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Quantitative Chemical Defense Traits, Litter Decomposition and Forest Ecosystem Functioning

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1. Introduction

In forest ecosystems, litter decomposition, which plays a critical role in nutrient cycling, is influenced by a number of biotic and abiotic factors, including quantitative chemical defense (Ross *et al.,* 2002), environmental conditions such as soil properties and climate (Badre *et al.,* 1998, Vanderbilt *et al.,* 2008), and decomposer community and its complex nature. However, Lavelle *et al.,* (1993) proposed a hierarchical model for the factors controlling litter decomposition. The levels of the hierarchal model are: climate (temperature and moisture)> physical properties of soil (clay and nutrients)>litter quality> macro and microorganisms (Lavelle *et al.,* 1993). Leaf litter quality, which is inherited from living leaves, has repeatedly been emphasized as one of the most important factors controlling the decomposition process (Swift *et al.,* 1979, Melillo *et al.,* 1982, Osono & Takeda 2005). Decomposition rate may be decreased with latitude and lignin content of litter but increased with temperature, precipitation and nutrient concentrations at the large spatial scale (Zhang *et al.,* 2008).

Bernhard-Reversa & Loumeto (2002) mentioned that litter fall serves three main functions in the ecosystem such as energy input for soil microflora and fauna, nutrient input for plant nutrition, and material input for soil organic matter building up. The first two functions are completed through decomposition and mineralization, and the third one through decomposition and humification.

Litter decomposition is a primary source of soil nutrients such as nitrogen and phosphorus, which are often limiting to plant growth in terrestrial ecosystems. The litter is broken down by insects, worms, fungi and microorganisms, organically-bound nutrients are released as free ions to the soil solution which are then available for uptake by plants. The variation in soil carbon and nutrient cycling has been clearly linked to variation in particular aspects of litter chemistry. For example, net N mineralization rates in monocultures of different grass species were correlated with root lignin content, suggesting that substrate chemistry is an important control over mineralization and/or immobilization processes (Hobby & Gough 2004).

De Santo *et al.,* (2009) revealed that litter decomposition rates at the boreal forest were significantly lower than at the temperate one and did not differ between needle litter and leaf litter. In the boreal forest mass-loss was positively correlated with the nutrient release. In this site, Mn concentration at the start of the late stage was positively correlated with lignin decay and Ca concentration was negatively correlated to litter mass loss and lignin decay. In the temperate forest neither lignin, N, Mn, and Ca concentration at the start of the late stage, nor their dynamics were related to litter decomposition rate and lignin decay (Santo *et al.,* 2009). On the other hand, litter quality had stronger effects on decomposition than the temperature in temperate forest (Rouifed *et al.,* 2010). In arid and semi-arid sites, photodegradation could be an influential factor for litter decomposition (Austin & Vivanco 2006). Powers *et al.,* (2009) used a short-term litter bag experiment to quantify the effects of litter quality, placement and mesofaunal exclusion on decomposition in 23 tropical forests in 14 countries. They concluded that decomposition in tropical forest is controlled by soil fauna and litter chemistry, which would vary with the precipitation regime.

Zhang *et al.,* (2008) stressed that the combination of total nutrient elements and C:N accounted for 70.2% of the variation in the litter decomposition rates. On the other hand, the combination of latitude, mean annual temperature, C: N and total nutrient accounted for 87.54% of the variation in the litter decomposition rates. They also indicated that litter quality is the most important direct regulator of litter decomposition at the global scale.

The management of scheme options can influence vegetation and wildlife value for delivering ecosystem services by modifying the composition of floral and faunal communities (Smith *et al.,* 2009). Most European temperate forests have been managed according to "classical" sustainable yield principles for a very long time. In France, vast areas of deciduous forests have been cultivated on short rotations for the production of fuelwood under so-called "low forest" regimes. Many of these forests are now being converted back to high forest management (FAO, 2011). Clear felling is common in harvesting operations in mature softwood stands in Northern America. Thinning is a very common and recommended management practice to manage the plantation and forest stands in general (Blanco *et al.,* 2011). Intensive forest management, which may include operations such as: site preparation; tree planting; tending; thinning; and fertilizer application is often influence the litter decomposition process. Litter decomposition in unmanaged systems is affected mainly by climatic variables (Aerts 1997, Blanco *et al.,* 2011).

However, for better understanding of litter decomposition process and forest ecosystem functioning, we need to know more detail about quantitative chemical defense and their effects on the litter decomposition process which influence the ecosystem functioning. This paper will discuss the quantitative defense traits of forest litter, their effects on litter decomposition and ecosystem functioning.

2. Quantitative chemical defense traits of litter

Quantitative chemicals are those that are present in high concentration in plants (5 – 40% dry weight). The most quantitative metabolites are digestibility reducers that make plant cell walls indigestible to animals. The effects of quantitative metabolites are dosage dependent and the higher these chemicals' proportion in the herbivore's diet, the less nutrition the herbivore can gain from ingesting plant tissues. Because they are typically

large molecules, these defenses are energetically expensive to produce and maintain, and often take longer to synthesize and transport (Nina & Lerdau 2003). These secondary compounds may be secreted within the cells, for example, in vacuoles, or excreted extracellularly. They include poisonous compounds whose concentration in the cell tends to be relatively low, e.g. alkaloids, cyanogenic glycosides and cardenolides. Some of these secondary metabolites accumulate to levels high enough to reduce the plant's digestibility and palatability for herbivores (McKey 1979; Lindroth & Batzli 1984; Lambers 1993).

However, quantitative chemical defensive traits of litter may divide into three main categories: 1. Lignin 2. Total phenolics 3. Tannins (Hydrolyzable tannins and Proanthocyanidins or Condensed tannins).

2.1 Lignin

Lignin is a polymer of aromatic subunits usually derived from phenylalanine. It is an important constituent of plant secondary cell walls and comprises the largest fraction of plant litter. Lignified leaves are rigid in structure, and highly recalcitrant to decay. Its chemical assay is difficult and different methods may lead to different results. Because it constitutes a barrier preventing decomposition of cellulose, lignin content of litter has been reported to control litter decomposition rate (Sterjiades & Erikson 1993).

2.1.1 Chemistry and occurrence of lignin

Lignins are complex polymers formed by the dehydrogenative polymerization of three main monolignols, *p*-coumaryl, coniferyl, and sinapyl alcohols (Fig. 1).

Gymnosperm lignins are mainly formed from coniferyl alcohol, together with small proportions of *p*-coumaryl alcohol. Angiosperm lignins are mainly formed from coniferyl and sinapyl alcohols with small amounts of *p*-coumaryl alcohol (Lewis 1999). Table 1 shows the % lignin content of different leaf litter.

2.1.2 Effects of lignin on litter decomposition

Lignin is an essential component of plant litter, and is among the most recalcitrant compounds, and consequently is of major importance in soil humus building. 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 (Meentemeyer 1978; Melillo *et al.,* 1982; Vitousek *et al.,* 1994; Hobbie 1996; Kitayama *et al.,* 2004). The ratio of lignin and N as a factor that is more related to decomposition than lignin content (Fig. 2).

On the other hand, hemicellulose and lignin concentrations were reported to be negatively correlated with decomposition (Vivanco & 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

& 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; Devi & Yadava, 2007). These increases showed partially linear relationships with accumulated mass loss (Berg *et al.,* 1984).

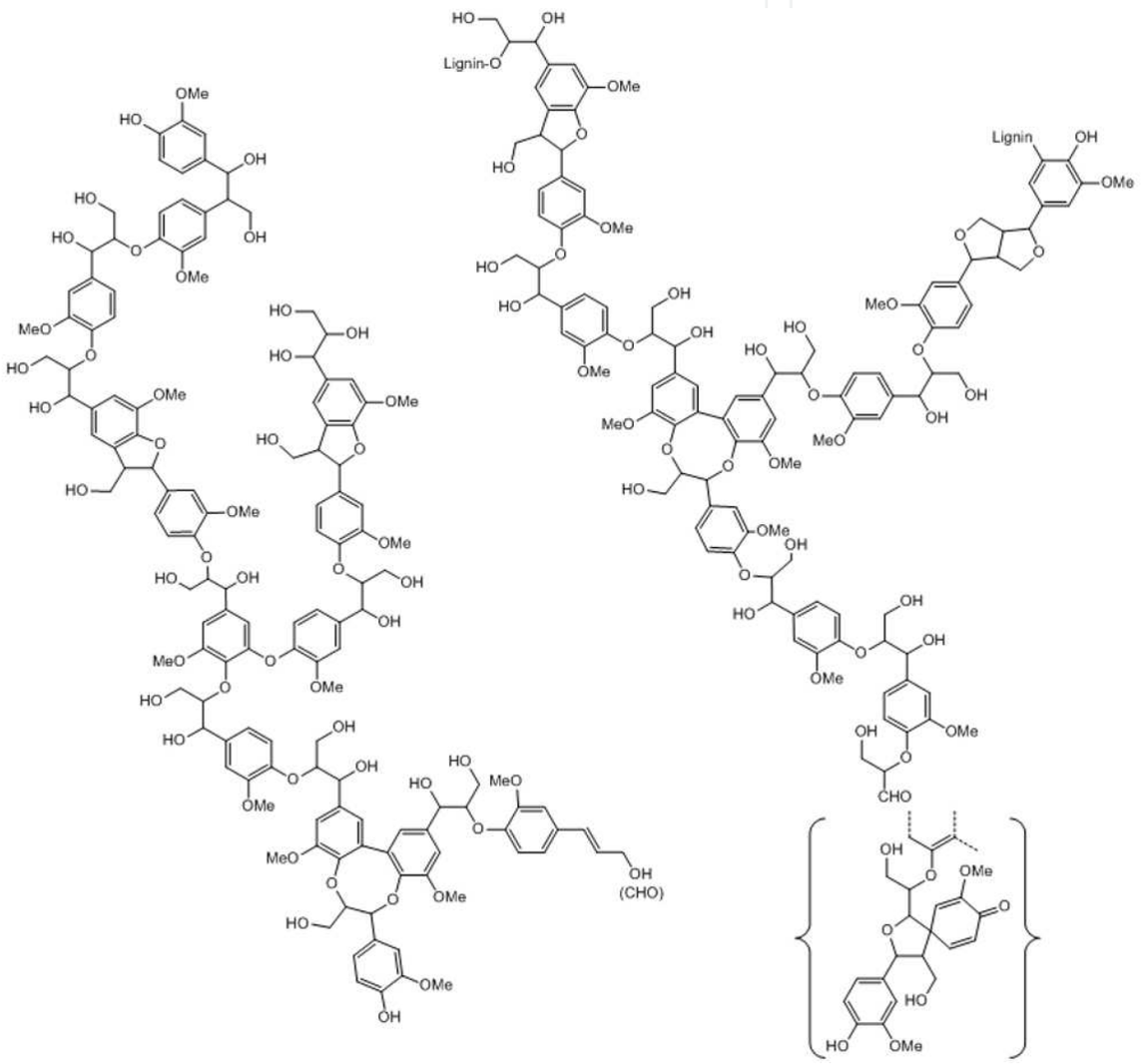


Fig. 1. Common structure of lignin.

Name of the species	Category of Plant	Lignin content of litter (%)
Acacia auriculiformis	Broadleaf tree	54.4
Acacia mangium	Broadleaf tree	43.1
Acer saccharum	Broadleaf tree	10.8
Alphitonia petriei	Broadleaf tree	40.4
Betula pubescens Ehrh	Broadleaf tree	14.0
Castanea sativa	Broadleaf tree	21.1
Dipterocarpus tuberculatus	Broadleaf tree	7.45
Eucalyptus grandis	Broadleaf tree	21.1
Gaultheria griffithiana	Shrub	5.0
Nothofagus dombeyi	Broadleaf tree	19.3
Nothofagus nervosa	Broadleaf tree	29.2
Nothofagus obliqua	Broadleaf tree	27.6
Picea orientalis	Coniferous tree	21.5
Pinus contorta Dougl	Coniferous tree	37
Pinus sylvestris L.	Coniferous tree	29.3
Populus nigra	Broadleaf tree	21.5
Quercus rubra	Broadleaf tree	23.1
Quercus dealbata	Broadleaf tree	6.0
Quercus fenestrata	Broadleaf tree	4.0
Quercus griffithii	Broadleaf tree	3.8
Rhododendron arboreum	Shrub	8.0
Tilia americana	Broadleaf tree	20.0
Broadleaves		21.57±14.23
Coniferous tree		29.26±7.75
Shrub		6.50±2.12

Table 1. The lignin content of different plant species litter (percentage of dry weight) (adapted from Rahman *et al.,* 2011).

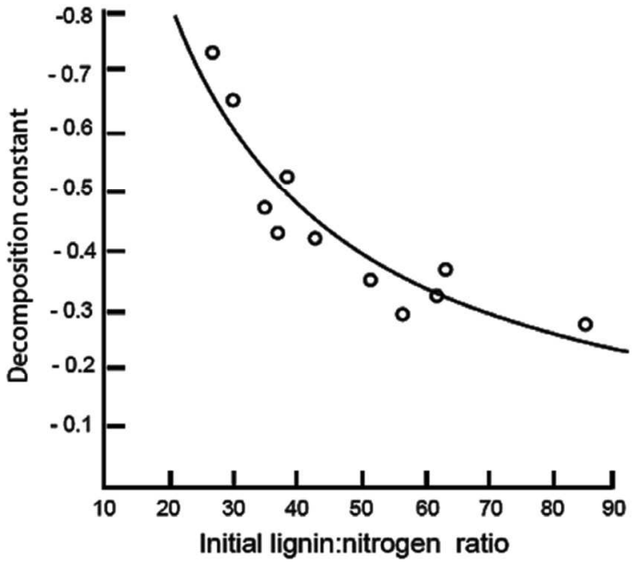


Fig. 2. Relationship between the decomposition constant (*k* = lose of dry mass, to initial lignin concentration of litter) and the lignin: nitrogen ratio of litter (adapted from Melillo *et al.,*1982).

As decomposition proceeds the litter becomes enriched with lignin and N along with other components (Devi & Yadava, 2007). Earlier works have shown that as the lignin concentration increases during litter decomposition, the decomposition rates get suppressed (Fogel & Cromack, 1977; Devi & Yadava, 2007). The suppressing effect of lignin on litter mass-loss rates can be described as a linear relationship in the later stages of decomposition, which, for pine litter, may start at ca. 20–30% mass loss (Fig. 3a). For these later stages, the slope and intercept of this negative relationship varies among sites under different climates (Berg *et al.*, 1993). The lowest effect of lignin concentration on mass-loss rates was found near the Arctic Circle (where long-term average actual evapotranspiration was about 385–390 mm).

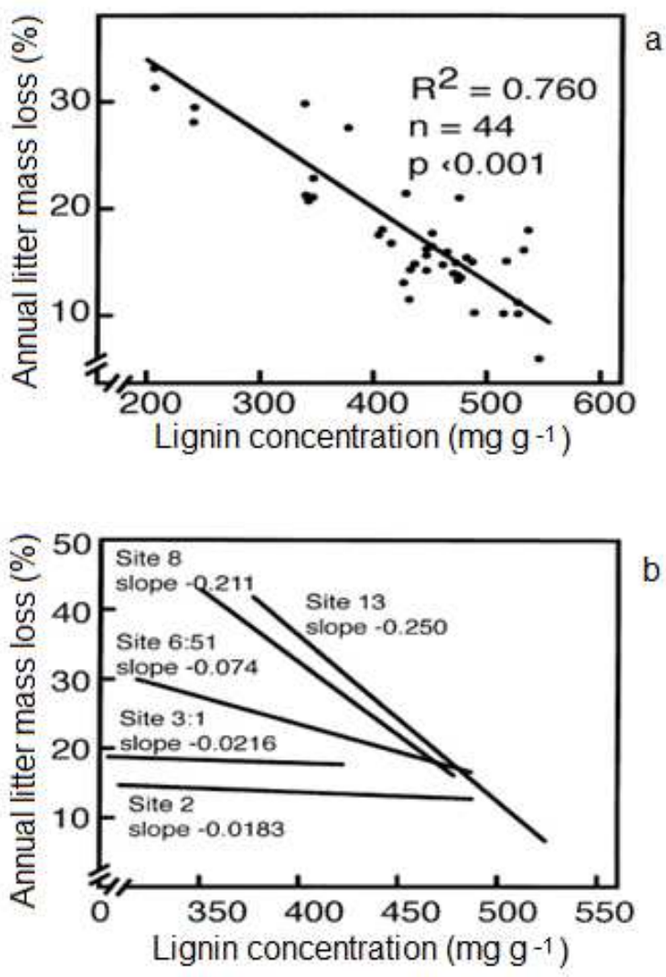


Fig. 3. Annual litter mass loss (%) as a function of initial lignin concentration at the start of each one year period. (a) The linear relationship indicated here, namely a decreasing rate with increasing lignin concentrations for one type of liter. (b) The same relationships under different climatic conditions (five climatically different sites with the AET values 385, 387, 472, 509 and 560 mm for sites 2, 3, 6:51, 8 and 13, respectively) indicate that the rate retarding effect of lignin is stronger in warmer wetter climates (adapted from Berg 2000).

In contrast, in Northern Germany and on the European continent the rate-regulating effect of lignin was found to be higher (Fig. 3 b). In a research on decomposition study from India, it is reported that lignin and fibre contents have showed a negative relation with weight loss of litter (Devi & Yadava, 2007). Many studies have reported a decline in the rate of weight loss of litter due to high initial lignin content (Singh & Gupta, 1977; Devi & Yadava, 2007). More recently, the scientists have found a highly significant, positive correlation between lignin contents and litter decay rates (Raich *et al.,* 2007).

2.2 Total phenolics

Phenolic compounds are one of the most abundant and widely distributed groups of substances in the plant kingdom with more than 8000 phenolic structures currently known (Harbone, 1980). They are products of the secondary metabolism of plants and arise biogenetically from two main primary synthetic pathways: the shikimate pathway and the acetate pathway (Paixao *et al.,* 2007).

2.2.1 Chemistry and occurrence of total phenolics

Phenolics are a heterogeneous group of natural substances characterized by an aromatic ring with one or more hydroxyl groups (Fig. 4). These substances are chemically diverse carbon-based secondary plant compounds occurring in plant tissues (Harborne 1997).

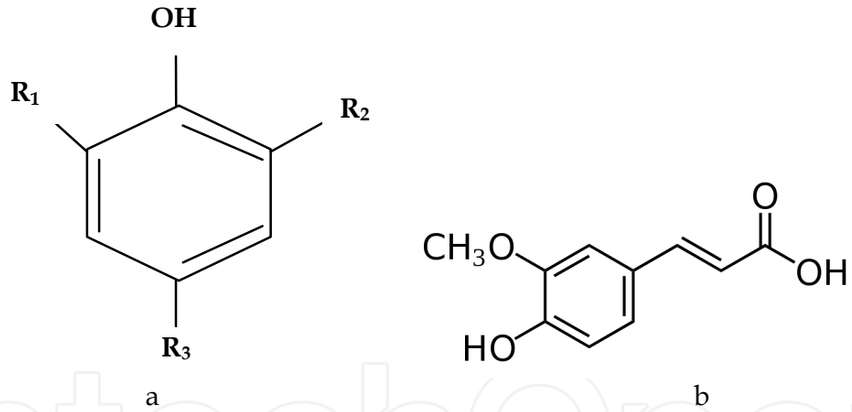


Fig. 4. Simple phenols (C_6), a. phenolic acids b. ferulic acid.

Phenols can be roughly divided into two groups: (1) low molecular weight compounds; and (2) oligomers and polymers of relatively high molecular weight (Hättenschwiler & Vitousek, 2000). Low molecular weight phenolics occur universally in higher plants, some of them are common in a variety of plant species and others are species specific. Because of the large variety of analytical methods and problems with choosing the appropriate standards, polyphenol concentrations reported in the literature vary immensely and might not be comparable with each other. Nevertheless, the two most frequently used polyphenol measurements (i.e. 'total phenolics' and Proanthocyanidins) are accepted reasonably well, and they commonly yield results in the range of about 1% to 25% of total green leaf dry mass (Hättenschwiler & Vitousek, 2000). The amount of phenolics in plant tissues varies with leaf species, age and degree of decomposition (Table 2) (Barlocher & Graca, 2005).

Name of the Species	Plant type	Phenolics (% leaf dry mass)
Acer saccharum (s)	Deciduous tree	15
		2.7
Alnus glutinosa (s)	Tree	6.6
		6.8-7.6
Carya glabra (s)	Deciduous tree	9.1
Eucalyptus globulus (s)	Evergreen tree	6.4
		9.8
Fagus sylvatica (s)	Deciduous tree	8.0
Quercus alba (s)	Tree	16.2
Sapium sebiferum (l, s)	Deciduous tree	3.0
Spartina alterniflora (y)	Perennial deciduous grass	0.4-1.5

Table 2. The phenolics concentrations (%) in selected plant tissues, including senescent leaves (s), live (l) and yellow-green to brown-dead grass leaves (y) (after Barlocher and Graca, 2005).

2.2.2 Effects of total phenolics on litter decomposition

Total phenolics are considered to be biologically active, e.g. by protecting plants against biotic (e.g. microbial pests, herbivores) or abiotic stresses (e.g. air pollution, heavy metal ions, UV-B radiation) (Hutzler *et al.,* 1998), by contributing to allelopathic reactions (Waterman & Mole 1994) and by retarding decomposition rates of organic matter (Hattenschwieler & Vitousek 2000). In particular, phenolics play a major role in the defense against herbivores and pathogens (Lill & Marquis 2001).

In addition, some phenolics may prevent leaf damage resulting from exposure to excessive light (Lee & Gould 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 & Graca (1996) observed a strong negative correlation between the phenol content of different native litter types and litter decomposition rates in a stream, whereas Canhoto & Graca (1999) showed that phenolics from *Eucalyptus* leaves decrease feeding by detritivores. Thus, effects 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 & 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 for *Kandelia candel* and *Bruguiera gymnorrhiza* leaf litter at various stages of decomposition (Fig. 5). The perception of phenols as inhibitors, however, is far too simple, and the variety of phenolic compounds can have many different functions within the litter layer and the underlying soil (Hattenschwiler & Vitousek 2000). Even intraspecific variation in litter polyphenol concentrations can strongly influence soil processes and ecosystem functioning (Schweitzer *et al.,* 2004). Phenols may influence rates of decomposition as they bind to N in

the leaves forming compounds resistant to decomposition (Palm & Sanchez 1990). Gorbacheva & Kikuch (2006) found that dynamics of easily oxidized phenolics may influence the litter decomposition rate in the monitored subarctic field. Some scientist mentioned that phenolics stimulate microbial activity and subsequently reduce plant available N (Madritch & Hunter 2004; Lin *et al.*,, 2006). These results contribute important information to the growing body of evidence, indicating that the quality of C moving from plants to soils is a critical component of plant-mediated effects on soil biogeochemistry and, possibly, competitive interactions among species. Gorbacheva & Kikuch (2006) found that the essential part of phenolics that participates in the formation of mobile forms of organic matter, leaches from the organic horizon and migrates through the soil profile.

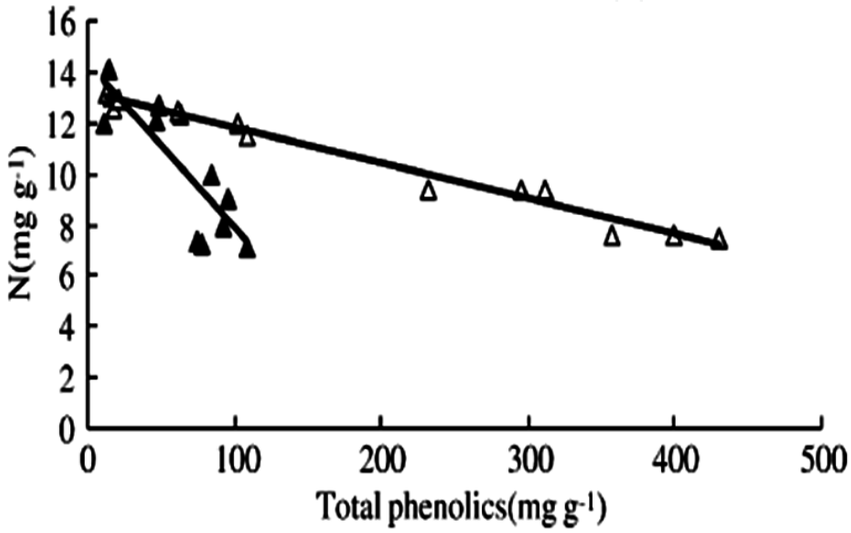


Fig. 5. Relationship between total phenolics and N contents during leaf decomposition of *Bruguiera gymnorrhiza* (Bg) and *Kandelia candel* (Kc). Symbols are: black triangle for Bg leaf; white triangle for Kc leaf (Adapted from Lin *et al.,* 2006).

2.3 Tannins

Tannin is the fourth most abundant biochemical substance in vascular plant tissue after cellulose, hemicellulose and lignin (Kraus *et al.,* 2003). Leaves and bark may contain up to 40% tannin by dry weight (Matthews *et al.,* 1997; Kraus *et al.,* 2003) and in leaves and needles tannin concentrations can exceed lignin levels (Benner *et al.,* 1990). Tannin reduce herbivore load either directly through toxicity or growth alteration or indirectly through reduction of palatability (Feeny 1970).

2.3.1 Chemistry and occurrence of Tannins

Tannins are heterogenous group of phenolics compounds derived from flavonoids and gallic acid. Bate-Smith & Swain (1962) defined tannin as water-soluble polyphenolic compounds ranging in molecular weight from 500 to 3000 Daltons that have the ability to precipitate alkaloids, gelatins and other proteins. Haslam (1998) has substituted the term "polyphenol" for "tannin", in an attempt to emphasize the multiplicity of phenolic group's characteristic of these compounds. Haslam also notes that molecular weights as high as 20,000 Daltons have been

reported, and that tannins complex not only with proteins and alkaloids but also with certain polysaccharides. However, tannins found in higher plants are divided into two major classes termed Proanthocyanidins or Condensed tannins and hydrolyzable tannins (Fig. 6).

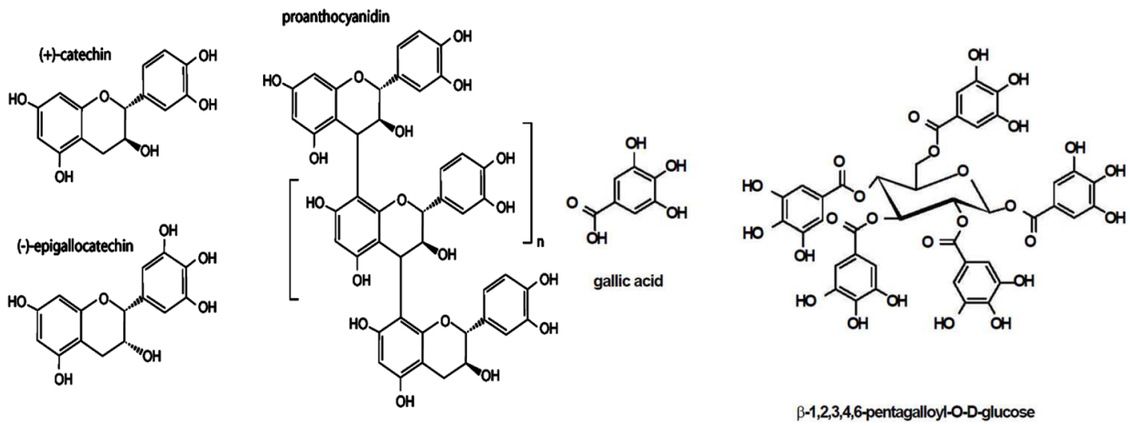


Fig. 6. Structures of tannins; a. Flavan-3-ols (+)-catechin and (-)-epigallocatechin, examples of monomeric precursors that polymerize to form macromolecular products such as linear proanthocyanidins composed of monomeric flavanoid units connected by C4-C8 linkages. b. hydrolyzable tannins β-1,2,3,4,6-pentagalloyl-O-D-glucose.

Tannins are distributed in species throughout the plant kingdom. They are commonly found in both gymnosperms as well as angiosperms. Tannins are mainly physically located in the vacuoles or surface wax of plants. Because tannins are complex and energetically costly molecules to synthesize, their widespread occurrence and abundance suggests that tannins play an important role in plant function and evolution (Zucker 1983). Tannins occur in plant leaves, roots, wood, bark, fruits and buds (Peters & Constabel, 2002; Ossipov *et al.,* 2003). Tannin distribution in plant tissues appears to vary from species to species. In leaf tissues, tannins have been reported to occur preferentially in the epiderm, hypoderm, periderm, mesophyll, companion cells and vascular tissues, as well as throughout the leaf tissue (Grundhöfer *et al.,* 2001). In roots, anatomical studies have identified a 'condensed tannin zone' in pine and eucalyptus located between the growing tip and the more developed cork zone (Peterson *et al.,* 1999; Enstone *et al.,* 2001). Hydrolyzable tannins have a more restricted occurrence than condensed tannin, being found in only 15 of the 40 orders of dicotyledons (Hättenschwiler & Vitousek 2000).

2.3.2 Effects of tannin on litter decomposition

N 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 & Sanchez, 1991; Gallardo & Merino, 1992; Driebe & 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.

In the past decades, many studies have shown that tannins are involved in defense mechanisms of plants against attack by bacteria, fungi, and herbivores (Zucker 1983; Scalbert 1991). There is not much knowledge about the mechanisms of action of the tannin (Zucker 1983; Scalbert 1991) even though modern analytical methods have improved the analysis of these complex structures (Mole & Watermann 1987; Schofield *et al.,* 2001). Proposals on the mechanism of action include tannins forming stable complexes with plant proteins to make the tissue unattractive and difficult to digest (Schofield *et al.,* 2001) and tannins acting like a toxin through highly specific reactions with digestive enzymes or directly at the cell membranes (Zucker 1983) or through depletion of essential iron by complexation (Mila *et al.,* 1996). 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; Provenza *et al.,* 1990; 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 & 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 inhibit soil nitrogen accumulation and the rate of terrestrial and aquatic decomposition (Hissett & 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 & Westley 1988; Lambers 1993). 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.

The studies by Schimel *et al.,* (1998) in the Alaskan taiga provide some of the most comprehensive examinations of the diversity of phenolics and condensed tannin effects on soil processes.

Secondary succession in these forests starts with *Salix/Alnus* communities and continues to an *Alnus/Populus*, a *Populus*, and finally a *Picea alba*–dominated community. *Populus balsamifera* was found to play a key role during succession by the production of polyphenols that interfere with soil processes. Plants from strongly N-limited ecosystems are generally defended by tannins, whereas N-based and structural defenses become more abundant with increases in N supply (Gartlan *et al.,* 1980).

For example, in the savannas of southern Africa, infertile miombo woodlands and savannas on soils derived from highly weathered granites have trees whose leaves are defended by

tannins, while on nearby savannas on higher-nutrient soils such as shales and young volcanic soils, plants are defended by spines. The prevalence of chemical defenses depends on ecosystem nutrient supply (Craine *et al.,* 2003). Fig. 7 represents the schematic overview of the effects of quantitative chemicals from leaf litter on various soil processes and its consequences for the nitrogen cycle and successional dynamics in terrestrial ecosystems.

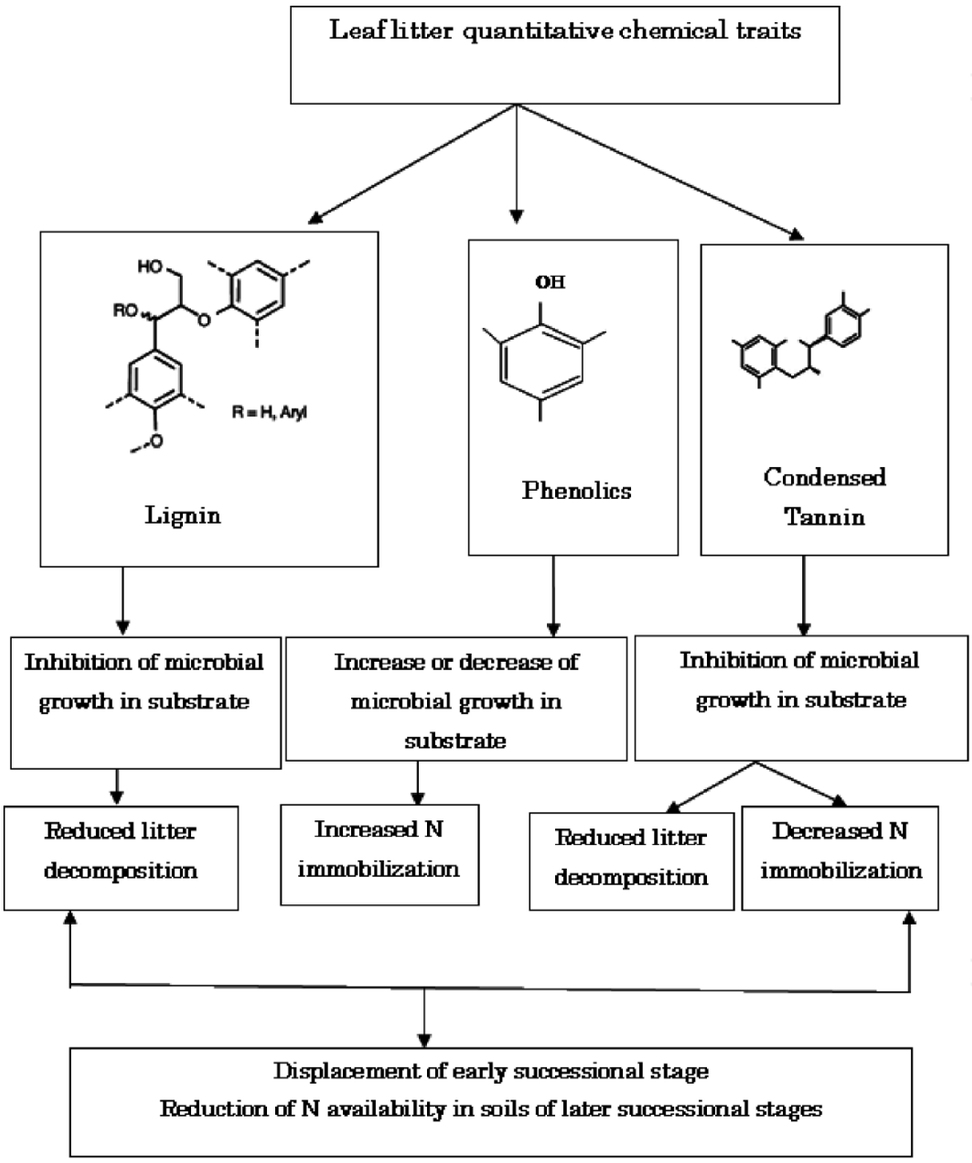


Fig. 7. Schematic reorientation of the effects of quantitative chemicals from leaf litter on various soil processes and its consequences for the nitrogen cycle and successional dynamics in terrestrial ecosystems (modified after Schimel *et al.,* 1998).

3. Litter decomposition and ecosystem functioning

Ecosystem is composed of three subsystems i.e., producer- consumer- and decomposer-subsystem. Ecosystem functioning is affected not only by the function of each subsystem but

also by interactions between them. Quantitative defense is the driving force of ecosystem functioning (fig. 8).

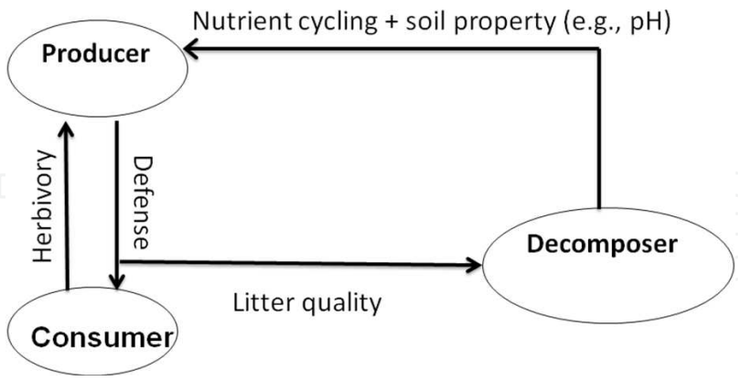


Fig. 8. Ecosystem functioning.

Wardle *et al.,* (1997) demonstrated the importance of tree species composition in determining turnover rate of organic matter and N mineralization by comparing the forests dominated by early successional, fast-growing species and those dominated by slow-growing climax species. This is a verification of the hypothesis in the boreal zone the climax of which is characterized by slow rate of decomposition of hardly decomposable spruce needle litter.

Plant litter decomposition is important to many ecosystem functions such as the formation of soil organic matter, the mineralization of organic nutrients, and the carbon balance (Austin & Ballaré 2010). It is estimated that the nutrients released during litter decomposition can account for 69-87% of the total annual requirement of essential elements for forest plants (Waring & Schlesinger 1985).

Decomposition and nutrient cycling are fundamental to ecosystem biomass production. Most natural ecosystems are nitrogen (N) limited and biomass production is closely correlated with N turnover (Vitousek & Howarth, 1991; Reich *et al.,* 1997). Typically external input of nutrients is very low and efficient recycling of nutrients maintains productivity (Likens *et al.,* 1970). Decomposition of plant litter accounts for the majority of nutrients recycled through ecosystems. Rates of plant litter decomposition are highly dependent on litter quality; high concentration of phenolic compounds, especially lignin, in plant litter has a retarding effect on litter decomposition (Hattenschwiler & Vitousek 2000). At the ecosystem level, chemical defense can influence litter decomposition and nutrient cycling rates (Hattenschwiler & Vitousek 2000; Kraus *et al.,* 2003). Ecosystems dominated by plants with low-lignin concentration often have rapid rates of decomposition and nutrient cycling (Chapin *et al.,* 2003). Simple carbon (C) containing compounds are preferentially metabolized by decomposer microorganisms which results in rapid initial rates of decomposition. More complex C compounds are decomposed more slowly and may take many years to completely breakdown. Phenols and tannins, affect nutrient cycling in soil by inhibiting organic matter degradation, mineralization rates and N availability (Kraus *et al.,* 2003).

3.1 Effects of management on litter decomposition

Litter decomposition rate may be regulated by species composition, leaf litter chemistry, management activities, or any of the combinations of them. The forest management activities

had significant effects on leaf litter decomposition. They also had significant effects on leaf litter chemistry during decomposition process. Clear cut or selective thinning method for timber harvesting may change litter decomposition by altering microclimatic conditions of the forest floor, leaf litter chemistry and composition of the microbial community (Li *et al.,* 2009; Blanco *et al.,* 2011). In a cold climate, selective thinning can increase the temperatures of the forest floor, and thus increase decomposition rate whereas selective thinning in a warm climate may slow decomposition by reducing the moisture content of surface organic matter (Li *et al.,* 2009; Blanco *et al.,* 2011). Blanco *et al.,* (2011) observed that thinning effects clearly influenced litter chemistry in Continental forest and Mediterranean forest, generally appeared sequentially, first nutrients and cellulose and then total C and lignin.

4. Concluding remarks and future direction

Leaf litter decomposition is the fundamental process of ecosystem functioning. Quantitative chemical is hypothesized to play a key role in regulating litter decomposition and to be important for the production of dissolved organic matter and CO_2. Lignin decomposition may be relatively slower in boreal forest than tropical forests. Results after three years of decomposition experiments of Canadian boreal forest, Moore *et al.,* (1999) concluded that lignin/N ratio, and some other climatic variables were valuable parameters for predicting mass loss.

Plants growing in tropical regions have higher polyphenolics concentrations in their tissues compared to temperate zone species (Coly 1983). Tannins are abundant in tropical tree foliage and have the potential effects on litter decomposition. Wieder *et al.,* (2009) used natural variations in species litter chemistry combined with a through fall removal experiment to understand how climate–chemistry interactions regulate tropical forest litter decomposition. Their results suggested that widely used predictors of litter decomposition based on chemical quality are still useful in tropical forests and that these wet systems also require an understanding of litter solubility to best prediction rates of decomposition.

The above discussion justifies that quantitative chemical traits can be used as a predictive tool for litter decomposability and ecosystem functioning. The decomposition of plant litter is an essential process in terrestrial ecosystems, resulting in carbon and nutrients being recycled for primary production. While a great deal of research has addressed quantitative chemical defense and their effect on decomposition and ecosystem functioning, there are many areas of quantitative chemical's biogeochemistry that are not known. There is still little information found regarding how different types of quantitative chemicals influence soil organisms, and how these chemicals' biodegradation affects the soil quality. An understanding of the role of quantitative chemicals in plant litter decomposition will allow for more accurate predictions of carbon dynamics in terrestrial ecosystems. When we can make a relationship between quantitative chemicals and decomposition then we can easily predict ecosystem functioning, which is important for conservation and restoration management of endangered ecosystems. Hence, it is imperative that future research focuses more attention on quantitative chemicals' biogeochemistry and their effects on litter decomposition, CO_2 emission and soil quality. There is a specific need to understand the role of lignin and of lignified cellulose, and their interactions during the late stages of decomposition. How do different types of lignin building blocks influence litter decomposition processes? What is the fate of quantitative chemicals after litter decomposition? Identifying and quantifying links

between quantitative chemical defense traits and litter decomposability would enhance our understanding of ecosystem functioning and will provide us with a predictive tool for modeling decomposition rates under different vegetation types.

5. Acknowledgements

We are thankful to Biogeochemistry, and Ecology journal editors for giving permission to use the figure in this manuscript.

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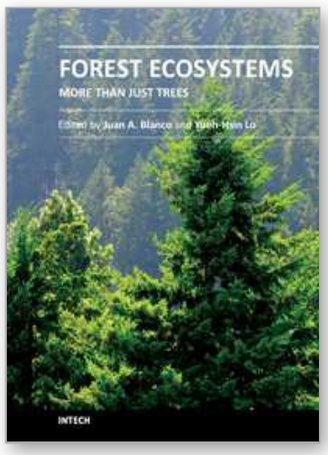
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Forest Ecosystems - More than Just Trees

Edited by Dr Juan A. Blanco

ISBN 978-953-51-0202-1
Hard cover, 464 pages
Publisher InTech
Published online 07, March, 2012
Published in print edition March, 2012

The common idea for many people is that forests are just a collection of trees. However, they are much more than that. They are a complex, functional system of interacting and often interdependent biological, physical, and chemical components, the biological part of which has evolved to perpetuate itself. This complexity produces combinations of climate, soils, trees and plant species unique to each site, resulting in hundreds of different forest types around the world. Logically, trees are an important component for the research in forest ecosystems, but the wide variety of other life forms and abiotic components in most forests means that other elements, such as wildlife or soil nutrients, should also be the focal point in ecological studies and management plans to be carried out in forest ecosystems. In this book, the readers can find the latest research related to forest ecosystems but with a different twist. The research described here is not just on trees and is focused on the other components, structures and functions that are usually overshadowed by the focus on trees, but are equally important to maintain the diversity, function and services provided by forests. The first section of this book explores the structure and biodiversity of forest ecosystems, whereas the second section reviews the research done on ecosystem structure and functioning. The third and last section explores the issues related to forest management as an ecosystem-level activity, all of them from the perspective of the "other" parts of a forest.

How to reference

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Mohammed Mahabubur Rahman and Rahman Md. Motiur (2012). Quantitative Chemical Defense Traits, Litter Decomposition and Forest Ecosystem Functioning, Forest Ecosystems - More than Just Trees, Dr Juan A. Blanco (Ed.), ISBN: 978-953-51-0202-1, InTech, Available from: http://www.intechopen.com/books/forest-ecosystems-more-than-just-trees/quantitative-chemical-defense-traits-litter-decomposition-and-forest-ecosystem-functioning

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