Effects of Litter Layer Enzymes on Litter Decomposition at Different Restoration Stages of Loropetalum chinense Communities in Guilin Karst Rocky Mountains: Postprint

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Date: 2018-04-28T00:00:00+00:00

Abstract

This study examined Loropetalum chinense communities at different restoration stages (shrub stage, shrub-arbor stage, and small arbor forest stage) in the karst hills of Guilin to investigate the effects of litter layer enzymes on litter decomposition rates. The results showed that after one year of decomposition, litter residual rates were 59.58% in the shrub stage, 61.79% in the shrub-arbor stage, and 62.02% in the small arbor forest stage. Litter decomposition rates decreased with succession. Across the three restoration stages, polyphenol oxidase, urease, and sucrase activities in the litter layer were lowest in December; polyphenol oxidase activity peaked in March, while urease and sucrase activities peaked in June. Cellulase activity showed consistent variation trends, reaching maximum values in June across all stages. Minimum cellulase activity occurred in March in the shrub stage and in September in both the shrub-arbor and small arbor forest stages. Enzyme activities in the litter layer consistently followed the pattern: sucrase > urease > cellulase > polyphenol oxidase. The effects of enzyme activities on decomposition rate varied among restoration stages. Correlation analysis revealed that sucrase activity was significantly positively correlated with decomposition rate in the shrub stage ($P < 0.05$), urease activity was significantly positively correlated with decomposition rate in the shrub-arbor stage ($P < 0.05$), but no significant correlations were observed in the small arbor forest stage. Path analysis indicated that sucrase, urease, and polyphenol oxidase were key factors influencing decomposition rate in the shrub stage, whereas urease, cellulase, and polyphenol oxidase were key factors in the shrub-arbor and small arbor forest stages.

Full Text

The Effect of Litter Layer Enzymes on Litter Decomposition in *Loropetalum chinense* Communities Among Different Recovery Stages in Karst Hills of Guilin

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DOI:10.11931/guihaia.gxzw201801025

Abstract

To explore the impact of litter layer enzymes on litter decomposition rate, *Loropetalum chinense* communities at different restoration stages (shrub stage, shrub-to-tree stage, and small tree stage) in karst hills of Guilin were selected as study subjects. The results showed that after one year of decomposition, the remaining mass of litter in the three restoration stages was 59.58% in the shrub stage, 61.79% in the shrub-to-tree stage, and 62.02% in the small tree stage. The litter decomposition rate decreased with vegetation succession. The activities of polyphenol oxidase, urease, and sucrase in the litter layer were lowest in December and highest in March (polyphenol oxidase) or June (urease and sucrase). Cellulase activity showed consistent trends across stages, peaking in June; it was lowest in March in the shrub stage and in September in the other two stages. Across all stages and periods, enzyme activities ranked as: sucrase > urease > cellulase > polyphenol oxidase. The effects of litter layer enzymes on decomposition rate varied among restoration stages. Correlation analysis indicated that sucrase activity was significantly positively correlated with decomposition rate in the shrub stage ($P < 0.05$), while urease activity showed a significant positive correlation in the shrub-to-tree stage ($P < 0.05$); no significant correlations were found in the small tree stage. Path analysis revealed that sucrase, urease, and polyphenol oxidase were important factors affecting litter decomposition in the shrub stage, whereas urease, cellulase, and polyphenol oxidase were key factors in the shrub-to-tree and small tree stages.

Keywords: *Loropetalum chinense* communities, litter decomposition, litter layer, enzyme activity, karst hills of Guilin

Introduction

Litter is an important component of forest ecosystems (Yu et al., 2009), serving as a food source for aboveground and underground decomposers (Guo et al., 2017). Forest litter plays a crucial role in improving soil physical and chemical properties, reducing soil erosion, and enhancing forest productivity (Xiao et al., 2010; Yang and Su, 2011; Jin et al., 2015). Litter decomposition is a vital source of materials and energy in forest ecosystems (Yu et al., 2015) and represents a key ecological process for maintaining forest productivity, soil nutrient cycling, and organic matter formation (Deng et al., 2015). Litter decomposition is a relatively long process that occurs through physical, chemical, and microbial pathways. The rate of litter decomposition is directly related to the activity of decomposition enzymes in the litter (Sinsabaugh & Findlay, 1995). Enzyme activity determines the rate of decomposition of litter and soil organic matter, influencing community structure, dynamics, and the productivity and soil nutrient supply capacity of forest ecosystems (Yang and Wang, 2004), thereby affecting species replacement, community composition, and vegetation restoration processes (Zhang et al., 1999). Research on the relationship between litter decomposition and enzymes is well-established, including factors affecting enzyme activity during decomposition (Adamczyk et al., 2009), methods for measuring enzyme activity (Zhang et al., 2006; Baerlocher, 2010), and the interrelationship between enzymes and litter decomposition (Allison & Vitousek, 2004; Kang & Freeman, 2009). Despite numerous studies on forest litter decomposition and enzymes, research continues to deepen due to the complexity of influencing factors.

Karst environments represent typical fragile ecosystems, with rocky desertification being one form of soil degradation in karst regions (Xiong et al., 2012; Cao et al., 2004). In recent years, vegetation restoration and protection have become priorities for rocky desertification management. Numerous factors influence litter decomposition in karst hills, and increased enzyme activity facilitates the decomposition of organic matter and nutrient release, which is important for improving forest soil fertility and restoring degraded ecosystems in karst areas (Zhang et al., 2008). *Loropetalum chinense* is a widely distributed woody plant in karst hills of Guilin, often forming dominant communities. Different restoration stages of *L. chinense* communities have already formed (Ma et al., 2013). This study examines litter decomposition in *L. chinense* communities in karst hills of Guilin to explore the effects of litter layer enzymes on decomposition during community succession, providing theoretical support for understanding litter decomposition mechanisms and vegetation restoration in karst hills.

1.1 Study Area Overview

The study area is located at Xicun Village, Ertang Township, southern suburb of Guilin City, Guangxi Zhuang Autonomous Region (110°15 E, 25°12 N) in northeastern Guangxi. The region features typical karst landforms at an altitude of 150–280 m. The climate is mid-subtropical humid monsoon, with long summers and short winters. The mean annual temperature is 18.9 °C, frost-free period is 300 days, mean annual precipitation is 1949.5 mm, and mean annual evaporation is 1490–1905 mm.

1.2.1 Experimental Design

This study used *L. chinense* communities as research subjects. Sample plot characteristics are shown in Table 1 . In early April 2014, three 400 m^2 (20 m × 20 m) plots were randomly established in fixed sample plots at the shrub stage, shrub-to-tree stage, and small tree stage of *L. chinense* communities. Four nylon mesh decomposition bags (50 cm × 50 cm, 1 mm mesh size) were placed in each plot at 50 cm above ground. From June to August 2014, freshly fallen, undecomposed leaf, branch, fruit, and bark litter were collected from the three restoration stages. In each plot, 20 g of litter was weighed according to the proportion of each component and placed in decomposition bags. In early September 2014, the litterbags were placed back in the original plots on the forest floor after removing surface litter, simulating natural decomposition conditions. A total of 108 bags were deployed across the three stages. Starting from placement, litterbags were retrieved every three months, with nine bags randomly collected from each stage for enzyme activity measurement. Retrieved litter was cleaned of surface soil and invading roots, oven-dried at 80 °C to constant weight, weighed, and used to calculate remaining mass and decomposition rate.

Enzyme activity measurement methods: Cellulase was measured by nitrosalicylic acid colorimetry, sucrase by 3,5-dinitrosalicylic acid colorimetry, urease by phenol-sodium hypochlorite colorimetry, and polyphenol oxidase by pyrogallol colorimetry.

1.2.2 Data Processing

Data were analyzed using SPSS 21.0 for variance analysis, correlation analysis, and path analysis. SigmaPlot 14.0 was used for graphing.

Table 1 Basic conditions of sampling sites of *L. chinense* communities

Restoration Stage	Slope Aspect	Slope Gradient (°)	Altitude (m)	Rock Bare Rate (%)	Average Diameter (cm)	Community Height (m)	Main Dominant Species
Shrub stage	SE, E	15–20	150–200	30–40	0.75a	—	*Loropetalum chinense*, *Bauhinia championii*, *Alchornea trewioides*, *Microstegium fasciculatum*
Shrub-to-tree stage	SE, E	20–25	200–250	30–35	3.91b	—	*Loropetalum chinense*, *Croton xiaopadon*, *Decaspermum esquirolii*, *Carex ischnostachya*, *Teucrium pernyi*
Small tree stage	SE, E	15–20	220–280	25–30	4.48b	—	*Loropetalum chinense*, *Croton xiaopadon*, *Bauhinia championii*, *Carex ischnostachya*

Note: a. Ground diameter, b. Diameter at breast height.

2.1 Litter Decomposition Dynamics

As shown in Figure 1 [Figure 1: see original paper], after one year of decomposition, litter remaining mass was 59.58% in the shrub stage, 61.79% in the shrub-to-tree stage, and 62.02% in the small tree stage. Litter decomposition rate decreased with succession. Decomposition rates peaked between March and June in the shrub and shrub-to-tree stages, and between June and September in the small tree stage. All three stages showed relatively slow decomposition between December and March.

Note: Litter decomposition times of 90 d, 180 d, 270 d, and 360 d correspond to December 2014, March 2015, June 2015, and September 2015, respectively.

Fig. 1 Litter decomposition dynamics of *L. chinense* community.

2.2 Litter Layer Enzyme Activity Dynamics

Litter layer enzyme activities showed distinct seasonal dynamics across the three restoration stages (Figure 2 [Figure 2: see original paper]). Polyphenol oxidase activity was lowest in December and highest in March across all stages (Figure a). Urease and sucrase activities were lowest in December and highest in June (Figure b, c). Cellulase activity patterns were generally consistent, peaking in June; the shrub stage showed lowest activity in March, while the shrub-to-tree and small tree stages had lowest activity in September (Figure d).

Annual mean enzyme activities differed significantly among stages (Figure 2). Mean annual polyphenol oxidase activity differed significantly among stages ($P < 0.05$), with March values being highest and significantly greater than other months ($P < 0.05$). In March, polyphenol oxidase activity was significantly higher in the shrub stage than in the other two stages ($P < 0.05$), which did not differ significantly. In September, activity was significantly higher in the small tree stage than in the shrub stage, which was significantly higher than in the shrub-to-tree stage ($P < 0.05$).

Mean annual urease activity differed significantly between the shrub-to-tree and small tree stages ($P < 0.05$), but neither differed from the shrub stage. Urease activity did not vary seasonally in the shrub stage, but in the other two stages, June activity was significantly higher than in March, September, and December ($P < 0.05$). December and March urease activities were significantly higher in the shrub stage than in the other stages ($P < 0.05$), while June and September activities did not differ among stages.

Mean annual sucrase activity differed significantly among stages ($P < 0.05$). In the shrub and small tree stages, June activity was significantly higher than in March, September, and December, while in the shrub-to-tree stage, seasonal differences were all significant (P < 0.05). Stage differences were significant in December and March but not in June and September.

Mean annual cellulase activity differed significantly among stages (P < 0.05). In the shrub and shrub-to-tree stages, June activity was significantly higher than in December, September, and March (P < 0.05), while in the small tree stage, all seasonal differences were significant (P < 0.05). Stage differences in December were significant (P < 0.05).

Note: 90 d, 180 d, 270 d, 360 d correspond to December 2014, March 2015, June 2015, September 2015, respectively.

Fig. 2 [Figure 2: see original paper] Seasonal dynamics of litter layer enzyme activities in *L. chinense* community.

2.3.1 Correlation Analysis

Simple correlation analysis between litter layer enzymes and decomposition rate showed that sucrase activity was significantly positively correlated with decomposition rate in the shrub stage, and urease activity was significantly positively correlated in the shrub-to-tree stage. No significant correlations were found in the small tree stage (Table 2).

Table 2 Relationships between litter enzymes activities and decomposition rate in *L. chinense* community

Stage	Urease	Sucrase	Cellulase	Polyphenol Oxidase	Decomposition Rate
Shrub stage	0.609*	0.804**	0.702*	0.918**	0.666*
Shrub-to-tree stage	0.661*	-0.773**	-0.658*	—	—
Small tree stage	—	—	—	—	—

Note: **P < 0.01, *P < 0.05. A1, A2, A3, A4, Y represent urease, sucrase, cellulase, polyphenol oxidase, and decomposition rate at each stage, respectively.

2.3.2 Path Analysis

Path analysis further revealed the relationships between enzymes and decomposition rate (Table 3). In the shrub stage, sucrase had a highly significant direct positive effect on decomposition rate, but exerted large indirect negative effects through urease and polyphenol oxidase. Urease and polyphenol oxidase had significant direct negative effects, but produced large indirect positive effects through sucrase. In the shrub-to-tree stage, urease had a highly significant direct positive effect, with small indirect negative and positive effects through cellulase and polyphenol oxidase, respectively. Cellulase and polyphenol oxidase had significant direct negative effects. In the small tree stage, urease had a significant direct positive effect, cellulase had a significant direct negative effect, and polyphenol oxidase had no significant effect.

Table 3 Path analysis between litter layer enzymes and decomposition rate in *L. chinense* community

Influence Factor	Shrub Stage	Shrub-to-tree Stage	Small Tree Stage
	Direct	Indirect	Total
Urease	-0.532*	1.198**	0.666*
Sucrase	1.034*	-0.513*	0.521*
Cellulase	-0.495*	-0.658*	-1.153*
Polyphenol Oxidase	-1.153*	1.855**	0.702*

Note: **P < 0.01, *P < 0.05. A1, A2, A3, A4, Y represent urease, sucrase, cellulase, polyphenol oxidase, and decomposition rate at each stage, respectively.

Discussion

Litter decomposition rate is closely related to local climate conditions, with temperature and precipitation being dominant factors (Aerts, 1997). This study found that decomposition rates peaked in June in the shrub and shrub-to-tree stages and in September in the small tree stage, likely because June–September is the summer-autumn period with high temperatures and abundant rainfall, enhancing microbial activity and leaching (Jin et al., 2015). All stages showed slow decomposition from December to March during the cool, dry winter-spring season when microbial activity and leaching were reduced (Jin et al., 2015). The decreasing decomposition rate with succession may be attributed to two factors. First, the small tree stage has more species with leathery leaves (Ma et al., 2012), which have well-developed cuticles and high concentrations of recalcitrant lignin, cellulose, and tannins that hinder decomposition (Qin et al., 2017). Second, it may relate to nutrient use efficiency of vegetation in karst areas (Zeng et al., 2016).

Beyond environmental factors, litter decomposition is closely linked to enzyme activity. Microbial degradation of litter essentially involves complex chemical reactions between litter and enzymes. Complete decomposition is accomplished through the combined action of various enzymes (Yan et al., 2010). Ji et al. (2013) found that enzyme activities in subtropical leaf litter showed clear seasonal dynamics, being higher in summer and lower in winter, with cellulase, sucrase, and urease activities being higher in early decomposition stages and declining over time. In this study, polyphenol oxidase activity peaked in March, consistent with Ge et al. (2014), possibly because root growth during the growing season promotes enzyme synthesis (Deng et al., 2009) and rapid microbial multiplication. Urease, sucrase, and cellulase activities peaked in June, likely due to temperatures favoring microbial growth (Deng et al., 2009). The predominance of hydrolases (sucrase, urease) suggests that specific microbial groups have high utilization of C, N, and organic matter during decomposition (Yan et al., 2010; Ge et al., 2014; Wang et al., 2006).

Different enzymes affect decomposition rates differently. Karst hills have unique habitat conditions, and litter decomposition rates for the same species may be generally higher in karst than non-karst areas, as the karst environment favors decomposition and nutrient cycling (Wang et al., 2013). Zhang et al. (2007) reported that broadleaf species had higher enzyme activities in the first litter layer, while coniferous species had higher activities in the second layer. Ji et al. found that urease and cellulase strongly influenced decomposition of three subtropical species, while polyphenol oxidase and peroxidase played clear degradation roles (Rietl & Jackson, 2012). Our path analysis identified sucrase as a key factor in the shrub stage, while urease and cellulase were important in the shrub-to-tree and small tree stages. Hydrolases facilitate decomposition of soluble substances, while polyphenol oxidase participates in decomposing complex organic compounds as decomposition progresses (Ge et al., 2014). Enzyme activities and types change with litter composition and quantity. Cellulases and -glucosidases appear mainly in early decomposition, while polyphenol oxidase and peroxidase increase later (Ge et al., 2013). Thus, key enzymes differ among restoration stages, possibly due to varying litter composition. However, Suseela et al. (2014) noted that litter mass loss and enzyme activity may not accurately reflect the complexity of specific compound degradation. The relationship between decomposition rate and enzyme activity may be determined by litter structural properties (Dilly & Munch, 1996). Given the diverse factors influencing enzymes and the unique karst environment, further research is needed to understand the relationship between decomposition rate and enzyme activity in *L. chinense* communities.

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