Degradation Characteristics of Polyphenols in Leaf Litter of Subtropical Evergreen Broad-Leaved Forests in the Sichuan Basin During Different Rainfall Periods (Postprint)

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Date: 2018-05-18T00:00:00+00:00

Abstract

Plant polyphenols are important constituents of forest litter, and their abundance partially determines litter decomposition rates. However, the degradation dynamics of polyphenols during litter decomposition remain poorly understood. Therefore, we investigated the degradation characteristics of polyphenols in leaf litter of six species during the first year across different rainfall periods using the litterbag method. The study focused on three representative coniferous species (Pinus massoniana, Cryptomeria fortunei, and Cunninghamia lanceolata) and three broad-leaved species (Cinnamomum camphora, Toona ciliata, and Quercus acutissima) from subtropical evergreen broad-leaved forests in the Sichuan Basin. The results revealed that from the trace rainfall period through the early rainy season, all six leaf litter types exhibited consistent degradation dynamics, with degradation rates increasing as precipitation increased; following the late rainy season, polyphenol content stabilized. During the first decomposition year, the degradation rates of polyphenols in the six leaf litter types followed the descending order: Toona ciliata (100%) > Cryptomeria fortunei (97.81%) > Cunninghamia lanceolata (94.45%) > Quercus acutissima (93.67%) > Pinus massoniana (93.06%) > Cinnamomum camphora (91.64%). During the two dry season periods in the early decomposition stage (trace rainfall period and spring low-rainfall period), all six leaf litter types showed substantial polyphenol degradation, accounting for 42.16%-71.20% of the annual degradation rate. Moreover, for the five leaf litter types except Cinnamomum camphora, massive polyphenol degradation and release occurred during the early rainy season, representing 44.46%-55.72% of the annual degradation rate. Additionally, the initial polyphenol content in leaf litter displayed a significant quadratic relationship with its degradation rate. Thus, rainfall is one of the key driving factors for polyphenol degradation in litter of humid subtropical evergreen broad-leaved forests, while

tree species composition is an internal factor influencing polyphenol degradation in litter.

Full Text

Preamble

ACTA ECOLOGICA SINICA
ChinaXiv Partner Journal
Vol. 38, No. 9, May 2018
DOI: 10.5846/stxb201703180461

The Polyphenol Degradation Characteristics of Leaf Litter at Different Rainy Stages in a Subtropical Evergreen Broad-Leaved Forest in the Sichuan Basin, China

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Abstract

Plant polyphenols are important components of forest litter, and their concentrations largely determine litter decomposition rates. However, the degradation dynamics of polyphenols during litter decomposition remain poorly understood. This study investigated the degradation characteristics of polyphenols in leaf litter of six representative tree species in the subtropical evergreen broad-leaved forest of the Sichuan Basin across different rainfall periods, from the micro-rainy stage to the early rainy stage, using the litterbag method. The six species included two conifers: *Pinus massoniana* and *Cunninghamia lanceolata*; and four broad-leaved species: *Cinnamomum camphora*, *Toona ciliata*, *Quercus acutissima*, and *Cryptomeria fortunei*.

The results showed consistent degradation dynamics across all six litter types, with degradation rates increasing as precipitation increased. Following the late rainy stage, polyphenol concentrations stabilized. During the first decomposition year, the ranking of polyphenol degradation rates was: *P. massoniana* (100%) > *C. fortunei* (97.81%) > *Q. acutissima* (94.45%) > *C. lanceolata* (93.67%) > *T. ciliata* (93.06%) > *C. camphora* (91.64%).

During the two dry stages of early decomposition (micro-rainy stage and spring brief-rainy stage), all litter types exhibited substantial polyphenol degradation, accounting for 42.16%–71.20% of annual degradation. For five species (excluding *C. camphora*), major polyphenol degradation occurred during the early rainy stage, representing 44.46%–55.72% of annual degradation. A significant quadratic relationship existed between initial polyphenol content and degradation rate, indicating that precipitation is a key driver of polyphenol degradation

in humid subtropical evergreen broad-leaved forests, while species composition represents an internal regulating factor.

Keywords: litter decomposition; polyphenols; seasonal rainfall; dry season; tree species; subtropical region

Introduction

Litter decomposition is a crucial forest ecosystem process that plays an irreplaceable role in maintaining forest productivity, soil organic matter formation, and vegetation community succession. The decomposition process is regulated by complex interactions among biotic and abiotic factors, including climate, litter substrate quality, and decomposer communities. Polyphenols are complex secondary metabolites synthesized by plants, characterized by polyphenolic structures that can be classified into hydrolyzable and condensed tannins. They are widely distributed in plant bark, leaves, and roots, with concentrations reaching up to 20%–40% in the bark of many coniferous species, second only to cellulose, hemicellulose, and lignin.

Although polyphenols cannot be metabolized through various pathways and thus do not directly affect plant growth and development, they play important ecological roles in plant evolution, including enhancing environmental adaptability, competitive ability, defense against herbivory, disease resistance, and allelopathic effects. They also provide significant ecological feedback for forest ecosystem processes. In coniferous litter, polyphenol concentrations are often high, and because these compounds are not readily translocated or reused by plants, litter polyphenol content serves as an important substrate quality indicator frequently used to predict decomposition rates—generally, higher polyphenol concentrations correlate with slower decomposition.

In the hot, humid subtropical evergreen broad-leaved forest zone, litter decomposition is dominated by biological degradation, with soil microorganisms and fauna making significant contributions. Fresh leaf litter first undergoes decomposition during several months of dry season before encountering the rainy season with better hydrothermal conditions. During seasonal rainfall periods, favorable moisture and temperature environments promote decomposer growth, reproduction, and activity, accelerating litter biodegradation. This process is influenced by decomposer communities, litter substrate quality, and environmental conditions, all of which change continuously throughout decomposition, leading to dynamic shifts in decomposer community structure and activity. Consequently, leaf litter of different quality may exhibit distinct degradation characteristics across different rainfall periods. However, research on how seasonal rainfall affects polyphenol degradation dynamics remains limited.

The Sichuan Basin, located in the upper reaches of the Yangtze River in a subtropical evergreen broad-leaved forest region, features a climate with concurrent rainfall and heat, distinct wet and dry seasons, and prolonged seasonal rainfall periods. Previous studies found that leaf litter decomposed 27.75%–72.09% dur-

ing the first year, with mass loss during the rainy season exceeding that in the dry season due to favorable hydrothermal conditions. This suggests that polyphenol degradation may accelerate during seasonal rainfall periods and be influenced by litter quality across different tree species.

This study examined six representative species (two conifers: *Pinus massoniana* and *Cunninghamia lanceolata*; four broad-leaved: *Cinnamomum camphora*, *Toona ciliata*, *Quercus acutissima*, and *Cryptomeria fortunei*) to characterize polyphenol degradation dynamics across different rainfall and temperature seasons. Using the litterbag method based on actual rainfall patterns, we aimed to provide fundamental theoretical insights into litter decomposition processes in subtropical evergreen broad-leaved forests.

1. Study Area Overview

The study was conducted at the Sichuan Agricultural University Modern Agricultural Research & Development Base in Qiquan Town, Chongzhou City, Sichuan Province (103°38 31 -103°39 22 E, 30°33 16 -30°33 54 N). The site is located in the western Sichuan Plain along the upper Yangtze River, within the Sichuan Basin' s subtropical humid monsoon climate zone. The area has an annual mean temperature of 16.0°C, annual precipitation of 1015.2 mm (concentrated in specific seasons), 1161.5 hours of annual sunshine, and a frost-free period of 283 days. The soil type is old alluvial yellow soil. The base covers 133.33 hm^2 at an elevation of 516 m. Detailed soil properties and vegetation conditions are described in reference [23].

2. Experimental Design and Sample Processing

In late November 2012, fresh leaf litter of *Pinus massoniana*, *Cryptomeria fortunei*, *Cunninghamia lanceolata*, *Cinnamomum camphora*, *Toona ciliata*, and *Quercus acutissima* was collected with nylon nets (mesh size 0.5 mm) from typical ecosystems in the Sichuan Basin. The litter was air-dried in the laboratory, and 10 g (accurately weighed) was placed in each 20 cm × 20 cm litterbag. Additional samples were oven-dried to constant mass to estimate initial dry mass and for determination of initial polyphenol content and other substrate quality indicators. Polyphenol content was determined using the Folin-Ciocalteu method. Initial substrate quality characteristics are detailed in reference [22].

On December 1, 2012, five replicate plots were established in open, flat areas without tall tree or shrub cover, spaced approximately 120 m apart. After removing surface vegetation and litter, litterbags were placed flat on the soil surface, with three bags per species in each plot (totaling 90 bags). iButton temperature loggers (DS1923-F5, Maxim/Dallas Semiconductor, Sunnyvale, USA) were installed to automatically record surface temperature every 120 minutes. Based on historical and actual rainfall data from Chongzhou, the experimental period was divided into: micro-rainy stage (LRS: 2013/12/1-2014/2/28), spring brief-rainy stage (SRS: 2014/3/1-2014/4/30), early rainy stage (ERS:

2014/5/1-2014/7/31), late rainy stage (LRS: 2014/8/1-2014/10/31), and winter brief-rainy stage (WRS: 2014/11/1-2014/11/30). Rainfall data for each period are detailed in reference [22].

Sampling occurred on February 28, April 30, July 31, October 31, and November 30, 2014. At each sampling, three litterbags per species were collected from each plot, oven-dried, weighed, and analyzed for remaining polyphenol content after careful removal of soil and new fine roots.

3. Data Calculation

Polyphenol degradation rate was calculated as:
(%) = (C × M - C × M) / (C × M) × 100%

Polyphenol degradation amount was calculated as:
(g) = C × M - C × M

Where M and M are the dry mass of litter in bags at placement and sampling time (g), respectively; C is initial polyphenol content (mg/g); and C is polyphenol content at sampling time (mg/g).

4. Statistical Analysis

Data were analyzed using Excel 2003 and SPSS 20.0. One-way ANOVA was used to compare differences in initial polyphenol content and degradation amounts across decomposition periods. When variances were unequal, Dunnett' s T3 test was performed. Least Significant Difference (LSD) tests were conducted for multiple comparisons. Significance was set at $P < 0.05$. Origin 9.0 was used for graphical presentation.

5. Results

5.1 Dynamics of Leaf Litter Polyphenol Content

Initial polyphenol content differed significantly among the six species, with *Quercus acutissima* showing the highest concentration (Table 1). All six litter types exhibited consistent dynamics: polyphenol content declined rapidly from the micro-rainy stage through the early rainy stage, then stabilized. By the end of the early rainy stage, all litter types had reduced polyphenol content to 5 mg/g, with *Toona ciliata* showing complete degradation.

Table 1 Initial polyphenol contents of six tree species foliar litter (mg/g)

Species	Polyphenols
Pinus massoniana	18.13 ± 1.32c
Cryptomeria fortunei	9.42 ± 0.17d
Cunninghamia lanceolata	19.77 ± 0.06c
Cinnamomum camphora	29.27 ± 0.62a

Species	Polyphenols
Toona ciliata	21.43 ± 0.12b
Quercus acutissima	27.17 ± 0.29a

Note: Different lowercase letters indicate significant differences among species (P < 0.05).

5.2 Dynamics of Leaf Litter Polyphenol Degradation

Polyphenol degradation dynamics were consistent across species, showing a linear increase with precipitation from decomposition onset through the early rainy stage (Figure 2). During the first decomposition year, degradation rates ranked as: *P. massoniana* (100%) > *C. fortunei* (97.81%) > *Q. acutissima* (94.45%) > *C. lanceolata* (93.67%) > *T. ciliata* (93.06%) > *C. camphora* (91.64%).

Substantial degradation occurred during the early rainy stage, accounting for 44.46%-55.72% of annual degradation (except for *C. camphora* at 28.78%). During the two dry stages of early decomposition (micro-rainy and spring brief-rainy stages), all species showed considerable degradation, representing 42.16%-71.20% of annual degradation.

Polyphenol degradation was regulated by both species and decomposition stage, with significant differences in degradation amounts across species and periods (Table 2). Initial polyphenol content determined final degradation rates, showing a significant quadratic relationship (Figure 4).

Table 2 Polyphenol degradation amount of six tree species foliar litter during each decomposition stage (mg/10g)

Species	MRS	SRS	ERS	LRS	WRS	Total
P. massoniana	39.35±8.02Abc	58.45±6.77Aab	77.25±2.92Aa	-3.47±0.48Cd	2.17±0.36BCc	174.73±0.66C
C. fortunei	49.26±17.80Ab	50.32±18.58ABb	131.19±12.[illegible]Aa	2.86±0.61Ab	2.49±0.32BCb	236.23±0.47B
C. lanceolata	39.18±5.13Ab	26.61±5.74Bb	84.82±6.25Aa	-1.53±1.38Ac	3.12±1.50Bbc	152.20±0.39E
C. camphora	28.56±2.29ABa	25.42±2.96Ba	21.82±1.24Bb	-1.22±0.39Bc	1.23±0.44Cb	75.82±0.040D
T. ciliata	48.98±15.83Aab	33.44±16.91ABab	194.13±17.91Aa	13.55±0.00C	10.35±7.32Bb	300.45±47.17A
Q. acutissima	97.70±40.14Aa	122.87±33.60ABa	-2.47±1.82ABb	10.24±1.98Ab	12.40±2.60Aa	240.70±0.59A

Note: Different uppercase letters in the same column indicate significant differences among species within a stage (P < 0.05). Different lowercase letters in the same row indicate significant differences among stages within a species (P <

0.05). MRS: micro-rainy stage; SRS: spring brief-rainy stage; ERS: early rainy stage; LRS: late rainy stage; WRS: winter brief-rainy stage.

Figure 1 [Figure 1: see original paper] Daily mean temperature and monthly actual precipitation during the incubation experiment

Figure 2 [Figure 2: see original paper] Dynamics of polyphenol contents in foliar litter of six tree species in the subtropical evergreen broad-leaved forest

Figure 3 [Figure 3: see original paper] Dynamics of polyphenol degradation rates in foliar litter of six tree species in the subtropical evergreen broad-leaved forest

Figure 4 [Figure 4: see original paper] Relationships between polyphenol degradation rates and initial polyphenol contents in foliar litter of six tree species in the subtropical evergreen broad-leaved forest

6. Discussion

Upon entering soil through litter and root exudates, polyphenols improve soil environment, enhance microbial activity, and increase nutrient availability. As major litter components, polyphenols can inhibit decomposition through allelopathic effects or formation of protein-tannin complexes, impeding decomposer activity while promoting humus formation and soil carbon sequestration. In subtropical evergreen broad-leaved forests, biological degradation dominates litter decomposition, which is essentially a biochemical process mediated by decomposer enzyme systems. Polyphenol oxidase, primarily derived from soil microorganisms and fauna, is the key enzyme degrading litter polyphenols, converting them into humus components while participating in lignin degradation.

Temperature and moisture affect decomposition by influencing decomposer community structure and activity. This study found significant polyphenol reduction during the micro-rainy and spring brief-rainy stages of early decomposition, despite low temperatures and drought conditions that limit microbial and faunal activity and reduce polyphenol oxidase activity. The substantial degradation during these dry stages (42.16%–71.20% of annual degradation) likely resulted from physical losses due to mechanical fragmentation caused by low temperature and drought. Previous research documented significant mass loss from mechanical fragmentation during this period, which also contributed to lignin and cellulose degradation.

As decomposition progressed into the rainy season with improved hydrothermal conditions, abundant soil microorganisms and fauna colonized the litter, accelerating decomposition. Polyphenol degradation intensified during the early rainy stage, with most litter types reducing polyphenol content to minimal levels (5 mg/g) by this stage' s end. Mechanical fragmentation during the preceding dry stages may have disrupted protein-tannin complexes, facilitating polyphenol degradation in the rainy season. Polyphenol oxidase activity increased during

the rainy period, and small molecular weight phenolics produced during decomposition were leached into soil by abundant precipitation. During the late rainy and winter brief-rainy stages, polyphenol concentrations remained stable, possibly due to formation of stable humus complexes.

This study demonstrates that polyphenol degradation is regulated by both tree species composition and decomposition stage, with significant differences in degradation amounts across species and periods. Different species contain varying polyphenol types and ratios, leading to distinct degradation characteristics across stages. While this study did not identify specific polyphenol components or hydrolyzable vs. condensed tannin ratios, future research should examine how different polyphenol fractions respond to seasonal rainfall.

Species composition determines initial litter quality, which regulates the entire decomposition process. The significant quadratic relationship between initial polyphenol concentration and degradation rate confirms that initial litter quality substantially influences polyphenol degradation dynamics. Decomposition stages affect this process by modifying rainfall, temperature, and other environmental factors that regulate soil biological community structure, activity, and extracellular enzyme function.

7. Conclusion

In the subtropical evergreen broad-leaved forest of the Sichuan Basin, polyphenol degradation in leaf litter of six tree species exhibited distinct dynamic patterns across decomposition stages, co-regulated by seasonal rainfall and species factors. Polyphenol content decreased rapidly from the micro-rainy stage through the early rainy stage, with the highest degradation amounts occurring during the precipitation-rich early rainy stage. Precipitation is a key driver of polyphenol degradation and release in humid subtropical evergreen broad-leaved forests, while species composition represents the internal factor regulating these dynamics. These results provide theoretical insights into litter decomposition processes in these ecosystems.

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Note: Figure translations are in progress. See original paper for figures.