Original Research Article

Seasonal patterns of litterfall in forest ecosystem worldwide

Haicheng Zhang a, Wenping Yuan a,*, Wenjie Dong a, Shuguang Liu b,c

a State Key Laboratory of Earth Surface Processes and Resource Ecology, Beijing 100875, China
b United States Geological Survey, Earth Resources Observation and Science Center, Sioux Falls, SD 57198, USA
c State Engineering Laboratory of Southern Forestry Applied Ecology and Technology, Central South University of Forestry and Technology, Changsha, Hunan 410004, China

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A B S T R A C T

The seasonal litterfall plays an important role in the process of forest carbon and nutrient cycles. The current dynamic vegetation models use a simplified method to simulate seasonal patterns of litterfall, and assume that litterfall inputs distributed evenly through the year for deciduous trees or occur once during the start of year for evergreen trees. In this study, we collected more than 400 litterfall measurements for different forest ecosystems from existing literature and monographs, and analyzed the seasonal patterns of litterfall over the various forest types. The results showed that the total annual litterfall varied significantly by forest types in the range of 3–11 Mg ha−1 yr−1. The seasonal litterfall patterns had diverse forms and varied obviously among the forest types. For tropical forests, the litter peaks occurred mostly in spring or winter, corresponding to the drought season; for temperate broadleaved and needle-leaved evergreen forests, litter peaks could occur at various seasons; and for temperate deciduous broadleaved and boreal evergreen needle-leaved forests, litter peaks were observed in autumn. Global analyses showed that seasonal patterns of litterfall were determined by both the physiological mechanism and environmental variables.

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1. Introduction

Litterfall is a particularly key process determining the carbon and nutrient cycling of forest ecosystems, and controls the main respiration substrates on the forest floor (Roig et al., 2005). Therefore, the magnitude of litterfall regulates the rate of soil respiration and soil organic carbon content indirectly (Schlesinger and Andrews, 2000; Sayer, 2006; Hansen et al., 2009). Moreover, litterfall maintains the soil fertility as it is the most important resource of soil organic matter and soil nutrients (Meentemeyer et al., 1981; Odiwe and Muoghalu, 2003; Gairola et al., 2009). Litterfall can also characterize the properties of the underlying surface by changing the hydraulic conductivity and albedo (Liu et al., 1997), and impact the responses and feedbacks of terrestrial ecosystems to climate systems (Winkler et al., 2010). Therefore, litterfall is the key parameter in measuring, modeling and predicting the terrestrial ecosystem dynamics (Liski et al., 2005).

The seasonal pattern of litterfall affects the dynamics of ecosystem carbon and nutrient cycling (Katz and Lieth, 1974; Das and Ramakrishnan, 1985; Xu et al., 2004). Many observations suggest that litterfall decomposition is characterized by faster decomposition during the initial periods (Olson, 1963; Yang et al., 2004; Liski et al., 2005; Aké-Castillo et al., 2006). For example, 40–50% of the dry weight of litterfall in an eastern Guatemalan forest was decomposed in the initial five weeks and 70% during the first six months (Ewel, 1976). A similar result was reported at Wuyi Mountain in China where the leaves of Castanopsis kawakamii and Ormosia xylocarpa lost 89 and 88% of their initial weight in the first 150 days period, respectively, compared with 11.7 and 9.5% in the following 600 days period (Yang et al., 2004). As a result, accurate prediction of litterfall start times and seasonal patterns determine temporal changes of soil respiration as well as carbon budget directly (Davidson et al., 1998; Janssens and Pilegaard, 2003; DeForest et al., 2009).

Numerous studies have shown significant differences in litterfall seasonal patterns within several ecosystem types and even for different tree species in the same ecosystems. The seasonal patterns of litterfall show unimodal, bimodal or irregular modes, and the litter peaks might occur in several months of the year (Woodruff, 1982; Lowman, 1992; Pausas, 1997; Scheer et al., 2009). For instance, Zelama (2008) reported that the seasonal patterns varied distinctly by species for a subtropical wet forest in Puerto Rico: 16 species were unimodal, another three species were bimodal and the litter peaks generally occurred in different...
months. Additionally, many studies have also suggested that environmental variables such as temperature, radiation, soil features and storms could influence the seasonal patterns of litterfall (Hermansah et al., 2002; Averti and Dominique, 2011). Pausas (1997) showed that the period of litter peaks for Pinus sylvestris in the eastern Pyrenees varied obviously between two adjacent years due to interannual variability of precipitation.

Many field observations have been conducted worldwide, and indicated that the seasonal patterns of litterfall were determined by physiological mechanisms (Slim et al., 1996; Sundarapandian and Swamy, 1999; Ndakara, 2011) and environmental variables (Hermansah et al., 2002; Martius et al., 2004; Zeleama, 2008). Several models of litterfall have been developed based on statistical analyses, mechanistic or remote sensing methods (Dixon, 1976; Box, 1988; Kikuzawa, 1991; Zeilhofer et al., 2012). Dixon (1976) developed an empirical litterfall seasonality model for temperate deciduous forests. Box (1988) integrated environment stress and foliage/defoliation habits to simulate litterfall seasonality at various biomes.

Current ecosystem carbon cycle models, however, seldom integrate these mechanisms and just use simplified algorithms to simulate the litterfall process (Kucharik et al., 2000; Ito and Okiawa, 2002; Sitch et al., 2003). The Lund–Potsdam–Jena Dynamic Global Vegetation Model (LPJ-GCM) assumes that all litterfall of the previous year falls into the ecosystem at the start of the next year (Sitch et al., 2003). Integrated Biosphere Simulator (IBIS) assumes that litterfall distributes evenly through the entire year (Kucharik et al., 2000; Ryan and Law, 2005). These assumptions are obviously inconsistent with numerous field observations, and resulted into large uncertainties in temporal changes of soil respiration within the current carbon cycle models (Gu et al., 2004; Ryan and Law, 2005). Therefore, it is quite important to identify the start and seasonal pattern of litterfall for improving carbon cycle models.

In this study, we collected and compiled substantial litterfall datasets and the related environmental conditions from published literature and monographs. Our specific objective was to assess the total annual litterfall, composition and seasonal patterns of litterfall for major forest types on a global scale, in particularly, examine the features and dominant environmental variables of seasonal patterns for various forest ecosystem types.

### 2. Data and methods

#### 2.1. Data sources

In this study, litterfall refers to plant material shedding in one year, and is composed primarily of leaves, twigs (usually <2 cm in diameter), flowers, fruits and bark. Dead roots and coarse woody detritus are not included. We collected literatures with litterfall measurements from databases including ISI Web of Knowledge, Springer Link, ScienceDirect, Journal of STORage (JSTOR) and China National Knowledge Infrastructure (CNKI). Several key words, including litterfall, litter, leaf fall, leaf phonology and leaf seasonality, were used to search the literatures at the above databases. The languages of the literatures included English, Chinese, French, Japanese, Spanish, Thai and Portuguese. Totally, more than 300 literatures and monographs were collected, and some had recorded the different parts of litterfall, including leaves, twigs and others. At a given site, the litterfall measurements of different tree species were considered to be different samples. In total, we collected 459 monthly litterfall samples from 267 observation sites, and 145 samples provided the composition of litterfall (Table 1). The sampling duration varied from 1 year to >10 years. The observation sites dispersed widely in various climate zones within latitudes 60°N–45°S (Fig. 1), and the elevation of the sites ranged from less than 10 m to more than 2000 m.

The litterfall measurement sites cover the seven different forest types: tropical evergreen forest (TEF), tropical rain-green forest (RGF), mangrove forest (Mang), temperate broadleaved evergreen forest (BEF), temperate summer-green forest (SGF), temperate needle-leaved forest (TNF) and boreal needle-leaved forest (BNF). Generally, Mang is included in TEF, but in the present study this was treated separately due to its unique characteristics (Matthews, 1997). Generally, the forest types for majority of the observation sites were specified in the references. For the unspecified observation sites, we determined the forest types according to the phonological characteristics of the constructive species and the latitude of the observation sites.

The corresponding environmental variables, including precipitation, temperature, solar radiation and wind speed, were extracted from the MERRA (Modern Era Retrospective-Analysis for Research and Applications) according to latitude and longitude of stations and the time when the experiments were done. MERRA is a NASA reanalysis for the satellite era using a major new version of the Goddard Earth Observing System Data Assimilation System Version 5 (GEOS-5), and produces an estimate of climatic conditions for the world, at 10 m above the land surface and at a resolution of 0.5° latitude by 0.6° longitude. The MERRA reanalysis dataset has been validated carefully at the global scale using surface meteorological data sets to evaluate the uncertainty of various meteorological variables (Yuan et al., 2010).

#### 2.2. Statistical analysis

We characterized the litterfall seasonal variability for each forest type by four indices: the percentage of the highest monthly litterfall (litter peak), the percentage of the lowest monthly litterfall (litter valley), the peak/valley ratio (PVR) and the coefficient of variation (CV) over the entire year. We summed the major seasonal patterns for each forest type according to the peak times. The samples with the same peak time would be classified into one group. Then the sample which presented a unique seasonal pattern and unparalleled peak time would be set aside.

To investigate the dominant environmental variable in seasonal variation of litterfall, the following method was used to determine the rank of environment variables with the maximum litterfall. We took temperature as an example to present our statistical approach. First, monthly average temperatures of each sample were sorted in descending order from 1 to 12, rank 1 indicating the highest and rank 12 the lowest. Second, we recorded the ranks of the monthly average temperature corresponding to the litter peak. For bimodal samples, both peaks were counted. The method of polynomial fitting was used for defining the peak time of litterfall measurements without apparent litter peak. Third, the frequency of each rank of 1–12 was counted. Then, we analyzed the

<table>
<thead>
<tr>
<th>Forest types</th>
<th>Ns</th>
<th>Nc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical evergreen</td>
<td>63</td>
<td>12</td>
</tr>
<tr>
<td>Tropical rain-green</td>
<td>58</td>
<td>24</td>
</tr>
<tr>
<td>Mangrove forest</td>
<td>56</td>
<td>15</td>
</tr>
<tr>
<td>Temperate broadleaved evergreen</td>
<td>113</td>
<td>38</td>
</tr>
<tr>
<td>Temperate summer-green</td>
<td>54</td>
<td>19</td>
</tr>
<tr>
<td>Temperate needle-leaved</td>
<td>67</td>
<td>26</td>
</tr>
<tr>
<td>Boreal needle-leaved</td>
<td>48</td>
<td>11</td>
</tr>
</tbody>
</table>

Table 1

The number of litterfall samples. Ns indicates the number of samples which just provide the total monthly amount of litterfall. Nc indicates the number of samples which provide both the total monthly amount of litterfall and the compositions.
3. Results

3.1. Litterfall production and composition

Mean annual litterfall varied obviously among and within various ecosystems in the range of 3–11 Mg ha⁻¹ y⁻¹. Litterfall was the lowest in BNF forests (3.3 Mg ha⁻¹ y⁻¹), intermediate in SGF, TNF and BEF (4.7–6.0 Mg ha⁻¹ y⁻¹), and these were all lower than that of TEF and RGF forests (7.0 Mg ha⁻¹ y⁻¹). Mang had the highest annual litterfall (10.7 Mg ha⁻¹ y⁻¹) (Fig. 2a), which was more than three times that of BNF.

Leaf litter contributed to total litterfall substantially. The percents of leaf litter vary slightly among forest types in a range of 64–73%. BNF owned the highest percent of leaf litter; TEF is the lowest (Fig. 2b). In contrast, twig litter composed about 17% of total litterfall. The other parts including fruit, flower and bark made up just 14% of total litterfall.

3.2. Seasonal patterns of litterfall

Litterfall production showed strong seasonal variability. According to PVR (34.8) and CV (166.5%) values, SGF showed the strongest seasonality. The largest monthly litterfall contributed 45.2% of the total annual litterfall and the lowest monthly contribution was only 1.3% (Table 2). RGF did not show a large seasonality compared to the evergreen broadleaved and needle-leaved vegetation types (Table 2). Overall, temperate and cool-temperate forests had a stronger seasonal variability than in tropical and subtropical areas.

The seasonal patterns of litterfall varied obviously among and within the various forest types (Fig. 3). The majority of samples had a unimodal seasonal pattern, but the litter peaks were generally found in different months. At RGF, the litter peaks occurred mostly in spring and winter, and autumn is the major season of litterfall at SGF and BNF. It should be noticed that at TEF, Mang, BEF and TNF,
the litter peaks occurred in various seasons. Moreover, many samples of TEF, Mang, BEF and TNF had bimodal seasonal patterns, with the first peak mostly in spring and the later peak in autumn or early winter. At TEF, BEF and TNF, a small number of samples showed uniform seasonal patterns, and the CV of monthly litterfall are less than 20%.

3.3. The environmental regulations

The litter peaks for most forest types depended strongly on environment. At TEF and RGF, the percentages of litter peaks in the driest three months were about 60 and 55%, respectively, and just 10% in the wettest three months. In addition to precipitation, solar radiation may also influence the seasonal patterns at tropical forests. There were about 55 and 50% of litter peaks in the most radiation-abundant three months at TEF and RGF, respectively (Fig. 4). The seasonal patterns for Mang were mostly related to temperature, and about 55% of the litter peaks were in the warmest three months, and nearly 30% in the warmest month. Both temperature and solar radiation impacted the seasonal patterns of litterfall for SGF strongly. About 32% of litter peaks occurred during the sixth warmest month (i.e. Rank 6 in Fig. 4). Nearly 50% of the litter peaks occurred during the eighth most radiation-abundant month. The seasonal patterns of BNF related significantly to solar radiation, and about 43% of the litter peaks occurred during the eighth most radiation-abundant month (i.e. Rank 8 in Fig. 4). Finally, none of the four variables showed significant correlation with the litter peaks for BEF and TNF.

4. Discussion

Litterfall is an important respiration substrate, and dominates the magnitude of heterotrophic respiration and the carbon budget. Previous studies showed that heterotrophic respiration released 50–75 Pg C to the atmosphere annually (Kucharik et al., 2000; Durel and Foley, 2003; Del Grosso et al., 2005; Yuan et al., 2011), equaling nearly ten times of annual emissions from burning fossil fuels (Schimel et al., 1996; Solomon et al., 2007). Seasonal patterns of litterfall, however, are processed in a simplified way, which induces large model uncertainties (Ryan and Law, 2005). Our results indicated obviously seasonal variability of litterfall which implied a substantial difference between model assumptions and field observations.

Environmental variables impact the seasonal patterns of litterfall greatly, and dominate environmental variables and mechanisms for seasonal patterns of litterfall generally vary over the various forest types. This study indicated that precipitation and radiation were the limiting factors for regulating litterfall at tropical forests (Fig. 4). In the dry season, leaf abscission takes place due to water stress as plant adaptation mechanism (Green, 1998; Valintini et al., 2008; Ndakara, 2011). Many existing studies also suggested that, in many tropical wet regions, radiation is the dominant environmental variable on seasonal patterns (Collins, 1977; Martinez-Yrizar and Sarukhan, 1990; Angulo-Sandoval and Aide, 2000). Forests in these wet regions usually shed the mature leaves coincident with the appearance of new leaves at the radiation-abundant periods (Moraes et al., 1999; Descheemaeker et al., 2006; Zelamea, 2008). Tropical forest ecosystems are diverse and formed by many tree species. The relationships with individual environmental variable are species- and component-dependent (Duke, 1988) and the total seasonal pattern is the result of the overlapping of seasonal patterns for individual or groups of species (Sundarapandian and Swamy, 1999; Zelamea, 2008; Ndakara, 2011). Thus, the litter peaks of tropical forests are not usually concentrated in a short time, and the intensity of seasonal variability is relatively weak.

Our results suggest temperature as limiting factor for mangrove forests, which is consistent with previous studies (Wafar et al., 1997; Sánchez-Andrés et al., 2010). It is known that high temperature can speed up the rate of transpiration and increase the salt content of mangrove leaves. In order to avoid being damaged by this high salinity, plants shed the mature leaves (Twigley et al., 1986; Shumway and Whittick, 1999). It is likely that precipitation would also affect the seasonal patterns of mangrove forests. Rainfall can reduce the salinity of soil water and lower the air temperature, which would help to reduce litterfall production. On the other hand, rainstorms can increase litterfall production greatly through physical mechanisms (Sim et al., 1996; Wafar et al., 1997; Chen et al., 2009).

The seasonal patterns of litterfall at BEF and TNF are multitudinous and show unimodal, bimodal or multimodal modes. The distribution of litter peaks on a global scale presents no significant individual correlations with precipitation, temperature, radiation or wind speed. Many existing studies suggest that the limiting factors for BEF and TNF generally vary with locations. Litter peaks occurring in autumn or winter are always caused by low temperature (Hennessey et al., 1992), and those in spring and summer primarily relate to radiation or drought (Birk, 1979; Briggs and Maher, 1983; Bellot et al., 1992; Weng et al., 1993; Enright, 1999; Wang et al., 2004). Overall, due to the diversity of component species and the related environmental conditions, the seasonal patterns of litterfall at BEF and TNF are diverse and cannot be characterized by a specific environmental variable.

For most temperate broadleaved deciduous forests, the fall of leaves and fruit occurred mostly in autumn. Therefore, the seasonal patterns of SGF are mostly unimodal, with a sharp peak in autumn (Fig. 3). Generally, low temperature is thought to be the limiting factor, and the mechanism has been explained sufficiently (Dixon, 1976; Ferrari, 1998; Givnish, 2002). However, in our study, solar radiation showed higher correlation with that of temperature. Previous studies suggested the reduction of solar radiation was one signal for leaf abscission in autumn, due to declining solar radiation reducing the rate of photosynthesis and influencing the transport of photosynthate (Taiz and Zeiger, 2002).

In boreal areas, most of the needle-leaved evergreen forests showed unimodal seasonal pattern with litter peaks in autumn (Fig. 3). Our study suggested solar radiation to be the dominant variable at BNF, as the litter peaks occurred mostly along with declining solar radiation. Moreover, previous studies also suggested that the phenology of many boreal forests was driven by temperature, and the litter peaks in autumn and winter were triggered by low temperature (Kramer et al., 2000). There are also some boreal forests with a bimodal seasonal pattern, with one litter peak in autumn and the other in spring coinciding with the budding of new leaves (Nihlgard, 1972; Lanier, 1979).
Fig. 3. Seasonal patterns of litterfall for each forest type. (a) TEF, (b) RGF, (c) Mang, (d) BEF, (e) SGF, (f) TNF, and (g) BNF. In each forest type, different seasonal patterns (e.g. TEF1, TEF2 etc.) were distinguished by the peak times. The samples with same peak time would be classified into one group. For each group, presented monthly percentages of litterfall are average values of samples belong to the group. The samples with distinctive peak times would be classified into “Other” and not be presented in line chart. The pie charts show the percentage of samples corresponding to the seasonal pattern shown in the line charts. The width of the line is proportional to the corresponding percentage of samples. Here, we set the seasonality of northern hemisphere as a benchmark and adjusted the seasons of southern hemisphere sites by exchanging January and July, February and August, and so on.
Fig. 4. The distributions of the highest litterfall according to rank of the environmental variables. Rank 1 is the highest value and rank 12 is the lowest.
5. Summary

We examined the seasonal patterns of litterfall at major forest types worldwide. The results suggested that total annual litterfall varied significantly by forests, with a range of 3–11 Mg ha⁻¹ y⁻¹, and that leaf litter was the main component. The seasonal patterns of litterfall had diverse forms and varied by forests. For tropical forests, the litter peaks were found mostly in spring or winter, corresponding to the drought season. For temperate broadleaved and needle-leaved evergreen forests, the litter peaks occurred in every season. For temperate broadleaved deciduous and boreal needle-leaved evergreen forests, the peaks were mostly in autumn. The limiting environmental variables generally differed among the forest ecosystems. For tropical forests, drought was always the limiting factor. For mangrove forests, high temperature caused the litter peaks with a unique mechanism. For temperate broadleaved and coniferous evergreen forests, the limiting factors usually varied by forests. For temperate broadleaved summer-green forests, low temperate was the main limiting factor. For boreal needle-leaved evergreen forests, the litter peaks were generally triggered by declining solar radiation. Our results will be benefit for developing litterfall modes in the future studies.

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