Interactive effects of elevated UV-B radiation and N deposition on decomposition of Moso bamboo litter

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A B S T R A C T

Being two important agents of global environmental change, elevated ultraviolet-B (UV-B) radiation derived from anthropogenic driven ozone depletion and enhanced nitrogen (N) deposition may strongly affect litter decomposition, a crucial factor in biogeochemical cycling. However, the interactive effects of both agents together on litter decomposition are still unclear even though each has been well-documented independently. We conducted a field-based experiment in subtropical China to investigate the combined effects UV-B radiation and N deposition on the decomposition of Moso bamboo (Phyllostachys pubescens) leaf litter over a 20 months period. It was found that the combined effect significantly accelerated litter decomposition, C loss, and lignin degradation as well as facilitating phosphorous (P) release, although it had no measurable effect on N release. Moreover, the interactive effects of both agents together far exceeded the effects of each separately. Results indicated that the positive combined effect of UV-B radiation and N deposition on litter decomposition and C loss could potentially impact Moso bamboo forest ecosystem C cycling. These findings provide a new perspective to further understand the interactive effects of global environmental changes on terrestrial ecosystem processes.

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1. Introduction

Elevated ultraviolet-B (UV-B, wavelength 280–320 nm) radiation and nitrogen (N) deposition are two important drivers of global environmental change. Due to ozone depletion, UV-B reaching the earth’s surface has increased by approximately 5% over northern mid-latitudes throughout the last 30 years and is expected to continue to increase until the mid twenty-first century (Herman, 2010). Reactive N production also increased from ~15 Tg N in 1860 to 187 Tg N yr⁻¹ in 2005 and is expected to continue to increase from 50% to 100% by 2030 (relative to 2000 figures) as a result of human activity (Galloway et al., 2008; Reay et al., 2008).

These increases in UV-B radiation and N deposition could profoundly influence terrestrial ecosystem processes, such as litter decomposition, a crucial factor of biogeochemical cycling. UV-B may increase litter decomposition by enhancing lignin photodegradation (Rozema et al., 1997; Austin and Vivanco, 2006; Song et al., 2012) or decrease litter decomposition by its impact on the abundance and community composition of microbial decomposers (Pancotto et al., 2003). N deposition also showed positive (Limpens and Berendse, 2003; Manning et al., 2008) and negative (Micks et al., 2004; Fang et al., 2007) effects on litter decomposition by altering soil N availability and soil enzymatic activity. To date, effects of enhanced UV-B (Newsham et al., 2001; Flint et al., 2003; Pancotto et al., 2003, 2005; Brandt et al., 2007; Smith et al., 2010; Kirschbaum et al., 2011) and N deposition (Knorr et al., 2005; Mo et al., 2006; Hobbie et al., 2012) on plant litter decomposition have primarily been investigated as effects of a single factor. However, the interactive effects of these two environmental agents together on litter decomposition have never been reported. It is therefore necessary to estimate the potential combined effects of both elevated UV-B and N deposition on litter decomposition.

These issues are of particular relevance in subtropical China, where UV-B radiation has increased with an annual ozone depletion rate of 0.27% (Liao et al., 2007; Zhou and Chen, 2008) and
annual N deposition rate was recorded with a maximum value of 64 kg N ha\(^{-1}\) yr\(^{-1}\) (Lü and Tian, 2007). This region was predicted to become the region in the world to receive the greatest N deposition rates by 2030 (Reay et al., 2008). Moso bamboo (Phyllostachys pubescens) forests, primarily distributed throughout subtropical China, cover an area of 3.37 million ha, which is 70% of the country’s bamboo forested area and 80% of \(P.\) pubescens global distribution (Song et al., 2011a). With its fast growth rate and high annual re-growth rate after harvesting, annual tree layer C fixation for a typical \(P.\) pubescens forest is c. 5 t ha\(^{-1}\), which is some 1.3 orders-of-magnitude compared to a typical tropical mountain rain forest (Zhou and Jiang, 2004). Owing to its enormous C sequestration potential as well as their other ecological benefits, such as water and soil conservation, moisture retention, rainfall interception, Moso bamboo forests play an increasingly important role in climate change mitigation and environmental protection (Song et al., 2011a). All of the listed ecological benefits are related to litter decomposition as this affects the realised growth rate of \(P.\) pubescens via its effects on nutrient availability. Under conditions of increasing UV-B and N deposition, it remains unclear how \(P.\) pubescens litter decomposition and nutrient release will respond to either single or combined factors. For this study, a 20 month field-based experiment was carried out to test the following hypotheses: (1) elevated UV-B radiation accelerates \(P.\) pubescens litter decomposition; (2) elevated N deposition also accelerates \(P.\) pubescens litter decomposition; and (3) the interactive effects of both factors combined on litter decomposition is stronger than each separately.

2. Materials and methods

2.1. Leaf litter collection

In March 2010, \(P.\) pubescens (Carrière) Lehaie leaf litter was collected at Zhejiang A & F University’s experimental field (long 119°44’E, lat 30°16’N). Samples were air-dried for a period of one month in a laboratory. Subsamples of air-dried samples were oven-dried at 65 °C to a constant weight to determine water content of air-dried samples. Oven-dried samples were then used to determine initial litter chemistry using the methods described below.

2.2. Experimental treatments

The decomposition experiment was carried out at the Zhejiang A & F University’s experimental field, located in the outskirts of Lin’an City, Zhejiang Province, China. The area has a monsoon subtropical climate with four distinct seasons. Mean annual rainfall is 1420 mm. Mean annual temperature is 15.6 °C, with a 2696 °C average effective accumulated temperature above 10 °C. The site has an average of 1939 daylight hours and 234 frost-free days per year. The experiment used four treatments: elevated UV-B radiation (UV-B), elevated N deposition (N), elevated UV-B radiation and elevated N deposition (UV-B + N), and a control group. Three replicate plots were created for each treatment. All plots and treatments were designed in randomized complete blocks. Soil in all plots was homogenized local red soil sieved through a 4 mm grate to remove coarse material. To focus solely on decomposition effects related to UV-B and N deposition, the experiment was carried out on bare ground devoid of vegetation.

Enhanced UV-B was regulated using artificial irradiance (Song et al., 2012) using fluorescent UV-B lamps (UV-B313EL, Beijing Lighting Research Institute, Beijing, China). Lamps were wrapped in cellulose triacetate film that allowed transmission of both UV-B and UV-A (315–400 nm) while removing all UV-C. Like many previous UV-B experiments (Hoorens et al., 2004; Smith et al., 2010), UV-A was not controlled in this experiment. Lamps operated between 9:00 a.m. and 4:00 p.m. under cloudless conditions and were adjusted monthly for height from ground to maintain an approximate 10% increase above ambient levels, measured using a UV-297 radiometer (Photoelectric Instrument Factory of Beijing Normal University, China).

Local N deposition was calculated at 30.9 kg N ha\(^{-1}\) yr\(^{-1}\) (Xie et al., 2008). Accordingly, 30 kg N ha\(^{-1}\) yr\(^{-1}\) ammonium nitrate (NH\(_4\)NO\(_3\)) was applied to the N treatment. NH\(_4\)NO\(_3\) was weighed and mixed with 100 ml water and distributed onto each plot using a sprayer at the start of every month. This made 12 equal applications over a one year period, equal to an annual increase of 0.5 mm rainfall (Mo et al., 2006; Fang et al., 2007). When NH\(_4\)NO\(_3\) was applied to the N treatment plots, the remaining treatments were irrigated using 100 ml of N-free water to avoid effects of water N transfer.

The UV-B + N treatment was carried out under both a 10% UV-B increase and a 30 kg N ha\(^{-1}\) yr\(^{-1}\) N addition, using the above methods. Lamp arrays using dummy lamps were constructed over both control and N treatment plots, which provided the same degree of shading as lamp arrays underwent in the UV-B and UV-B + N treatments.

2.3. Litter decomposition and chemical analysis

The widely used litterbag method was employed to determine the rate of leaf litter decomposition. Litterbag size was 15 × 15 cm and constructed from 0.5 × 1.0 mm mesh-size polypropylene fabric. All were filled with 10 g air-dried leaf litter. In May 2010, a total of 144 litterbags were positioned on the soil surface of 12 homogenized decomposition treatment plots so they would be in contact with the organic layer. Each plot contained 12 litterbags for four sampling. Three samples from each plot per measurement duration were averaged as the value per plot. Plots were maintained to prevent weeds from growing into the litterbags.

Three litterbags were retrieved from each plot after a period of 4, 8, 14, and 20 months, after which adhering soil particles were removed by gentle washing and brushing. Litter was oven-dried at 65 °C and weighed. 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.

Oven-dried litter was ground with a grinder (DFI-50A, Wenling LINDA machinery co. ltd., Wenling, China). Total carbon (C) and N were determined using a Sumigraph NC-80 high-sensitivty CN analyser (Shimadzu, Japan). Phosphorus (P) concentration was determined using a modified Kjeldahl method. This was followed by photometric analysis. Finally, lignin concentration was determined using the ADF-sulphuric method (Song et al., 2011b).

2.4. Data and statistical analysis

Net plant litter dry weight for each retrieved litterbag was expressed as a percentage of the initial plant litter dry weight of each litterbag. The first-order exponential decay model (Olson, 1963) using the \(X_t/X_0 = e^{-kt}\) form was fitted to the decomposition data where \(X_t\) is the net oven-dry weight remaining at time \(t\), \(X_0\) is the initial oven-dry weight, and \(k\) is the annual decomposition rate constant (yr\(^{-1}\)).

Nutrient release via litter decomposition was expressed as a percentage of initial nutrient content, which was calculated by determining nutrient content at each sampling and dividing it by the initial nutrient content (Pancotto et al., 2003; Brandt et al., 2010) \(E = \left[\left(M_t \times C_t\right)/\left(M_0 \times C_0\right)\right] \times 100\%\) where \(E\) is nutrient release (%); \(M_0\) is the initial oven-dry mass (g); \(C_0\) is the initial nutrient concentration (mg g\(^{-1}\)); \(M_t\) is the oven-dry mass at time \(t\);
and $C_t$ is the nutrient concentration at time $t$. Lignin content change via decomposition was calculated as a percentage of initial lignin content following the equation above.

One-way analysis of variance (ANOVA) was used to test differences between annual decomposition rates, litter mass loss, and nutrient release at each sampling time for the four experimental treatments. These analyses were carried out using SPSS 13.0 for Windows (SPSS Inc., Chicago, Illinois).

3. Results and discussion

3.1. UV-B effects

UV-B treatment did not accelerate litter mass loss and decomposition rate ($k$) throughout the decomposition experiment (Fig. 1A). Fourteen months into the trial, there was a slower C percentage loss in the UV-B treatment than the control treatment, after that, this difference disappeared (Fig. 2a). UV-B significantly reduced N release ($P < 0.05$) but had no effect on P release and lignin degradation (Fig. 2b, c, d).

The absence of significant UV-B effects on $P. \text{pubescens}$ litter decomposition in this study was contradictory to hypothesis 1 (that elevated UV-B accelerates $P. \text{pubescens}$ litter decomposition). UV-B may increase the rate of decomposition by enhancing lignin photodegradation (Rozema et al., 1997; Austin and Vivanco, 2006). Previous experiments carried out by the authors of this study also found that increasing UV-B by 31% accelerated litter decomposition of $Cinnamomum \text{camphora}$ and $Cyclobalanopsis \text{glauca}$, two common species found in subtropical China (Song et al., 2012). However, some studies have also reported that UV-B had no effect on litter decomposition (Kirschbaum et al., 2011; Song et al., 2011b; Usein et al., 2011) or even led to a decrease (Newsham et al., 1997; Pancotto et al., 2003). For this study, the nonsignificant UV-B effect on the decomposition rate may be related to the low UV-B enhancement dosage (only 10%). Our meta-analysis on UV-B effects on litter decomposition demonstrated that only intermediate enhancement in UV-B dose (from 30% to 70%) can accelerate litter decomposition (Song et al., 2013). In consideration of the UV-B enhancement trend in the future (Herman, 2010), we may safely predict that the elevated UV-B would not have significant effect on $P. \text{pubescens}$ litter decomposition. Pancotto et al. (2003) observed that UV-B could suppress microbial activity and would thus restrain litter C release. This could partly account for the slowest C release found under the UV-B treatment for the present study.

Leaf litter N release is predominantly driven by initial N content and the stoichiometric requirements of microbial decomposers (Parton et al., 2007). Berg and Staaf (1981) found that N release takes place when initial N content is between 0.6% and 2.8%. In the present study, the initial litter N content (0.94%) (Table 2) was in the lower range of the threshold. Berg and Staaf (1981) reported and thus led to N release under all four treatments. UV-B could suppress decomposition and activity of microbial decomposers (Pancotto et al., 2003; Jeffery et al., 2009) and thus resulted in slower N release. However, previous studies from the authors of this study observed that elevated UV-B (31%) had no obvious effect on $Pinus \text{massoniana}$ and $C. \text{camphora}$ N release (with 0.72% and 0.40% N content, respectively) and even accelerated $Cunninghamia \text{ lanceolata}$ and $C. \text{ glauca}$ N release (with 0.40% and 0.67% N content, respectively) in the subtropics (Song et al., 2011b, 2012). These conflicting findings could be a result of interspecific differences and complexities of litter N release under elevated UV-B.

P release from decomposing litter is closely correlated to the C:P ratio within the 200 to 480 critical range (Gosz et al., 1973; Manzoni et al., 2010). Generally, P release initiates when the litter C:P ratio is less than 480 (Gosz et al., 1973). However, this stoichiometric control varies across climatic regions and ecosystems. Manzoni et al. (2010) demonstrated that the values of the critical C:P ratio are very high in the tropic sites with high rainfall due to the compound effects of increased decomposer respiration, high decomposer C:P ratio, and physical losses (especially leaching of organic matter under high rainfall regimes). In the present study, the initial C:P ratio of $P. \text{pubescens}$ litter was 717 (Table 2), exceeding this critical range. Even so, P release still occurred under all four treatments. This is consistent with the findings by Manzoni et al. (2010). Similar to N release, P release from decomposing litter showed positive, negative, and even no response to UV-B (Pancotto et al., 2005; Song et al., 2011b; this study).

Negligible effects of UV-B exposure on lignin loss was also observed by previous studies (Gehrke et al., 1995; Brandt et al., 2007; Song et al., 2011b). However, a few litter decomposition studies carried out in arid and semi-arid ecosystems found that UV-B accelerated lignin loss (Austin and Vivanco, 2006; Day et al., 2007). These differences in experimental results likely resulted from a number of environmental factors, namely humidity, soil, and concentration of reactive gases such as oxygen (Austin and Ballaré, 2010).

3.2. N deposition effects

Litter mass loss under N treatment became significantly faster than under control and UV-B treatments ($P < 0.05$) by the end of the decomposition experiment although these differences did not exhibit for the first 14 months ($P > 0.05$). The litter decomposition rate was also significant higher under N treatment than under UV-B and control treatments (Table 1). Eight months into the trial, there was a greater C percentage loss in the N treatment than the control

<table>
<thead>
<tr>
<th>Table 1</th>
<th>The litter decomposition rate ($k$-value) calculated by the first-order exponential decay model ($X_t/X_0 = e^{-kt}$) and correlation coefficient ($R^2$) for $P. \text{pubescens}$ leaf litter under four different treatments.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>$k$-value* (year$^{-1}$)</td>
</tr>
<tr>
<td>UV-B</td>
<td>0.33 ± 0.01c</td>
</tr>
<tr>
<td>N</td>
<td>0.37 ± 0.02b</td>
</tr>
<tr>
<td>UV-B + N</td>
<td>0.43 ± 0.01a</td>
</tr>
<tr>
<td>Control</td>
<td>0.32 ± 0.01c</td>
</tr>
</tbody>
</table>

* Values are means ± SD ($n = 3$). Different lowercase letters denote significant differences ($P < 0.05$) among treatments.
and UV-B treatments. After a period of eight months, these differences tended to decrease (Fig. 2a). N treatment increased P release but had no affect on N release and lignin degradation (Fig. 2b, c, d). N addition accelerated the *P. pubescens* litter decomposition rate (Table 1) and therefore supported hypothesis 2 (that elevated N deposition accelerates *P. pubescens* litter decomposition). Other studies also reported similar findings (Limpens and Berendse, 2003; Manning et al., 2008). It is generally believed that N deposition may improve soil N availability and soil enzymatic activity, and for that reason can accelerate litter decay (Knorr et al., 2005; Manning et al., 2008). Fang et al. (2004) found that the positive effects of N addition on soil available N was negligible during early experimental stages but became significant as the experimental period progressed in a subtropical forest ecosystem in China. Similarly, in the present study, N addition showed significant positive effect on litter decay only after the first 14 months (Fig. 1). These results implied that N addition effects on N availability to soil microbes may have been delayed and thus resulted in the effects of N addition on decomposition became apparent with the time of experiment.

Andersson et al. (2004) found that the effects of N addition on microbial decomposer activity varied with decomposition stage. N addition increased soil enzymatic activity at the early stage, which was beneficial to C release, but decreased C availability during the latter stage, which led to the sharp C loss observed in the first four months and subsequent slow C loss thereafter under N treatment in this study.

*P. pubescens* litter N content was adequate enough to meet decomposer’s demand for N in this experiment. Thus, exogenous N addition may not have accelerated N release. Mo et al. (2007) observed that N addition suppressed pine (*P. massoniana*) needle P release. They speculated that even though N addition can possibly increase microbial activity and P demand, insufficient pine needle P content alone cannot meet microbial demands in itself. In the present study, *P. pubescens* litter contained sufficient P to meet microbial demand and thus exhibited faster P release under the N addition treatment than the control group.

Lignin is a recalcitrant material that is resistant to microbial decomposition. Only specialized fungi may break down these structures into biologically usable forms (Austin and Ballaré, 2010; Swift et al., 1979). It has been reported that N deposition impeded lignin degradation by restraining white-rot fungi (Fog, 1988; Thirukkumaran and Parkinson, 2000). However, Hobbie and Vitousek (2000) found N deposition did not impact lignin degradation enzyme activity and lignin degradation in tropic forest in Hawaii. The present study also observed that N deposition did not

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### Table 2

<table>
<thead>
<tr>
<th>N (mg g⁻¹)</th>
<th>P (mg g⁻¹)</th>
<th>C (mg g⁻¹)</th>
<th>Lignin (mg g⁻¹)</th>
<th>C:N</th>
<th>Lignin:N</th>
<th>C:P</th>
</tr>
</thead>
<tbody>
<tr>
<td>9.4 ± 0.1</td>
<td>0.7 ± 0.01</td>
<td>502 ± 17.1</td>
<td>191 ± 1.7</td>
<td>53.2 ± 2.1</td>
<td>20.2 ± 0.1</td>
<td>717 ± 28.3</td>
</tr>
</tbody>
</table>
influence lignin degradation. These inconsistent results may be related to the difference in soil microbial composition, especially fungi, between different ecosystems (Wang et al., 2006).

3.3. Interactive effects of UV-B and N deposition

Litter mass loss and C loss was significantly faster under the UV-B + N treatment (P < 0.05) at all sampling times throughout the entire 20 month decomposition experiment (Figs. 1 and 2a). The litter decomposition rate was also highest under the UV-B + N treatment (P < 0.05) (Table 1). UV-B + N treatment accelerated P release and lignin degradation but had no affect on N release (Figs. 2b, c, 2d).

The most rapid litter decomposition and C loss under the UV-B + N treatment (Fig. 1, Table 1) supported the third hypothesis (that the interactive effects of the two factors combined on litter decomposition is stronger than each separately), which would have far-reaching consequences on Moso bamboo forest ecosystem processes under climate change. Although N addition accelerated litter decay, UV-B had only negligible effects. Taking this into account, a possible reason for this stronger interactive effect could be that UV-B photodegradation partly destroyed the physical structure of the litter surface (Austin and Ballaré, 2010; Austin and Vivanco, 2006), leading to conditions by which vitalized soil microbial and enzymatic activity (due to N addition) facilitated litter decay and C loss. This conjecture, however, must still be substantiated by further investigation.

Litter decomposition plays a key role in terrestrial ecosystem C cycling (Olson, 1963; Austin and Vivanco, 2006). Ngao et al. (2005), for example, reported that approximately 80% of total C was lost from fresh leaf litter while the remaining fraction (20%) entered the soil organic matter pool during litter decomposition. Therefore, the rate of litter C loss would profoundly influence the distribution pattern and dynamics of forest ecosystem C. For the present study, the combination of UV-B radiation and N deposition significantly accelerated P. pubescens litter decomposition and C loss, far exceeding the effects each factor would have separately. What this indicated was that the combination of both environmental agents together would largely decrease the forest floor C storage capacity of Moso bamboo, potentially impacting C sequestration and C cycling dynamics of Moso bamboo forest ecosystems.

Positive effects of N addition on microbial decomposers possibly offset negative effects of the UV-B treatment. Consequently, UV-B + N treatment did not exhibited lower N release than the control treatment. Partly due to UV-B photodegradation effect on litter, the positive effect of N addition on P release was further enhanced and thus faster P release appeared under UV-B + N treatment. UV-B and N treatments, either alone or combined, altered the timing of N and P release (Fig. 2b, c), which also affects N and P cycling and soil’s ability to meet plant nutrient requirements. N and P are two primary limiting factors on terrestrial ecosystem primary productivity, especially pertaining to how P reacts in tropical forest environments (Elser et al., 2007; Vitousek et al., 2010). Greater than 90% of N and P taken up by plants derive from nutrients released during litter decomposition (Chapin III et al., 2002). Observations from this study showed that only UV-B hindered N release while N alone and, especially, N and UV-B together, facilitated P release, which could potentially alter Moso bamboo forest ecosystem productivity and C cycling.

Since lignin slowly degrades during litter decomposition, it therefore controls litter decay rates, particularly during the latter stage of litter decomposition (Austin and Ballard, 2010). Rapid litter mass loss observed under the UV-B + N treatment in the present study could be partly explained by the rapid lignin loss that occurred under this treatment (Fig. 1). Lignin degradation is regarded as a key variable in predicting terrestrial ecosystem carbon dynamics (Austin and Ballaré, 2010). Therefore, the interactive effects of UV-B and N in conjunction with increasing lignin loss observed in this study may have contributed to greater litter mass loss and increased C cycling in the Moso bamboo forest investigated.

4. Conclusions

Elevated UV-B and N deposition are two important drivers of global environmental change that impact plant litter decomposition. Exposure to the combined effect of elevated UV-B and N deposition during P. pubescens leaf litter decomposition resulted in a significant acceleration of the litter decomposition rate, C loss, and lignin degradation. P release also increased, but N release remained unaffected. Interactive effects far exceeded the effect of each factor separately. Litter decomposition is a crucial link between C cycling and nutrient turnover in terrestrial ecosystems. Taking this into account, results from this study suggest that increasing UV-B and N deposition could have a profound effect on Moso bamboo forest ecosystem biogeochemical cycling. Findings from this study will contribute to the further understanding of the interactive effects of enhanced UV-B and N deposition on terrestrial ecosystem C dynamics and primary productivity.

Acknowledgements

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