

# The Role of Quantitative Traits of Leaf Litter on Decomposition and Nutrient Cycling of the Forest Ecosystems

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## Abstract

Decomposition of plant material is an important component in the study of forest ecosystem because of its critical role in nutrient cycling. Different tree species has different nutrient release patterns, which are related to leaf litter quantitative traits and seasonal environmental factors. The quantitative traits of leaf litter are important predictors of decomposition and decomposition rates increase with greater nutrient availability in the forest ecosystems. At the ecosystem level, litter quantitative traits are most often related to the physical and chemical characteristics of the litter, for example, leaf toughness and leaf mass per unit area, and lignin content tannin and total phenolics. Thus, the analysis of litter quantitative traits and decomposition are highly important for the understanding of nutrient cycling in forest ecosystems. By studying the role of litter quantitative traits on decomposition and nutrient cycling in forest ecosystems will provide a valuable insight to how quantitative traits influence ecosystem nutrient dynamics. Such knowledge will contribute to future forest management and conservation practices.

**Key Words:** litter decomposition, quantitative traits of leaf litter, nutrient cycling, forest ecosystems.

## Introduction

Litter production and litter decomposition are key processes of nutrients cycling in forest ecosystems. Litter decomposition is the main way of transfer of organic matter and mineral elements from vegetation to the soil surface (Vitousek and Sanford 1986; Moraes et al. 1999; Berg and McLaugherty 2008; Oladoye et al. 2008). Plant production depends on the recycling of nutrients within the system; recycling depends on the decomposition of organic matter and release of the nutrients it contains (Temel 2003).

Although ground vegetation in sparse open stands can make a substantial contribution to total litterfall in the stand, litter from the trees is generally the largest natural source for the inflow of organic material and nutrients to the forest floor (Berg et al. 1999). Different species have different nutrient release patterns, which are related to litter quantitative traits (quality) and seasonal environmental factors (Khiewtam and Ramakrishnan 1993; Wang et al. 2008). The humus profile is usually thinner in deciduous and sclerophyllous forests and than in coniferous forests (Van Wesemael and Veer 1992) suggested that the lower

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rate of decomposition of the leaf litter in the Japanese cedar (*Cryptomeria japonica* D. Don) plantation and red pine (*Pinus resinosa* Ait.) forest, compared to that of the oak forest may be due to their chemical properties (Kavvadias et al. 2001).

Litter decomposition rates are influenced by at least three general factors: the composition and activity of the decomposer community, the quantitative traits of the litter and the physicochemical environment (Anderson and Swift 1983; Heal et al. 1997; Kavvadias et al. 2001). Species' type had a large influence on the decomposition rate ( $k$ ), most probably through its influence on leaf quality and morphology (Salinas et al. 2011).

Litter quantitative traits (quality) become a better determinant of decomposition rates than climate (Meentemeyer 1978; Aerts 1997; Tatenno et al. 2007). For instance, decomposition rates of Scots pine needles vary across boreal forests more according to substrate quality rather than to climatic conditions (Berg and McClaugherty 2008). Similarly, a prevailing effect of litter quality over climate has been reported for wet tropical forests (Tanner 1981; Weider et al. 2009). Litter decomposability is negatively correlated with the level of quantitative defense of leaves (Kurokawa and Nakashizuka 2008). Litter turnover rate is strongly controlled by tree species effect, and therefore, by litter quality in cool temperate and boreal forests (Wardle et al. 1997; Reich et al. 2005). Above ground and below ground ecosystem functioning in forests is closely linked with each other through litter quality or quantitative defensive traits of leaves (Wardle 2002).

At the ecosystem scale, litter quantitative traits are most often related to the physical and chemical characteristics of the litter, for example leaf toughness and LMA, and lignin content (Aber et al. 1990; Aerts 1997; Pérez-Harguindeguy et al. 2000; Freschet et al. 2011), tannin and total phenolics (Rahman and Motiur 2012). Chemical composition is one of the main factors controlling the decomposition rate of litter. This was postulated already by Tenney and Waksman (1929) and several studies have later stressed the importance of inorganic and organic components in controlling turnover rate of organic matter and release of nutrient elements (Melillo et al. 1982; Berg et al. 1993; Johansson 1994). Boring and Hendricks (1992) revealed that generally, litter with high

lignin and low Nitrogen (N) concentration has a slower decomposition rate and immobilizes more N than litter with low lignin and high N content. Information on levels of inorganic and organic components in tree litter is thus of great importance for studying the carbon dynamics in forest ecosystems. Decomposition of leaf litter is also an integral and significant part of biochemical nutrient cycling and food webs; this refers to both the physical and chemical breakdown of litter and the mineralization of nutrients (Boulton and Boon 1991; Baker et al. 2001). Decomposition of plant material is an important component in the study of forest ecosystem because of its critical role in nutrient cycling. Thus the analysis of litter quantitative traits and decomposition is highly important for the understanding of nutrient cycling in forest ecosystems. This paper will discuss the role of leaf litter quantitative traits on decomposition and nutrient cycling of forest ecosystems.

#### *Leaf litter quantitative traits*

Litter quality has been considered as an important factor controlling the decomposition rate (Singh et al. 1999; Sundarapandian and Swamy 1999; Ribeiro et al. 2002). Leaf litter quantitative traits can be described following major groups:

##### **Quantitative physical traits of leaf litter**

Quantitative physical traits of leaf litter may be divided into following categories

1. Leaf litter toughness
2. Leaf mass per unit area (LMA)

The toughness of plant litter, which may be related to anti-herbivore defense of living leaves, can also affect decomposition and nutrient release (Gallardo and Merino 1993; Cornelissen and Thompson 1997; Pérez-Harguindeguy et al. 2000). LMA also has the great effect on the decomposition rate of litter. Litter decomposition rates in general are negatively correlated with LMA (Lambers et al. 1998).

##### **Quantitative chemical traits of leaf litter**

Leaf litter quantitative chemical traits have been measured as lignin, tannins, phenols, carbohydrates (e.g. cellulose and hemicellulose) (Aber et al. 1990; Aerts 1997;

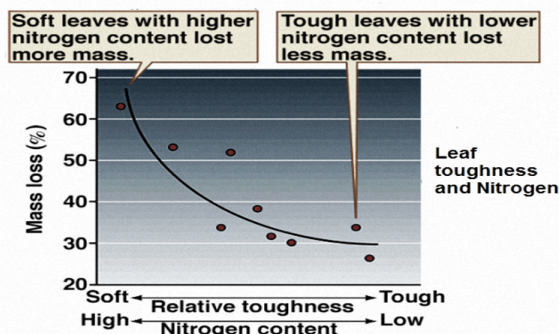
McClaugherty and Berg 2011; Rahman and Motiur 2012).

*Roles of quantitative traits on leaf litter decomposition*

**Role of quantitative physical traits on decomposition**

Leaf toughness is one of the good predictors for predicting the litter decomposition rate (Quinn et. al 2000; Pérez-Harguindeguy et al. 2000; Anderson 2008; Freschet et al. 2011). Leaf toughness may slow breakdown the rate of litter is reported by several related studies (Goncalves et al. 2006; Moretti et al. 2007). The negative association found between leaf toughness and decomposition rate suggest that the structural defenses of the living leaves, persisting in litter, could have been responsible for slow decomposition (Pérez-Harguindeguy et al. 2000). Gallardo and Merino (1993) found that the best predictor of mass loss is the ratio of leaf toughness to nitrogen content. The tougher leaves with lower concentrations of nitrogen decomposed at a lower rate (Fig. 1).

LMA also can influence the decomposition rate of litter. Low-LMA leaves with high nutrient contents decompose much faster, leading to increased carbon and nutrient cycling (Cornelissen et al. 1999; Poorter et al. 2009). Community-level LMA had a strong negative impact on the primary productivity and decomposition rate of the successional communities (Poorter et al. 2009). A study from China demonstrated that leaf area had little effect on decomposition (Huang et al. 2004).

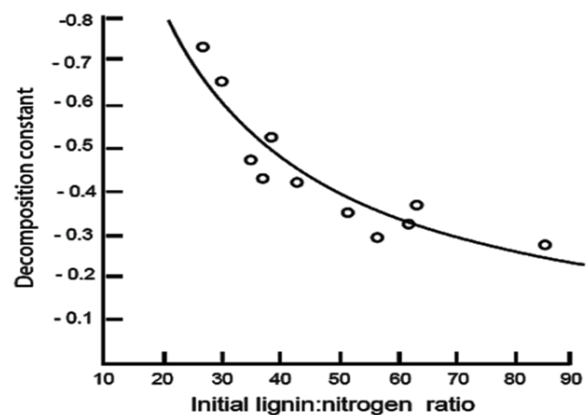


**Fig. 1.** Influence of leaf toughness and nitrogen content on decomposition (data from Gallardo and Merino 1993, adapted from Manuel and Molles 2009).

*Roles of quantitative chemical traits on leaf litter decomposition*

**Role of lignin on leaf litter decomposition**

Lignin concentration in leaves (or lignin to mineral ratios) has been widely used as an index of organic-matter quality. For instance, lignin concentrations alone, or lignin to N ratios in leaves could explain the rate of decomposition; negative correlations have been reported between lignin concentrations (or lignin to mineral ratios) and decomposition rates (Fig. 2) (Meentemeyer 1978; Melillo et al. 1982; Vitousek et al. 1994; Hobbie 1996; Kitayama et al. 2004). Lignins strengthen leaves significantly (Coley et al. 1985; Wright and Illius, 1995; Pérez-Harguindeguy et al. 2000) and litter with high lignin concentration is known to be resistant to decomposition (Meentemeyer 1978; Gallardo and Merino 1993; Wardle et al. 1998). On the other hand, hemicellulose and lignin concentrations were reported to negatively correlated with decomposition (Vivanco and Austin 2008). The initial lignin content of leaf litter influenced the rate of decomposition. The species exhibiting higher initial lignin contents showed lower rates of decomposition of leaf litter. For example, the decomposition of *Quercus dealbata* litter is slower than that of *Quercus fenestrata* (Laishram and Yadava 1988). However, the concentrations of the lignin fraction increased as decomposition proceeded, reaching relatively steady levels in the range of 45-51% (Berg 2000; Sarjubala and Yadava 2007). These increases showed partially linear relationships with accumu-

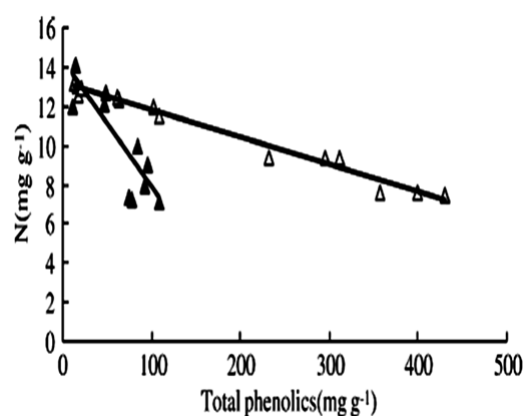


**Fig. 2.** Relationship between the decomposition constant and the lignin: nitrogen ratio of litter (adapted from Melillo et al. 1982).

lated mass loss (Berg et al. 1984). Raich et al. (2007) found a highly significant, positive correlation between lignin contents and decay rates. This finding is supported by measurements of soil organic matter contents in the same sites, which correlated negatively with foliar lignin contents. It would appear that the decomposer organisms in their study sites did not just tolerate lignin, they preferred it. Perhaps organisms can trump chemistry in controlling litter decomposition in tropical rain forests (Anderson and Swift 1983; Lavelle et al. 1993). Regardless, this result contradicts models that predict that lignin depresses litter turnover rates (Meentemeyer 1978) and highlights the potential problem that exists when individual factors are presumed to control the rate of a process that is under multivariate control (Raich et al. 2007).

#### Role of total phenolics on leaf litter decomposition

Phenolics may be an important determinant of plant C quality and significantly affect decomposition and soil nutrient availability (Horner et al. 1988; Schimel et al. 1996; Kraus et al. 2003; Meier and Bowman 2008). Phenolics may prevent leaf damage resulting from exposure to excessive light (Gould and Lee 2002). The bulk of phenolics remain present during leaf senescence and after death, these compounds may also affect microbial decomposers (Harrison 1971) and therefore delay microbial decomposition of plant litter (Salusso 2000). Canhoto and Graça (1996) observed a strong negative correlation between the phenol content of different native litter types and litter decomposition rates in a stream, whereas Canhoto and Graça (1999) showed that phenolics from *Eucalyptus* leaves decrease feeding by detritivores. Thus, roles of phenolics on detritivores may be one reason for the low decomposability of *Eucalyptus* litter. The initial concentration of total phenolics in litter is positively correlated with dry organic carbon loss (Madritch and Hunter 2004). High amount of phenolics compounds in plants tissue decrease N concentration, which impedes the litter decomposition (Xuefeng et al. 2007). Barta et al. (2010) confirmed that a low amount of phenolics and low phenolics/N ratio in plant litter is closely related to higher differences in microbial respiration rates and mineral N release during the four months of litter decomposition in spruce forest. Lin et al. (2006) observed a negative correlation between total phenolics and N contents



**Fig. 3.** Relationship between total phenolics and N contents during leaf decomposition of *Bruguiera gymnorrhiza* (Bg) and *Kandelia candel* (Kc). Symbols are: black triangle for Bg leaf; white triangle for Kc leaf (Adapted from Lin et al. 2006).

for *Kandelia candel* and *Bruguiera gymnorrhiza* leaf litter at various stages of decomposition (Fig. 3). Phenols may influence rates of decomposition as they bind to N in the leaves forming compounds resistant to decomposition (Palm and Sanchez 1991). Gorbacheva and Kikuch (2006) found that dynamics of easily oxidized phenolics may influence the litter decomposition rate in the monitored sub-arctic field.

#### Role of tannin on leaf litter decomposition

Nitrogen and lignin concentration or C: N and lignin: N ratios are often used to predict rates of litter decomposition. However, a number of studies have shown that tannin and/or polyphenol content is a better predictor of decomposition, net N mineralization and N immobilization (Palm and Sanchez 1991; Gallardo and Merino 1992; Driebe and Whitham 2000; Kraus et al. 2003). Coq et al. (2010) mentioned that litter decomposition in tropical rainforest correlated well with condensed tannin concentration. They concluded that leaf litter tannins play a key role in decomposition and nutrient cycling in the tropical rainforest. Leaves with high initial contents of condensed tannins, seem to decompose slowly in both terrestrial (Valachovic et al. 2004) and aquatic ecosystems (Wantzen et al. 2002). Condensed tannin may play an important role in aquatic leaf litter decomposition, as they may deter invertebrate shredders (Wantzen et al. 2002). Condensed tannin deters herbivore feeding by acting as toxins and not as digestion

inhibitors by protein precipitation. Other researchers have obtained data that suggest the toxic nature of tannins (Robbins et al. 1987; Clausen et al. 1990). Alongi (1987) noticed that if decomposers are inhibited by high contents of tannins in their food, strong effects on litter breakdown would be expected. Handayanto et al. (1997) found a strong negative correlation between N mineralization rates and the protein precipitation capacity of litter material, a measure of tannin reactivity. Litter material high in tannin content is commonly associated with reduced decomposition rates (Gallardo and Merino 1992; Kalburtji et al. 1999). The convergent evolution of tannin-rich plant communities has occurred on nutrient-poor acidic soils throughout the world. Tannins were once believed to function as anti-herbivore defenses, but more and more ecologists now recognize them as important controllers of decomposition and nitrogen cycling processes. Tannins may also reduce insect predation because they increase the leaf toughness (Haslam 1988). Kraus et al. (2003) summarized that tannins may limit litter decomposition in a number of different ways: (1) by themselves being resistant to decomposition (2) by sequestering proteins in protein-tannin complexes that are resistant to decomposition (3) by coating other compounds, such as cellulose, and protecting them from microbial attack (4) by direct toxicity to microbes, and (5) by complexing or deactivating microbial exoenzymes.

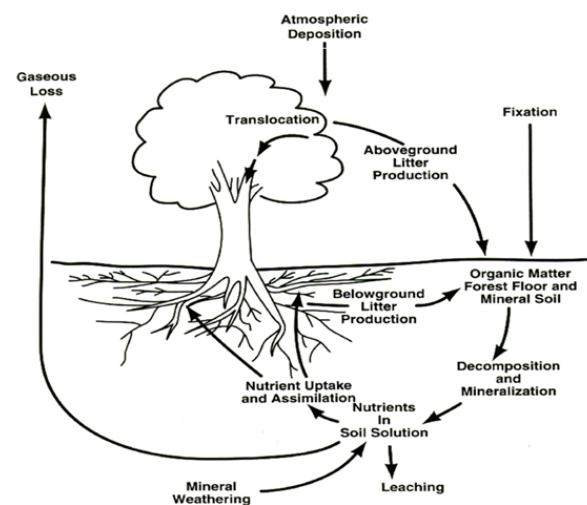
**Role of carbohydrates (cellulose and hemicelluloses) on leaf litter decomposition**

Cellulose is a polysaccharide which is assembled from glucose monomer units, and, which is the main constituent of plant cell walls. It is a linear homopolymer composed of (1→4)-β-glucopyranose. Cellulose can account for between 30 and 60% of plant materials (dry wt.), and its decomposition is of major importance to the biogeo-chemical cycling of carbon (C) and essential plant nutrients (Paul and Clark 1996; Chew et al. 2001). Bunt (1988) reported that cellulose plays a major role in N immobilisation since it breaks down very rapidly and has a high C: N ratio. Initial C/N and N/P ratios were demonstrated to be important factors of regulating litter decomposition rate (Zhou et al. 2008). On the other hand, plant litter of a lower C: N ratio may be more susceptible to decomposition and mineralization (Pal et al. 2010).

*Nutrient cycling in forest ecosystem*

Ecologists refer to the use, transformation, movement, and reuse of nutrients in ecosystems as nutrient cycling. Because of the physiological importance of nutrients, their relative scarcity and their influence on rates of primary production, nutrient cycling is one of the most significant ecosystem processes studied by ecologists. Three nutrient cycles play especially prominent roles: the nitrogen cycle, the carbon cycle and the phosphorus cycle. However, elements such as phosphorus (P), carbon (C), nitrogen (N), potassium (K), and iron (Fe) are used over and over. Elements that are required for the biological processes of organisms are called nutrients (Barnes et al. 1998). Nutrients enter terrestrial ecosystems through geological, hydrological and biological process. Since a cycle can start anywhere; but it will start with the 1) uptake of nutrients by plant roots and their mycorrhizae. 2) allocation of nutrients to biomass construction and maintenance. 3) nutrient reabsorption from senescing tissue, 4) return of nutrients to the soil via above- and below-ground litter, and 5) microbially mediated release of inorganic nutrients to the soil solution (mineralization) during organic matter decomposition. Fig. 4 shows the schematic diagram of nutrient cycling of forest ecosystem.

Forest ecosystem’s nutrient cycling is structured by autotrophic plants, which incorporate minerals into organic



**Fig. 4.** A conceptual diagram of nutrient cycling of forest ecosystem (adapted from Barnes et al. 1998).

compounds. After senescence or death, litter enters the decomposition process in which organic matter is broken down and nutrients are released in an inorganic form, i.e. mineralized. This plant-litter-soil cycle is considered the core of ecosystem cycling, which dominates the dynamics of ecosystem N cycling (Knops et al. 1996; Schlesinger 1997; Knops et al. 2010). In most natural terrestrial ecosystems, this internal ecosystem nutrient recycling exceeds the inputs-outputs fluxes by a large amount, especially for N and P (Schlesinger 1997). However, comparative study of litterfall, litter decomposition and nutrient return in a monoculture *Cunninghamia lanceolata* and a mixed stand in southern China by Wang et al. (2008) showed that the C return of leaf litter varied from 167 g m<sup>-2</sup> year<sup>-1</sup> (in pure stand) to 213 g m<sup>-2</sup> year<sup>-1</sup> (in mixed stand) (Table 1). C was generally returned to soil in the highest amount, followed by N with a range of 4.3-7.0 g m<sup>-2</sup> year<sup>-1</sup> and Ca with a range of 3.0-3.3 g m<sup>-2</sup> year<sup>-1</sup>. On the other hand, the returns of P, K and Mg through leaf litter were much smaller than those for C, N and Ca. No significant differences existed in the returns of C, Ca and Mg between pure and mixed stands (Wang et al. 2008). N release during litter decomposition becomes more important with higher litter quality, decreasing soil C: N ratios and decreased SOM stabilization.

#### *Role of leaf litter quantitative traits on nutrient cycling*

The toughness of plant litter can affect decomposition and nutrient release. Litter decomposition rates in general are positively correlated with N content and negatively so with LMA (Lambers et al. 1998). Low-LMA leaves with

high nutrient contents decompose much faster, leading to increased carbon and nutrient cycling (Cornelissen et al. 1999; Poorter et al. 2009).

Lignin is one of the most slowly decomposing components of dead vegetation, contributing a major fraction of the material that becomes humus as it decomposes. The resulting soil humus generally increases the photosynthetic productivity of plant communities growing on a site as the site transitions from disturbed mineral soil through the stages of ecological succession, by providing increased cation exchange capacity in the soil and expanding the capacity of moisture retention between flood and drought conditions. Lignin and nitrogen contents control carbon dioxide production and nitrogen mineralization in soils. Prescott (2005) revealed that N deposition or fertilization of forested ecosystems with high-lignin litter may lead to greater accumulations of humus or soil organic matter, and greater sequestration of C.

Phenolics can reduce soil nutrient availability, either indirectly by stimulating microbial nitrogen (N) immobilization or directly by enhancing physical protection within soil. Phenolic-rich plants may therefore negatively affect neighboring plant growth by restricting the N supply (Meier and Bowman 2008). However, more recent studies show that both phenolics and tannins are also important in shaping a plant's soil nutrient environment (Hättenschwiler and Vitousek 2000; Kraus et al. 2004). Phenols can also interact with nutrient cycling in various ways beyond a simple negative correlation between phenol concentration and decomposition rate. These interactions can be considered to fit within two groups of mechanisms - effects on the activ-

**Table 1.** Nutrient return (gm<sup>-1</sup>year<sup>-1</sup>) via leaf litter to forest soil in a monoculture *Cunninghamia lanceolata* and mixed with *M. macclurei* stands (adapted from Wang et al. 2008)

|                      | C                   | N                    | P                      | K                      | Ca                     | Mg                     |
|----------------------|---------------------|----------------------|------------------------|------------------------|------------------------|------------------------|
| Monoculture          |                     |                      |                        |                        |                        |                        |
| <i>C. lanceolata</i> | 167±36 <sup>a</sup> | 4.3±1.1 <sup>a</sup> | 0.10±0.04 <sup>a</sup> | 0.19±0.05 <sup>a</sup> | 3.32±0.86 <sup>a</sup> | 0.62±0.26 <sup>a</sup> |
| Mixed stand          |                     |                      |                        |                        |                        |                        |
| <i>C. lanceolata</i> | 122±31              | 3.6±0.8              | 0.09±0.03              | 0.17±0.03              | 2.33±0.71              | 0.45±0.22              |
| <i>M. macclurei</i>  | 91±18               | 3.4±0.7              | 0.38±0.12              | 0.62±0.21              | 0.71±0.28              | 0.27±0.13              |
| Total                | 213±47 <sup>a</sup> | 7.0±1.3 <sup>b</sup> | 0.48±0.13 <sup>b</sup> | 0.79±0.29 <sup>b</sup> | 3.04±0.87 <sup>a</sup> | 0.72±0.30 <sup>a</sup> |

Values followed by different litter within the same column are different significantly at 5% level according to the Tukey's honestly significant difference test.

ity of soil organisms, and physico-chemical effects on the pools and forms of nutrients (Hättenschwiler and Vitousek 2000).

Tannins inhibit soil nitrogen accumulation and the rate of terrestrial and aquatic decomposition (Hissett and Gray 1976). Tannins make plant tissues unpalatable and indigestible for animals. Tannins impede digestion of plant tissues by blocking the action of digestive enzymes, binding to proteins being digested or interfering with protein activity in the gut wall (Howe and Westley 1990; Lambers 1993). Tannins play a major role in nutrient dynamics, especially in that of nitrogen (Kraus et al. 2003) and have an integral control on the activity of soil bacteria and fungi (Field and Lettinga 1992). A number of experiments indicate that plant-derived polyphenols can affect a variety of soil processes some of which could increase nutrient availability to plants (Hättenschwiler and Vitousek 2000). Phenolic substances can comprise a substantial pool of C substrates in the soil, which may increase microbial activity, resulting in short-term immobilization of N (Kraus et al. 2004; Castells et al. 2005; Halvorson et al. 2009).

The decomposition of cellulose provides much of the carbon and energy needs of soil microorganisms. Hemicellulose is the sources of energy and nutrients for soil microflora. When subjected to microbial decomposition, hemicelluloses degrade initially at a faster rate and are first hydrolyzed to their component sugars and uronic acids. The hydrolysis is brought about by the number of hemicellulolytic enzymes known as “hemicellulase” excreted by the microorganisms. On hydrolysis, hemicelluloses are converted into soluble monosaccharide, which is further converted to organic acids, alcohols, CO<sub>2</sub> and H<sub>2</sub>O and uronic acids are broken down to pentoses and CO<sub>2</sub>. As litter decomposes, microorganisms become inextricably associated with the decaying litter creating a substrate- microbe complex. The soil microorganisms will decay the litter in order to gain nutrients and energy for growth and reproduction. During the decomposition process, microorganisms convert the carbon structures of fresh residues into transformed carbon products in the soil.

## Conclusion

The main conclusions can be drawn from the above-

mentioned discussion that the quantitative traits of leaf litter is important predictors of decomposition and decomposition rates increase with greater nutrient availability in the forest ecosystems. This discussion also a more complete understanding of how quantitative traits of leaf litter influence litter decomposition, as variations in chemistry can affect nutrient cycling and long-term soil organic matter dynamics.

Forests provide a multitude of essential functions globally. In addition to supplying building materials for humans, the forests of the world play a key role in C cycling, influence large-scale precipitation patterns, provide clean water and provide habitat for most of the world's biodiversity. As the demands placed on forest ecosystems increase with the growing human population, the need to better understand these systems and their individual components becomes ever more vital. By studying the role of litter quantitative traits on decomposition and nutrient cycling in forest ecosystems we will gain valuable insight to how quantitative traits may influence ecosystem nutrient dynamics. Such knowledge will hopefully contribute to future forest management and conservation practices.

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