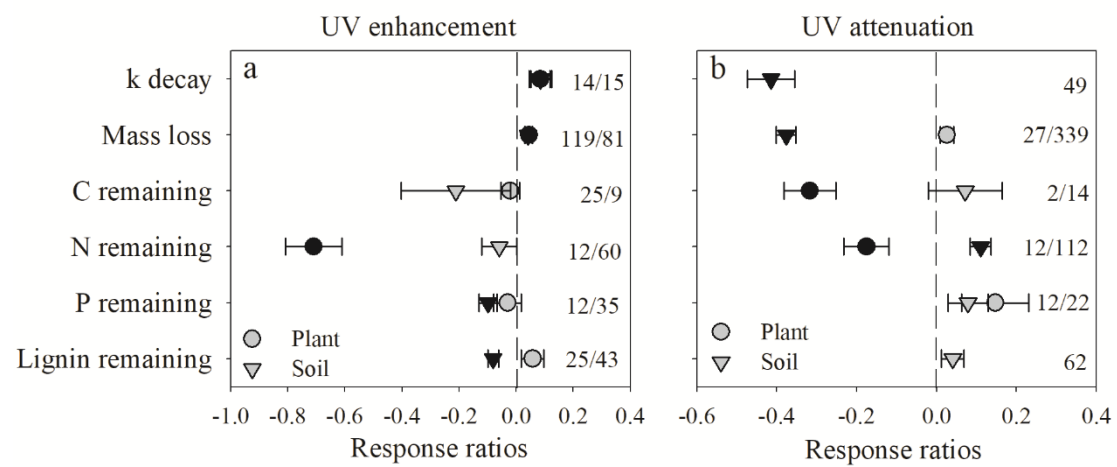


Figure 2

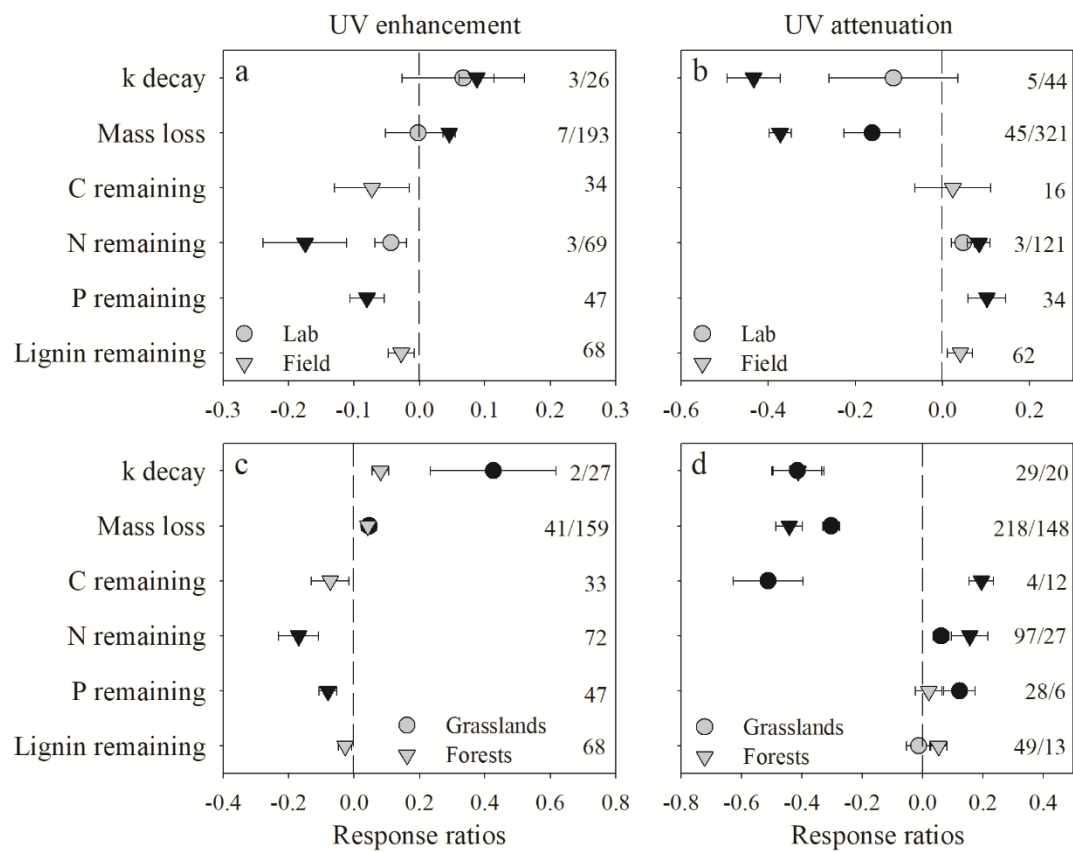


Figure 3

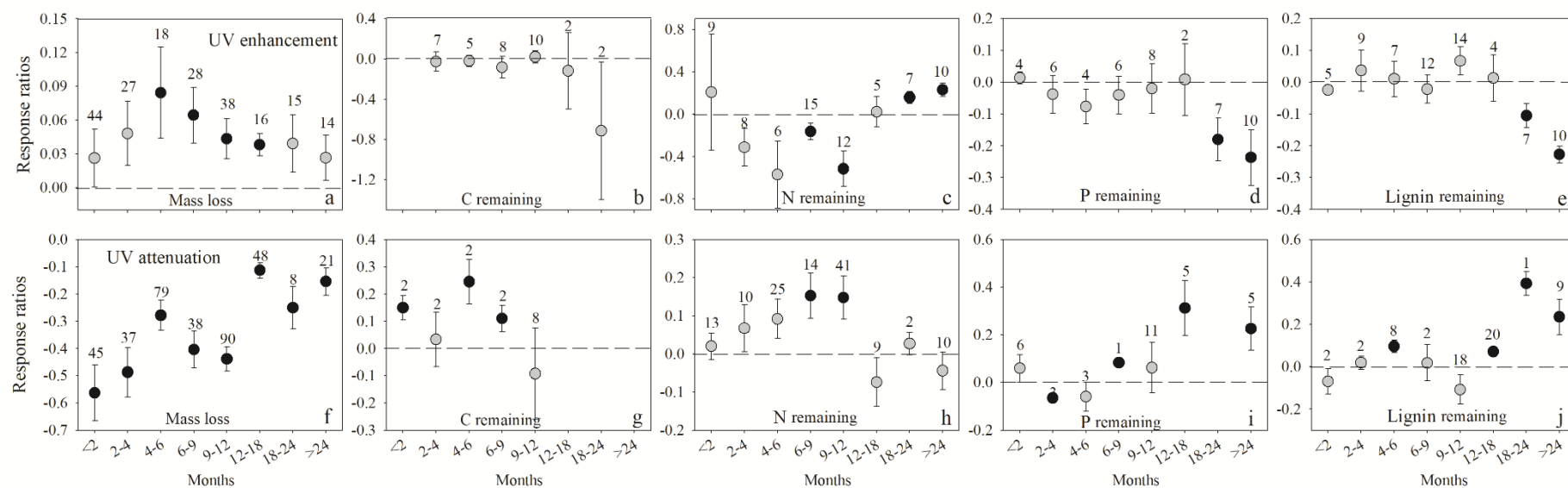


Figure 4

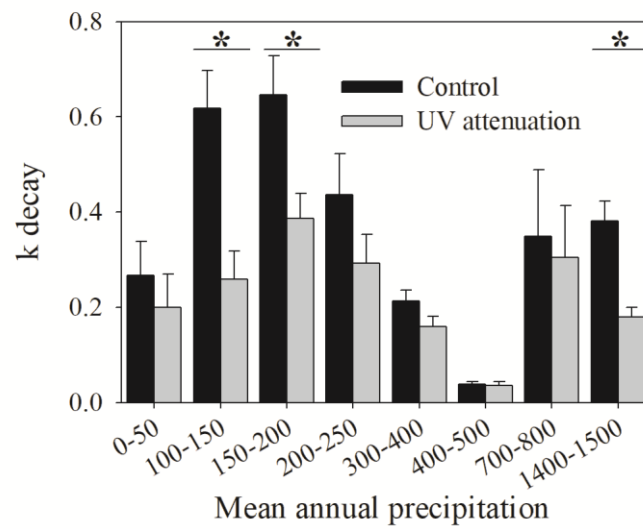


Figure 5

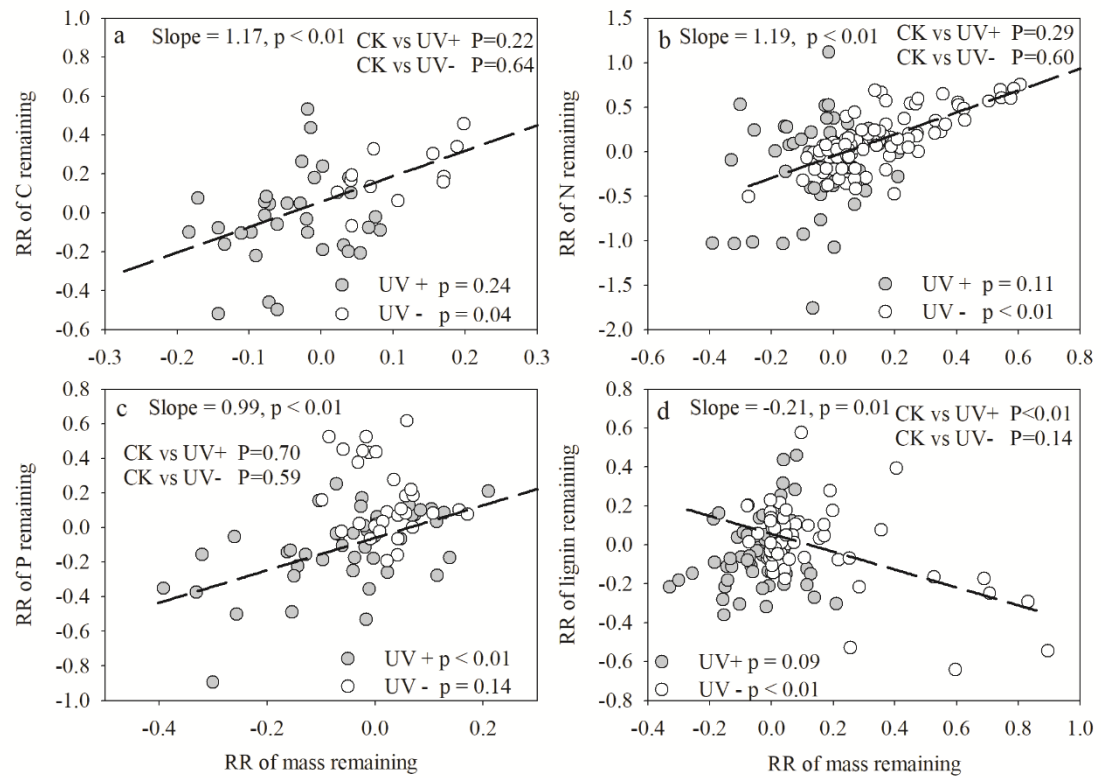


Figure 6