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Authors

Marinho, Osmarina A
Martinelli, Luiz A
Duarte-Neto, Paulo J
[et al.](#)

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**Photodegradation Influences Litter Decomposition Rate in a Humid Tropical Ecosystem,
Brazil**

Osmarina A. Marinho^{1*}, Luiz A. Martinelli¹, Paulo J. R. Duarte-Neto², Edmar A. Mazzi¹,
Jennifer Y. King³

¹ Center of Nuclear Energy in Agriculture, University of Sao Paulo, Piracicaba, SP, Brazil,
13400-970.

² Department of Statistics and Computing, University of Pernambuco, Recife, PE, Brazil, 52171-
900.

³ Department of Geography, University of California, Santa Barbara, CA, USA, 93106-4060.

*Corresponding author at: Center of Nuclear Energy in Agriculture, University of Sao Paulo,
Piracicaba, SP, Brazil, 13400-970.

E-mail address: osmarina.marinho@usp.br (O.A. Marinho)

ABSTRACT

Solar radiation in general and UV radiation in particular have been recognized to stimulate plant litter decomposition through photochemical mineralization of organic molecules such as lignin and through facilitation of microbial decomposition in dryland ecosystems. However, little is known about how photodegradation may influence decomposition in other ecosystems not subject to moisture limitations and under what conditions photodegradation may be favored. Decomposition in humid tropical ecosystems is a complex process, and it can be influenced by a number of environmental factors that are distinct from arid and semi-arid ecosystems. To assess the mechanisms underlying photodegradation by ultraviolet B (UV-B) radiation in a humid tropical ecosystem, we designed a 300-day field experiment in a tropical site in Brazil with high levels of annual precipitation, compared to arid ecosystems, and exposed litter to three levels of radiation (full sun, UV-B removed, and shade) combined with a biocide treatment. Results show that after nearly one year of exposure, the microbial biomass was not affected by UV-B incidence, and this effect has not yet been fully understood for tropical ecosystems. Modeled using an exponential deceleration equation, the removal of UV-B radiation decelerated the plant litter decomposition rate by almost 35% compared to litter exposed to full sun. Interestingly, shaded litter exhibited similar mass loss compared to litter exposed to full sun. Furthermore, differences in the decay constant among radiation treatments due to the UV-B effect were independent of lignin loss. Overall, our study suggests that UV-B radiation contributed to plant litter decomposition through carbon losses but had no discernible effect on nitrogen, lignin, or cellulose loss specifically. Importantly, our results demonstrate that photodegradation occurs under humid tropical conditions, and further studies are necessary to examine the mechanisms of carbon loss.

Keywords: Abiotic, exponential deceleration model, Atlantic Forest, polyphenols, climate change, mesic environment.

1. INTRODUCTION

Annually, plant litter and soil organic matter decomposition release ten times more carbon to the atmosphere than fossil fuel combustion globally (IPCC, 2007; Lee *et al.*, 2012). On the soil surface, plant litter can be decomposed either by microorganisms or by solar radiation. Pauli (1964) was the first one to raise the possibility of organic matter photodegradation; however, in just the last decade, investigation of photodegradation of plant litter in terrestrial ecosystems has increased (King *et al.*, 2012). Still, much less is known about the role of solar radiation than the role of microorganisms in plant litter decomposition (Austin *et al.*, 2016).

Ultraviolet B (UV-B) radiation (280-320 nm) is considered to have a large impact on ecological processes, affecting several regulatory mechanisms in organisms such as growth and reproduction (e.g., Caldwell *et al.*, 1998; Brandt *et al.*, 2009; Ballaré *et al.*, 2011; Day *et al.*, 2015 and references therein). Atmospheric conditions modulate the intensity of UV-B radiation; changes in ozone layer, cloud cover, and aerosol concentration are likely to change UV-B radiation (Ballaré *et al.*, 2011; Bais *et al.*, 2015). In turn, such atmospheric properties are also heavily influenced by changes in land use, such as deforestation, as the incidence of radiation on the soil surface can increase due to lack of vegetation cover (Ballaré *et al.*, 2011).

UV-B radiation is especially important for decomposition in arid and semiarid ecosystems, where microbial activity is low (Austin & Vivanco, 2006; Day *et al.*, 2007; Smith *et al.*, 2010). In these regions, UV-B radiation not only causes direct photolysis, but also causes photoprimering, by breaking recalcitrant compounds, which consequently enhances the susceptibility of litter tissue to microbial decomposition (Austin & Ballaré, 2010; King *et al.*, 2012; Wang *et al.*, 2015; Austin *et al.*, 2016; Wang *et al.*, 2017). It has been suggested that lignin is susceptible to photodegradation due to UV radiation absorption by aromatic rings (Austin & Ballaré, 2010). However, the studies about that susceptibility of lignin have shown contradictory results up to now with some studies showing this susceptibility (Day *et al.*, 2007; Austin & Ballaré, 2010) while other studies suggest the occurrence of photoprimering through other compounds such as cellulose (Lin & King, 2014; Baker *et al.*, 2015). Nevertheless, in addition to studies indicating a general stimulatory effect of UV-B radiation in litter decomposition (Song *et*

69 *al.*, 2013a), studies have found that not only UV-B, but also UV-A and blue-green radiation
70 cause photodegradation of plant litter (Brandt *et al.*, 2009; Austin *et al.*, 2016).

71 As already mentioned, the effects of solar radiation on plant litter decomposition are
72 much less understood than microbial degradation (Pancotto *et al.*, 2003; Austin *et al.*, 2016;
73 Wang *et al.*, 2017). This is especially true in wetter ecosystems of the subtropical and tropical
74 regions, since most studies of photodegradation have been conducted in arid and semiarid zones
75 of the globe. In subtropical China, studies by Song *et al.* (2012, 2013b) present conflicting
76 evidence for the role of photodegradation under subtropical conditions with some litter types
77 showing accelerated decomposition with exposure to UV-B radiation while others do not. Wu *et al.*
78 (2018) suggest that photodegradation is important in decomposition of coarse woody debris in
79 subtropical forests in China. Some studies have examined the influence of precipitation or
80 moisture on photodegradation (Henry *et al.*, 2008; Smith *et al.*, 2010; Liu *et al.*, 2014), but these
81 studies were not conducted in tropical field settings. Furthermore, even though the predicted
82 increase of UV radiation is small in the tropics, this region receives more solar radiation across
83 the year than mid and high latitudes (Bias *et al.*, 2015). Therefore, advancing understanding of
84 how solar radiation affects plant litter decomposition in tropical and subtropical regions of the
85 globe is essential for predicting changes in biogeochemical processes with global change
86 (Almagro *et al.*, 2015). No published studies to date have focused on quantifying the importance
87 of photodegradation in tropical forests of Brazil.

88 We conducted a field litterbag experiment to investigate the effects of photodegradation
89 in a tropical region where the mean annual precipitation is approximately 2000 mm. Due to the
90 high levels of precipitation in this region, we hypothesized that removal of UV-B radiation might
91 not influence rates of decomposition compared to full sunlight. Furthermore, even though the
92 overall rates of decomposition might not be affected by radiation level in this ecosystem, we
93 hypothesized that differences in litter chemistry could emerge during the litter decomposition
94 process under different radiation regimes.

2. MATERIALS AND METHODS

2.1. Study site

This study was conducted in the *Serra do Mar* State Park at the Santa Virginia research station, São Paulo, southeast Brazil (23°24'S, 45°11'W). The *Serra do Mar* is a mountain rift system located in dense montane forest (evergreen rainforest) and features a humid tropical climate. The soils are classified as Typic Dystrudepts at the end of the Atlantic Plateau forming coastal scarps. The vegetation in the research station is classified according to the Brazilian classification system as Ombrophylus Dense Forest (Martins *et al.*, 2015), having on average 150 tree species per ha (Sanchez *et al.*, 2013). The mean altitude is 1000-1100 m above sea level, and the mean annual precipitation and temperature are 1990 mm and 16 °C, respectively (Rocha, H; unpublished data). Seasonality in this region is mild, and our study was conducted during the rainy season, avoiding the dry period of the year. The site has extensive sun exposure and receives direct radiation all year round.

2.2. Experimental design

The litter decomposition experiment was initiated early in the rainy season (September 17th, 2015). Senescent leaves of *Tibouchina sellowiana*, a dominant pioneer tree species in the forest, were collected at the study site in August 2015, using a netting system attached underneath the trees. Ten grams of whole senescent leaves were placed in each litterbag (nylon with 2 mm mesh size; 20 cm by 20 cm) in such a way as to avoid overlapping. To manipulate radiation, we placed 1 m²-PVC frames at 40 cm from the soil surface, each covered with plastic films with different transmittance properties according to the three radiation treatments (Austin & Vivanco 2006) as follows: (1) **full sun** (Aclar films which transmit >90% of total solar radiation); (2) **UVB^{-I}** (Mylar films, 125 µm thickness (Mylar® DuPont) which block the UV-B spectrum (280 -315 nm)), and (3) **shade** (Mylar films covered with silver aerosol paint, which blocks > 90% of solar radiation). The plastic transmission properties were tested using a spectrometer (USB4000, Ocean Optics). Under each PVC frame, all above-ground vegetation was removed to avoid shading. Perforations (grid of 2 mm² holes at 5 cm spacing) were made in the plastic films to allow precipitation to pass through, and plastic films were periodically

evaluated for damage and replaced when necessary. On each litterbag collection date, three repeated measures of soil temperature under the PVC frames were performed using a temperature probe inserted to 5 cm depth, and soil moisture was measured gravimetrically by collecting a soil sample to 20 cm depth under each PVC frames. Soil moisture and temperature data were checked for homogeneity of the experimental treatments using ANOVA for each collection time. Total ambient solar radiation and precipitation during the experiment were obtained from an eddy-covariance flux tower located less than 1 km from the study site.

In order to investigate if microbial activity could mask the effect of radiation on decomposition, the biocide treatments were sprayed with an aqueous solution containing a dose equivalent of 15 g m⁻² of fungicide (Ortocide, N-(trichloromethyltio phthalimide)) and 15 g m⁻² of bactericide (Casugamicina). This biocide solution was applied five times over the course of the experiment. The same volume of distilled water was sprayed on the other half of the plots (control). Starting at the third collection date, as suggested by the literature, we also incorporated naphthalene pellets into the soil to help control microbial activity (Austin & Vivanco, 2006; García-Palacios *et al.*, 2013).

Each treatment was replicated four times (four replicate plots), totaling 24 plots (3 radiation treatments x 2 biocide and control treatments x 4 replicates). Litterbags were collected on five collection dates (14, 35, 66, 217, and 300 days after the start of the experiment) for a total of 120 litterbags.

Soil microbial biomass C was determined according to the fumigation-extraction method described by Vance *et al.* (1987). A soil sample (10 cm depth) from beneath each PVC frame was collected at the end of the experiment in order to evaluate the efficacy of biocide in suppressing microbial biomass and the effects of UV-B radiation under these conditions.

2.3. Mass loss and litter chemistry analysis

In order to estimate mass loss during litter decomposition, one litterbag was randomly collected from each plot (four litterbags per treatment) five times after the beginning of the experiment. Litterbags were cleaned to remove visible plants and soil matter and then oven dried at 50 °C for 48 h before weighing. Subsamples of litter from each litterbag were ashed at 563 °C for 3 hours to express mass remaining on an ash-free dry mass basis (AOAC, 2011). For

determination of carbon and nitrogen concentrations in the litter, a subsample of litter was ground to powder and then encapsulated for analysis using an elemental analyser (Carlo Erba model 1110, Milan, Italy).

As recommended by Udén *et al.* (2005), neutral detergent fibre content was analysed according to Mertens (2002), and acid detergent fibre (ADFom) and lignin (LIG) were determined sequentially following the methodology proposed by Van Soest *et al.* (1991). Cellulose was calculated by the difference between ADFom and LIG. Total polyphenols were evaluated using the methodology proposed by Makkar (2000). All chemical analyses of lignin, cellulose, and total polyphenols were based on the content of dry matter (DM). The initial litter chemistry was determined on four replicates through the same procedures as described above.

2.4. Decomposition model

The following three decomposition models were evaluated: the single exponential equation (1E model, equation 1) proposed by Olson (1963), the double exponential (2E model, equation 2) proposed by Lousier & Parkson (1976), and the exponential deceleration (D model, equation 3) proposed by Rovira & Rovira (2010),

$$1E \text{ model: } X_t = X_0 e^{-kt} \quad (1)$$

$$2E \text{ model: } X_t = a e^{(-k_1 t)} + (1 - a) e^{(-k_2 t)} \quad (2)$$

$$D \text{ model: } X_t = X_0 e^{-(at - \frac{b}{m}(e^{-mt} - 1))} \quad (3)$$

where t is the time of decomposition expressed in years; X_t is the litter mass at time t ; and X_0 is the initial litter mass. While the first model (equation 1) considers a single decomposition rate k , the double exponential model (equation 2) considers two constant decomposition rates, k_1 and k_2 , i.e. the rate of decomposing organic matter for the labile and recalcitrant pools. In this case, a is the initial amount of labile pool and $1-a$ is the initial amount of recalcitrant pool. As the first model, the exponential deceleration model (equation 3) considers a single litter pool; however, it describes a decrease in the decomposition rate over time with changes in the substrate from labile to more recalcitrant organic matter compounds, where m in equation 3 represents decreasing rate of k (equation 1); a is the basal rate; and b is the amplitude of k (equation 1).

2.5. Data analysis procedure

The effect of the treatments and their interactions on decomposition were evaluated using a model selection approach. Decisions about the model comparison were based on Akaike's Information Criterion corrected for small sample size (AICc) in which the model that had the best fit with the lowest number of variables would have the lowest AICc value, and differences were considered when ΔAIC was more than two units (Burnham & Anderson, 2002; Hobbs & Hilborn, 2006). AIC combines the Kullback–Leibler (K–L) distance (the amount of information lost by using a model to approximate the truth) with maximum likelihood estimation by using likelihood to estimate the relative K–L distance between competing models (Burnham & Anderson, 2002).

We first selected, among the three decomposition models presented above, the one that best describes all data, using all main factors (biocide and radiation treatments) and their second order interactions (the full model). After that, based on the above model selection approach and using the best decomposition model, we conducted a hierarchical procedure from the full model and compared it with simpler models, first taking off the second-order interactions, followed by each factor. This procedure was conducted using the "R code for Model Selection" (Castanho *et al.*, 2012). In this code, the likelihood functions are constructed in such way that the estimation of k and m are based on a linear sum of treatments (factors) and interaction effects (see supplementary material from Castanho *et al.*, 2012 for more details).

For mass remaining and litter quality parameters (C, N, lignin, cellulose, and total polyphenols), the results were presented as percent of their initial value against time of decomposition. In order to investigate temporal changes in litter quality, a preliminary three-way analysis of variance (ANOVA) found significant interaction between the treatments and time of decomposition, indicating that data should be checked for each period of time independently (Lin & King, 2014; Lin *et al.*, 2015). For differences in soil temperature, soil moisture, and soil microbial biomass, we also used analysis of variance (ANOVA). Data were tested for normality using Shapiro-Wilks test; log transformations were used for cellulose and total polyphenols to ensure normality. The *post-hoc* Tukey's HSD (Honestly Significant Differences) test was used to compare means. The effects were considered statistically significant at $p < 0.05$. Statistical analyses were conducted using R version 3.3.2 (R Core Team, 2016).

3. RESULTS

3.1. Experimental treatments

In general, there were no significant differences in soil temperature or soil moisture among radiation treatments (Supplementary Figure 1). Solar radiation, monthly precipitation, and monthly mean air temperature followed the typical pattern found for the latitude and longitude of the experiment location (Supplementary Figure 2).

The use of biocide to suppress microbial activity was ineffective or only temporarily effective, since no statistical differences in the soil microbial biomass carbon (SMBC) were found between control and biocide treatment plots at the end of the experiment (Supplementary Figure 3). Additionally, SMBC was not affected by any radiation treatment.

Regarding the effect of biocide treatment on litter chemistry across radiation treatments, we observed that biocide did not have a consistent effect on characteristics of litter chemistry measured in this study. Remaining mass, nitrogen remaining, and total polyphenols remaining were slightly higher in the biocide treatment compared to the control on some sampling dates; however, the other litter characteristics (carbon, lignin, and cellulose remaining) showed no differences or the opposite trend (Supplementary Figure 4). These results and the lack of evidence of an effective biocide treatment were taken into account in the hierarchical model selection process for modeling factors influencing mass loss (described below).

3.2. Decomposition rate and mass remaining

Decomposition rate was significantly slowed by the lack of UV-B radiation compared to that under full sun exposure, as described below. Litter mass showed a typical rapid loss during the first month, and there was no difference in the mass loss rate among the treatments in the first two months. After this period, mass loss proceeded at a slower rate in the UVB^[-] treatment compared to full sun and shade treatments (Figure 1). In order to know if this difference is statistically significant, it is necessary to select the best model to describe mass loss with time.

The D model had a better fit compared to 1E and 2E models; therefore, the D model was considered the most adequate to describe the decomposition process in this study (Table 1). Because the 1E model is commonly used in decomposition studies, the results are presented in

Table 2 only for comparison. Under the D model, the best fit includes all main effects (radiation and biocide treatments) without interaction between them. However, by independently excluding radiation and biocide treatments, the AICc increased 9.7 and 2.4 in magnitude, respectively. This indicates that even though the decomposition process had been affected by both factors, radiation treatments were more important in affecting decomposition rate than the biocide treatment (Table 2). There is large uncertainty about the real effectiveness of the biocide treatment, since ΔAIC was close to two units when this treatment was removed. We opted, therefore, to use the D model that only includes radiation treatments (D_R).

In the D_R model, the m coefficient (deceleration rate of k) of the UVB^[-] treatment was significantly higher than that of full sun and shade treatments, suggesting that the lack of UV-B radiation may retard litter decomposition (Figure 2). Compared to full sun, the UVB^[-] treatment decelerated the litter decomposition rate by almost 35% (ratio of full sun to UVB^[-] treatments; Figure 2).

3.3. Litter chemistry

After 300 days of decomposition, there was a distinct temporal pattern in litter chemistry among radiation treatments. A major decrease in relative concentrations of most elements and compounds was observed in the first two weeks of decomposition, while a decrease in carbon was observed for every radiation treatment during the whole experiment (Figure 3A). Differences among radiation treatments were only significant after 66 days of decomposition. Loss of C was lower in the UVB^[-] than under full sun, suggesting that the lack of UV-B radiation retards carbon loss (Figure 3A).

Overall, N loss was faster during the initial stage of decomposition without significant differences among treatments (Figure 3B). The carbon to nitrogen (C:N) ratio became significantly higher in the UVB^[-] treatment, compared to both other radiation treatments, only at the last sampling date (Figure 3C).

Lignin was not affected by the UVB^[-] treatment in relation to the full sun treatment (Table 4, Figure 4A). However, loss of lignin was slower in the shade treatment during the 300-day experiment than in the other two treatments (Figure 4A). Cellulose decreased slightly without a clear effect of UVB^[-] treatment (Table 4, Figure 4B). The polyphenols also exhibited a rapid loss during the initial stages of decomposition (Figure 4C). However, polyphenol loss was

significantly lower in the UVB^[-] treatment toward the end of the experiment, suggesting that the lack of UV-B radiation retards polyphenol breakdown (Table 4).

4. DISCUSSION

4.1. Litter decomposition rate

In contrast to our hypothesis, removal of UV-B radiation (UVB^[-] treatment) was enough to decelerate litter mass loss rate to the same extent in this tropical ecosystem in 10 months as has been observed in arid climates on timescales ranging from 4 months to 3 years (Austin & Vivanco, 2006; Brandt *et al.*, 2007; Day *et al.*, 2007; King *et al.*, 2012; Song *et al.*, 2013a; Lin & King, 2014; Day *et al.*, 2015; Wang *et al.*, 2015; Day *et al.*, 2018). Since the effects of photodegradation are expected to become more apparent during later stages of decomposition, the results from this 10-month-long experiment suggest that photodegradation is an important contributor to litter turnover in tropical ecosystems. Surface litter environment measurements are not available, but measurements of soil temperature and soil moisture did not show significant differences among radiation treatments through time (Supplementary Figure 1). Based on this and previous work employing the same experimental approach (Austin & Vivanco, 2006), we excluded a possible microclimate effect created by the use of different plastics. Removal of UV-B radiation clearly resulted in higher mass remaining after 300 days of exposure (Figure 1). Our experimental area receives approximately 2000 mm of precipitation per year, and despite this high amount of precipitation, the effect of UV-B radiation on decomposition was notable, suggesting that this effect can occur in any ecosystem where litter is exposed to UV-B radiation (Day *et al.*, 2007; Smith *et al.*, 2010; Austin *et al.*, 2016).

Decomposition rates are reported to increase under full sunlight compared to shade conditions in arid environments (Austin & Vivanco, 2006). However in our study there was no difference in decomposition rates between full sun and shade treatments (Figure 2). In addition, radiation had no evident suppression effect on soil microbial biomass in our study (Supplementary Figure 3). Similar findings have also been described by Wang *et al.* (2015) and Baker *et al.* (2015) where UV-B radiation was responsible for increasing the efficiency of extracellular enzymes for microbial activity. On the other hand, there are several examples in

which UV-B radiation had a detrimental effect on microbial communities, suppressing microbial growth and damaging microbial DNA (Rohwer & Azam, 2000; Caldwell *et al.*, 2007).

In our study, we expected that photodegradation would become more evident with suppressed microbial activity. However, our approaches for controlling microbial activity and measuring its effectiveness were inadequate in this study. Due to logistical and resource constraints, we were only able to measure microbial biomass once, at the end of the experiment, and the results show a weak trend of lower microbial biomass C with biocide treatment (Supplementary Figure 3). Consequently we could not evaluate the effect of microbial activity on mass loss pathways in this study. We speculate here that this lack of biocide effect was due to the high microbial activity found in tropical soils (Chapin *et al.*, 2011), and a one-time measurement could not reflect microbial activity during the entire study. The fast cycle of recolonization and regrowth of soil microbes in the tropics would probably require a much larger and more consistent application of biocide, which can compromise the safety of the natural ecosystem due to the use of substances that are considered toxic for the environment. Therefore, it remains unclear how microbial suppression through the use of biocide would affect decomposition via photodegradation in areas with high microbial activity.

Our experiment also showed an unexpected result in relation to arid zones: the decomposition rate under the shade treatment was as high as found for the full sun treatment. We speculate that in the shade treatment, litter decomposition is driven by high soil moisture allied to high soil temperature, conditions which favor high rates of microbial decomposition. Furthermore, fungal communities tend to be sensitive to light, which inhibits spore germination (Caldwell *et al.*, 2007; Barnes *et al.*, 2015). Thus, the absence of direct solar radiation favors fungal communities that are considered the main decomposers of plant litter and account for 60 to 90% of microbial biomass in forest soils (Chapin *et al.*, 2011).

4.2. Litter chemistry

In this study, carbon and total polyphenols were significantly affected by the lack of UV-B radiation (UVB^[-] treatment). The lack of UV-B radiation decreased the loss of carbon and polyphenols during the decomposition process (Figure 3A and Figure 4C). As a consequence, the C:N ratio at the end of the experiment was significantly higher in the UVB^[-] treatment than in the other radiation treatments (Figure 3C). It seems that the C:N ratio in the UVB^[-] treatment

was affected by changes in C, but not in N, since our results did not show any consistent UV-B effect on N concentration across the entire experiment (Figure 3B). This finding is in line with the results of Brandt *et al.* (2010) who found that N dynamics were unaffected by UV-B exposure, but contradicts a meta-analysis study by Wang *et al.* (2015) in which litter N was reduced due to UV radiation exposure as a result of altering microbial processes. These opposing trends illustrate how the effect of UV radiation on N dynamics is still controversial.

Recent studies have found that UV radiation contributes to the decomposition process by facilitating microbial decomposition via the breakdown of recalcitrant compounds, an effect called “photopriming” (Wang *et al.*, 2015; Austin *et al.*, 2016). Furthermore, as photopriming facilitates microbial decomposition, decreases in the C:N ratio due to UV-B radiation exposure will increase substrate quality and accelerate microbial decomposition (Chapin *et al.*, 2011). Similar findings were also described by Wang *et al.* (2017) in an experiment conducted in a Chinese semi-arid ecosystem, where UV exposure increased litter biodegradability, changing litter chemistry while facilitating microbial decomposition in the last stage of the process. The stage of decomposition (early vs. late) may be a key factor in understanding the role of photopriming in overall decomposition rates, as indicated by Hewins *et al.* (2019) and suggested in modeling work by Adair *et al.* (2017). In their Chihuahuan Desert experiment, Hewins *et al.* separated radiation exposure from field decomposition and found no photopriming effect (Hewins *et al.* 2019). On the other hand, Day *et al.* (2018) showed that litter mass loss is strongly predicted by microbial respiration rates in the Sonoran Desert. Therefore, the increase of C:N ratio we observed in the end of the decomposition process in the UVB^[-] treatment suggests that a similar process of microbial facilitation could be occurring in wetter regions.

In our experiment, the lack of UV-B radiation did not show a strong effect on the loss of lignin and cellulose (Figure 4A and 4B), which are considered light-absorbing recalcitrant compounds that may experience photodegradation (Day *et al.*, 2007; Henry *et al.*, 2008, Austin & Ballaré, 2010; Austin *et al.*, 2016). Indeed some studies have shown that UV-B radiation caused a higher cellulose loss (Brandt *et al.*, 2007; Lin & King, 2014) and in some cases increased lignin loss as well (Day *et al.*, 2007; Austin & Ballaré, 2010). On the other hand, other studies did not show the same effect (e.g., Brandt *et al.*, 2010). Among others, King *et al.* (2012) have suggested that lignin may not be the most susceptible compound to be photodegraded by UV-B radiation. In addition, the analytical method for lignin in our study does not distinguish

between plant lignin and lignin-like microbial by-products (Preston *et al.*, 2006), which could be expected to increase under conditions of high biological activity. Nevertheless, when litter is shaded, a significantly smaller loss of lignin was observed during most of the decomposition process compared to the other radiation treatments (Figure 4B), which highlights the importance of solar radiation in lignin loss. However, the mechanisms which break down this compound and the relevant parts of the spectrum to the process are not yet clear (King *et al.*, 2012; Day *et al.*, 2015).

Polyphenols showed the strongest radiation treatment effect (Figure 4C). Gallo *et al.* (2009) suggested that photodegradation of polyphenols can accelerate litter mass loss. Furthermore, our results also show a surprisingly higher loss of polyphenols in the shade treatment compared to other radiation treatments (Figure 4C), which suggests that in tropical ecosystems, the high microbial activity may be efficient in the breakdown of recalcitrant compounds such as polyphenols.

Our results demonstrate that the removal of UV-B radiation decreased plant litter decomposition rates in a wet tropical region. Therefore, it seems that UV-B radiation has a positive effect on decomposition, especially in the late stages, after 217 days, when the lack of UV-B radiation led to decreased C losses and increased litter C:N ratios. On the other hand, the lack of UV-B radiation did not affect lignin degradation or soil microbial communities as was observed in some studies (e.g. Austin & Ballaré, 2010).

The understanding of changes in litter chemistry during decomposition remains an important gap in studies of temporal dynamics in decomposition (Parsons *et al.*, 2014; García-Palacios *et al.*, 2016), and the degree to which this process is influenced by solar radiation in tropical ecosystems remains unclear. Our findings should be interpreted with caution, since only one tree species was tested. Clearly, investigation of the effects of UV-B radiation on decomposition of other litter types under tropical conditions is in order.

In summary, our study provides evidence for a broader role of photodegradation, extending the importance of UV-B radiation in plant litter decomposition to ecosystems without moisture limitations. Furthermore, because the magnitude of photodegradation will vary depending on climate conditions, it needs to be better understood and incorporated into mechanistic models in order to accurately predict changes associated with climate change.

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The authors have no competing interests to declare.

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