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Seasonal patterns of litterfall in forest ecosystem worldwide

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ABSTRACT

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} y^{-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.

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 9.9% 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 (Woodroffe, 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

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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; Zelamea, 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 foliation/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 Oikawa, 2002; Sitch et al., 2003). The Lund–Potsdam–Jena Dynamic Global Vegetation Model (LPJ-DGVM) 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.

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.

Forest types	Ns	Nc
Tropical evergreen forest (TEF)	63	12
Tropical rain-green forest (RGF)	58	24
Mangrove forest (Mang)	56	15
Temperate broadleaved evergreen forest (BEF)	113	38
Temperate summer-green forest (SGF)	54	19
Temperate needle-leaved forest (TNF)	67	26
Boreal needle-leaved forest (BNF)	48	11
All forests	459	145

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 rank 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