

Decomposition Characteristics of Litterfall from Ten Typical Plant Species in Forested Wetlands of South Carolina, USA: Postprint

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Abstract

Leaf litter decomposition is a crucial ecological process controlling material cycling in forest wetlands and represents an important component of global C, N and other elemental cycles. Using leaf litter from 10 typical plant species in South Carolina, USA as the research subject, a 2-year decomposition experiment was conducted to determine biomass residual rates, decomposition rate constant k , and C, N residual percentages at various decomposition stages, and to explore the influence of initial leaf litter chemical properties on the decomposition rate constant k . The results showed: (1) The biomass of the ten types of leaf litter degraded to 14.5%-66.2% of the initial amount within two years, with interspecific differences exceeding fourfold; the decomposition rate constant k ranged between 0.26-1.64 a^{-1} , with coniferous litter decomposition rates < broadleaf litter decomposition rates; (2) The decomposition rate constant k was extremely significantly positively correlated with initial leaf litter acid-soluble fraction (AS) ($P < 0.001$), and significantly negatively correlated with initial C content, acid-insoluble fraction (AIF), and AIF/N ratio ($P < 0.05$); (3) The C residual percentage in leaf litter continuously decreased to 10.2%-66.1%, whereas the N residual percentage exhibited different patterns of change depending on species and decomposition stage. The results indicate that differences in initial C fractions of leaf litter are the primary cause of the large interspecific variation in decomposition rates in forest wetlands, and that interspecific differences should be fully considered when assessing C and N cycles in forest wetlands.

Full Text

Preamble

Leaf Litter Decomposition of Ten Plant Species in a Forested Wetland in South Carolina, USA

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Abstract

Leaf litter decomposition is a critical ecological process controlling carbon (C) and nitrogen (N) cycling in forested wetlands. However, most decomposition studies have focused on non-flooding forests, leaving the C and N dynamics during litter decomposition in mixed forested wetlands poorly understood. This study conducted a two-year litter decomposition experiment in a representative freshwater forested wetland in Georgetown, South Carolina, USA, examining leaf litters from ten local plant species: *Asimina triloba*, *Nyssa aquatica*, *Acer rubrum*, *Fraxinus pennsylvanica*, *Liquidambar styraciflua*, *Celtis occidentalis*, *Taxodium distichum*, *Ulmus americana*, *Pinus palustris*, and *Platanus occidentalis*. We measured the C and N contents of initial and decomposed litter samples and analyzed the initial chemical composition, including extractives, acid-soluble, acid-insoluble, and ash fractions. The percentages of remaining biomass, C, and N, as well as the decomposition rate constant (k), were calculated and correlated with initial mass, C and N contents, and chemical composition.

The results showed that after two years of decomposition, the percentage of remaining biomass varied substantially across species, ranging from 14.5% to 66.2% of the initial biomass (up to a fourfold difference). Meanwhile, the decomposition rate constant k ranged from 0.26 a⁻¹ (*P. palustris*) to 1.64 a⁻¹ (*A. triloba*), with broadleaf litter decomposing faster than coniferous litter. The decomposition rate constant was positively correlated with the initial acid-soluble fraction (AS) of the litter ($p < 0.001$) and negatively correlated with initial C content, acid-insoluble fraction (AIF), and AIF/N ratio ($p < 0.05$), indicating that initial litter chemistry was a key factor determining decomposition rate. Similarly, the remaining C content gradually decreased to 10.2%-66.1% of the initial C content, with the greatest loss in *A. triloba* and the lowest in *P. palus-*

tris. In contrast, N content was either immobilized or mineralized during decomposition depending on plant species and decomposition stage. For example, the N content of *N. aquatica*, *P. occidentalis*, and *P. palustris* was immobilized during early decomposition and released at later stages. However, N was consistently immobilized in the litter of *U. americana*, *C. occidentalis*, *A. rubrum*, and *A. triloba*, and consistently released from the litter of *F. pennsylvanica*, *L. styraciflua*, and *T. distichum*.

Thus, this study demonstrates that, similar to litter decomposition in non-flooding forests, initial litter chemistry could explain the large variation observed in decomposition rates of different plant species at individual sites. In addition, there are also large differences in the C and N dynamics during litter decomposition among plant species. Accordingly, our study highlights the importance of fully considering inter-species differences when evaluating the C and N cycling of forested wetlands.

Keywords: forested wetland; leaf litter; decomposition rate constant; initial carbon fractions; C and N dynamics

1. Introduction

Forested wetlands are critical transition zones between terrestrial and aquatic ecosystems, characterized by high productivity and active biogeochemical cycling, with likely different carbon (C) and nitrogen (N) turnover rates compared to non-flooding upland forests. Leaf litter decomposition is a vital ecological process that controls C and N cycling in forested wetlands, determining nutrient availability for plants and soil organic matter formation. The decomposition process returns nutrients from leaf litter to the soil, influencing the nutrient cycling function of wetland ecosystems and representing an important component of global C and N cycles.

Litter decomposition in both wetland and non-wetland forest ecosystems is determined by three factors: chemical factors (litter chemical composition), physical factors (climate and environmental conditions), and biological factors (microorganisms and invertebrates involved in decomposition). Initial litter chemical composition is a key factor controlling decomposition rate and patterns, with initial chemical properties such as lignin content, initial element concentrations (especially N), C/N ratio, N/P ratio, and carbon fractions including non-polar extractives, water-soluble components, and acid-soluble components showing significant correlations with decomposition rate.

Unlike non-forested wetlands, hydrological conditions are the most important environmental factor in wetland ecosystems, controlling organic matter production and transformation processes. Seasonal wetting promotes dissolution of chemicals and release of elements from leaf litter, providing moisture required for heterotrophic microbial decomposition, resulting in faster litter decomposition

rates in forested wetlands compared to non-forested wetlands under equivalent conditions. While most litter decomposition experiments have been conducted in non-forested wetlands with relatively thorough understanding of decomposition characteristics and mechanisms in terrestrial ecosystems, studies on the mechanisms and characteristics of litter decomposition in forested wetlands remain limited, making research on forested wetland litter decomposition processes important for understanding biogeochemical cycling in these ecosystems.

Hobcaw Barony Natural Reserve, located east of Georgetown County, South Carolina, experiences minimal human disturbance and has served as a wading bird colony since the 1980s. It is an important habitat for wild insects and aquatic organisms, hosting the largest bird colony in South Carolina and playing a significant role in biodiversity conservation. The reserve is also a typical area for studying element cycling in freshwater forested swamps, tidal forested swamps, and coastal salt marshes. This study selected the freshwater forested wetland in Hobcaw Barony as the research site to analyze the decomposition characteristics and interspecific differences of plant leaf litter.

2. Study Area

The litter decomposition experiment was conducted in a seasonal freshwater wetland north of Hobcaw Barony (70.8 km²) near Winyah Bay, Georgetown, South Carolina, USA (79°12 33.37 W, 33°22 2.88 N). The site features a typical subtropical climate with an annual precipitation of 1,312 mm. January temperatures reach a minimum of -2.5°C, while July temperatures peak in the typical range for the region. The site is a typical seasonal coniferous-broadleaf mixed forest wetland in the southeastern United States, co-managed by Clemson University and the Wallace F. Pate Environmental Research and Education Fund.

The lowland plant communities in the study area are dominated by *Taxodium* spp. (bald cypress) and *Nyssa* spp. (water tupelo), including *Taxodium distichum* (bald cypress) and *Nyssa aquatica* (water tupelo). Surrounding transition zones and uplands include *Pinus* spp. (pines), *Quercus* spp. (oaks), *Acer* spp. (maples), and *Ulmus* spp. (elms), with *Acer rubrum* (red maple) and *Ulmus americana* (American elm) being common. Water levels fluctuate seasonally, with high water levels in late winter and low levels from summer to late autumn. Typically, the water level is above the soil surface, but during severe droughts it can drop more than 50 cm below the surface.

3. Experimental Materials

This study collected leaf litter from ten typical plant species in the research area: *Nyssa aquatica* (water tupelo), *Taxodium distichum* (bald cypress), *Fraxinus pennsylvanica* (green ash), *Acer rubrum* (red maple), *Liquidambar styraciflua*

(sweetgum), *Celtis occidentalis* (hackberry), *Pinus palustris* (longleaf pine), *Platanus occidentalis* (American sycamore), *Ulmus americana* (American elm), and *Asimina triloba* (pawpaw). The litter of *Pinus palustris* and *Nyssa aquatica* was collected within the study site, while litter of other species was collected from similar habitats in the Congaree National Forest wetland park approximately 150 km northwest of the site due to difficulty collecting sufficient quantities in the native site. All leaf litter was collected using suspended collection nets and transferred to the laboratory for processing within 15 months. Preliminary experiments showed no significant differences in chemical properties of the same species litter between sites.

4. Experimental Design and Sample Processing

After collection and species separation, the leaf litter was dried at 70°C for 72 hours. Dried leaf samples were placed in 20 cm × 15 cm nylon litterbags with 0.15 mm mesh, with approximately 3.00 g of litter per bag. On March 15, 2011, the litterbags were placed on the litter surface in Hobcaw Barony and secured with wire. Samples were collected at 30 days, 61 days, 194 days, 370 days, and 735 days, yielding 30 samples per species.

Collected samples were cleaned of surface sediment with low-temperature ultrapure water (4°C), dried at 72°C for 72 hours, weighed, and recorded. Dried samples were ground with a plant grinder (Retsch ZM 200) and passed through a sieve. Carbon, hydrogen, and nitrogen contents at different decomposition stages were measured with an elemental analyzer (Elementar vario EL cube). Ash content percentage was determined by placing samples in a muffle furnace (Nabertherm LE 6/11/B150) at 575°C.

Chemical fractionation followed the method of Ryan et al. [31], modified by using qualitative filter paper. The procedure involved: (1) extracting 20.0 mg of ground, sieved, dried sample with chloroform-methanol at room temperature; (2) treating the extracted and dried sample with sulfuric acid at room temperature; (3) rinsing the residue with ultrapure water to pH = 7, drying at 105°C for 24 hours, cooling, and weighing; and (4) placing the remaining residue in a muffle furnace at 550°C, cooling in a desiccator, and weighing the ash. Fractions were calculated as follows [31]: Extractives, Acid-Soluble fraction (AS), and Acid-Insoluble fraction (AIF).

5. Data Analysis

The decomposition rate constant (k) was calculated using Olson's exponential decay model [32]: $W/W_0 = e^{-kt}$, where W_0 is the initial litter mass, W is the mass at time t , and t is the decomposition time. The percentage of remaining C (or N) was calculated as: (C (or N) mass at a decomposition stage

/ initial C (or N) mass) $\times 100\%$. We used ANOVA and the S-N-K method for multiple comparisons of litter biomass remaining percentages and simple linear regression and correlation analysis to explore relationships between decomposition rate constants and initial litter chemical properties. Statistical analyses were performed using SigmaPlot.

6. Results

6.1 Litter Biomass Remaining

All ten species showed consistent patterns of biomass remaining over time, with biomass decreasing as decomposition progressed. After two years, the remaining biomass varied significantly among species, ranging from 14.5% in *Asimina triloba* to 66.2% in *Pinus palustris*. The order of remaining biomass from lowest to highest was: *Asimina triloba* (14.5%) < *Liquidambar styraciflua* (17.3%) < *Platanus occidentalis* (29.0%) < *Acer rubrum* (37.6%) < *Nyssa aquatica* (55.7%) < *Fraxinus pennsylvanica* (62.5%) < *Taxodium distichum* (62.4%) < *Ulmus americana* (66.2%) < *Pinus palustris* (66.2%) and *Celtis occidentalis* (62.5%).

[Figure 1: see original paper] Dynamic changes in percent remaining biomass during decomposition of ten foliar litters

6.2 Litter Decomposition Rate

Using Olson's exponential decay model [32], we simulated decomposition rates for the ten species. The decomposition rate constant k ranged from 0.26 to 1.64 a^{-1} , with larger k values indicating faster decomposition. The k values differed substantially among species, with broadleaf litter decomposing faster than coniferous litter. *Asimina triloba* showed the highest k value (1.64 a^{-1}), while *Pinus palustris* had the lowest (0.26 a^{-1}). The time required to decompose 50% and 95% of initial biomass (T_{50} and T_{95}) varied accordingly.

Comparison of percent remaining biomass, decomposition rate constants, T_{50} , and T_{95} for ten foliar litters

6.3 Initial Litter Chemical Composition

Initial chemical composition varied significantly among the ten species. Extractives ranged from 0.1% to 14.8%, acid-soluble components (AS) from 22.2% to 51.6%, and acid-insoluble fractions (AIF) from 48.0% to 73.1%. Initial C content ranged from 45.3% to 52.8%, N content from 0.6% to 2.1%, C/N ratio from 22.5 to 83.4, and AIF/N ratio from 28.6 to 104.2. The decomposition rate constant k was positively correlated with initial AS ($p < 0.001$) and negatively correlated with initial C content, AIF, and AIF/N ratio ($p < 0.05$ or $p < 0.01$). No significant correlations were found with extractives or ash content.

[Figure 2: see original paper] Relationship between initial ash, carbon fractions, and decomposition rate constant using simple linear regression

[Figure 3: see original paper] Relationship between initial C, N indicators, and decomposition rate constant using simple linear regression

6.4 Carbon and Nitrogen Dynamics

The percentage of remaining C decreased over time for all species, ranging from 10.2% to 66.1% after two years. The pattern of N remaining percentage varied among species and decomposition stages. Some species showed N immobilization followed by release, while others showed consistent immobilization or consistent release throughout the decomposition period. The C/N ratio dynamics also varied, with some species showing continuous decreases while others exhibited more complex patterns.

[Figure 4: see original paper] Percent remaining C, N, and C/N ratio dynamics for ten litter species at different decomposition stages

7. Discussion

7.1 Litter Decomposition Rate Patterns and Mechanisms

Previous studies have shown that coniferous needles decompose slower than broadleaf litter, and evergreen leaves decompose slower than deciduous leaves. Our finding that the evergreen conifer *Pinus palustris* had a decomposition rate constant ($k = 0.26 \text{ a}^{-1}$) lower than all species except *Platanus occidentalis* confirms that this pattern holds in forested wetlands. This difference is related to litter physical and chemical properties: broadleaf species have higher soluble component contents and lower leaf tensile strength, while coniferous needles have higher cuticle and wax contents, larger leaf area, and slower decomposition rates that depend primarily on microbial activity.

Initial chemical composition is a key factor controlling litter decomposition rate. We found that decomposition rate constant k was negatively correlated with initial C content, consistent with studies in terrestrial ecosystems. The negative correlation between k and AIF and AIF/N ratios aligns with findings from subtropical evergreen forests and subalpine meadows, further demonstrating that high AIF content inhibits litter decomposition. The positive correlation between k and AS fraction indicates that acid-soluble components promote decomposition.

While some studies suggest that initial C/N ratio significantly affects decomposition rate, we found no correlation between k and initial C/N ratio in this forested wetland. This may be related to the high productivity of forested wetlands, where high N availability in surface water and soil satisfies microbial requirements, making initial litter N content less influential on decomposition

rate. The effect of initial carbon fractions on decomposition rate depends on fraction type: no correlation with extractives, negative correlation with AIF, and positive correlation with AS. This is related to the hydrological characteristics of forested wetlands and the stage-based nature of litter decomposition. Extractives dissolve rapidly in the early decomposition stage and have little effect on the two-year decomposition rate, while AIF (primarily lignin) exerts increasing inhibition during later decomposition stages.

7.2 Carbon and Nitrogen Dynamics and Mechanisms

Previous research indicates that C release patterns during decomposition are not species-specific, though the magnitude is related to initial chemical properties. In our study, C remaining consistently decreased across all ten species because easily decomposable non-structural substances such as sugars and starches are degraded first, with C gradually released as litter dry weight decreases. Initial litter chemistry, particularly N content, influences N dynamics during decomposition. High N content litters may release N, while low N content litters immobilize N. Our results further demonstrate that for forested wetlands, the threshold initial N content determining N dynamics during decomposition is approximately 1.4%. Species with initial N content below this threshold (e.g., *Pinus palustris* and *Acer rubrum*) consistently immobilized N, while those above it showed varied patterns.

7.3 Potential Effects of Plant Community Succession on Element Cycling

One purpose of examining interspecific differences in decomposition rates is to assess whether plant community succession accelerates or slows nutrient release rates. Over the past decade in our study area, the density and basal area of *Acer rubrum* and *Liquidambar styraciflua* have decreased significantly, while those of *Taxodium distichum* have increased. Our finding that *Taxodium* litter decomposes faster than *Acer* suggests that community succession in this area may reduce *Acer* litter input while slightly slowing overall litter decomposition. However, because *Liquidambar* litter immobilizes more N than *Taxodium*, the net effect on ecosystem N cycling is complex. Thus, plant community succession in this forested wetland may not necessarily alter overall litter-mediated C and N cycling rates, as changes in species composition involve trade-offs between quantity and quality of litter input.

8. Conclusion

This study revealed that litter decomposition rates among different species in the study site varied up to fourfold over two years, with differences related to initial litter chemistry. Higher initial acid-soluble fractions promoted rapid decomposition, while higher acid-insoluble fractions and AIF/N ratios slowed

decomposition. Carbon remaining percentages decreased gradually over time across all species, while nitrogen remaining patterns varied depending on initial N content. The large interspecific variation in decomposition rates and N dynamics suggests that evaluating C and N cycling in forested wetlands must fully consider species differences. Initial carbon fraction differences are the primary cause of large interspecific variation in decomposition rates, and these differences may influence element turnover during plant community succession.

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