JGR Biogeosciences

RESEARCH ARTICLE

10.1029/2020JG006204

Key Points:

- Leaf and total litterfall exhibited a strong and similar seasonal pattern
- There was an “S-shaped” increasing pattern in the annual litterfall
- Contrasting climatic factors controlled seasonal and annual litterfall dynamics

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

A. Z. Wang and G. H. Dai,
waz@iae.ac.cn;
daiguanhua@126.com

Citation:

Wang, C. G., Zheng, X. B., Wang, A. Z., Dai, G. H., Zhu, B. K., Zhao, Y. M., et al. (2021). Temperature and precipitation diversely control seasonal and annual dynamics of litterfall in a temperate mixed mature forest, revealed by long-term data analysis. *Journal of Geophysical Research: Biogeosciences*, 126, e2020JG006204. <https://doi.org/10.1029/2020JG006204>

Received 13 DEC 2020

Accepted 8 JUN 2021

Author Contributions:

Conceptualization: A. Z. Wang, G. H. Dai

Data curation: X. B. Zheng

Formal analysis: C. G. Wang

Funding acquisition: C. G. Wang

Investigation: G. H. Dai, B. K. Zhu, Y. M. Zhao, S. J. Dong, W. Z. Zu,

W. Wang, Y. G. Zheng, J. G. Li

Methodology: A. Z. Wang, G. H. Dai

Supervision: A. Z. Wang, G. H. Dai

Writing – original draft: C. G. Wang

Writing – review & editing: M.-H. Li

Temperature and Precipitation Diversely Control Seasonal and Annual Dynamics of Litterfall in a Temperate Mixed Mature Forest, Revealed by Long-Term Data Analysis

C. G. Wang¹ , X. B. Zheng², A. Z. Wang² , G. H. Dai² , B. K. Zhu³, Y. M. Zhao³, S. J. Dong³, W. Z. Zu³, W. Wang³, Y. G. Zheng³, J. G. Li³, and M.-H. Li^{1,4,5}

¹Key Laboratory of Geographical Processes and Ecological Security in Changbai Mountains, Ministry of Education, School of Geographical Sciences, Northeast Normal University, Changchun, China, ²Research Station of Changbai Mountain Forest Ecosystems, Chinese Academy of Sciences, Antu, China, ³Natural Conservation Management Center, Changbai Mountain Protection and Development Zone, Antu, China, ⁴Swiss Federal Research Institute WSL, Birmensdorf, Switzerland, ⁵Erguna Forest-Steppe Ecotone Research Station, CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, China

Abstract Litterfall is a good indicator of overall forest functions in forest ecosystems. Globally, forest litterfall has been extensively investigated, however, there is a lack of long-term data analysis to show the various litterfall components in relation to environmental factors on the monthly and yearly scales. Here, monthly (May–October) and annual (1981–2018) litterfall including leaves, twigs, bark, reproductive, and miscellaneous fractions were collected in a mixed mature *Pinus koraiensis* forest on Changbai Mountain in Northeast, China, across 30 years. Based on these long-term litterfall data, we analyzed the seasonal and annual variations in different litterfall fractions and the internal/external drivers. We observed that both the leaf and total litterfall exhibited a strong, similar seasonal pattern, with the highest levels between September and October, and the annual litterfall had an “S-shaped” increasing pattern from 1981 to 2018. The other litterfall fractions showed distinct monthly and yearly fluctuations across the 30 years. Mean monthly evapotranspiration and temperature (minimum and maximum) were the best predictors for monthly litterfall. By contrast, the models that best predicted the annual litterfall production included mean annual precipitation and mean monthly precipitation and temperature in May and October. Our study, using a unique dataset of detailed long-term litterfall dynamics, has potentially major significance for enhancing our understanding of the role of climatic factors controlling forest litterfall amount and seasonality in temperate mixed mature forests. This insight is of paramount importance for modeling and estimating soil carbon sequestration and nutrient cycling of temperate forests under climate change.

Plain Language Summary Forest litterfall is very important for nutrient cycling in forest ecosystems. Many researchers have studied forest litterfall, but still, there is an obvious lack of long-term data analysis to show the relationships between forest litterfall and environmental factors. In this study, we analyzed the monthly and annual litterfalls of various components (leaf, reproductive, twig, bark, and miscellaneous litterfall) collected over 30 years in a mixed broad-leaved *Pinus koraiensis* old-growth forest on Changbai Mountain in northeastern China, in relation to climatic factors. We found that the highest monthly values of both leaf and total litterfall occurred during September–October, and the annual litterfall of all components had an increasing trend from 1981 to 2018. The monthly litterfall was strongly influenced by the mean monthly evapotranspiration and temperature (minimum and maximum). The annual litterfall was mainly influenced by the mean annual precipitation, mean monthly precipitation, and temperature in May and October. These long-term data based findings have important implications for better understanding the role of climatic factors on forest litterfall dynamics under climate change.

1. Introduction

The fall of leaves is considered to be an essential survival strategy of trees when their environmental growth conditions get unfavorable for net primary production, such as colder temperature or soil drought by strong solar radiation of sunny days (Erkan et al., 2018; Rowland et al., 2018; Zhu et al., 2021). A great deal of

organic matter and mineral elements are transferred through leaf litterfall from the aboveground vegetation to the soil surface in forest ecosystems (Liu et al., 2004; Nakagawa et al., 2019). To some extent, leaf litterfall production plays a key role in determining the dynamic of forest ecosystems, carbon and nutrient cycling, and ultimately forest productivity (Li et al., 2010; Zhou et al., 2007). Forest litterfall involves leaf litterfall and other important components including reproductive organs (flowers and fruits) and woody materials (bark and twigs). The production patterns of these litterfall parts are also used as good indicators of overall forest function such as carbon allocation to photosynthesizing tissues and reproductive organs in forest ecosystems (Rowland et al., 2018). However, very little information is available on the dynamics of forest reproductive and woody litterfall fractions (Bhatti & Jassal, 2014). Thus, investigating all types of aboveground litterfall allows us to gain important insight into the determinants of seasonal and inter-annual variations in litterfall production of forest ecosystems (Portillo-Estrada et al., 2013).

Integrated Biosphere Simulator, a comprehensive model of the global simulations of water, carbon balance, and vegetation structure, assumes that litterfall distributes evenly throughout the entire year, but this assumption is obviously inconsistent with numerous field observations (Kucharik et al., 2000; Ryan & Law, 2005). Globally, various seasonal patterns of litterfall production such as unimodal, bimodal, multimodal, or irregular modes are observed in forest ecosystems (Zhang et al., 2014). The variability of forest litterfall results in large uncertainties in the estimation of forest carbon cycling (Leff et al., 2012; Zhang et al., 2014). Furthermore, numerous previous studies have shown significant variations in the inter-annual patterns of litterfall production among or within forest ecosystems (Bhatti & Jassal, 2014; Zhou et al., 2007). For example, pine forest (pioneer community) in the subtropical zone has the lowest mean annual litterfall, but a rapidly increased rate of litterfall production with time. In contrast, evergreen broadleaved forest (regional climax) had a relatively stable litterfall production over the observation period of 1982–2001 (Zhou et al., 2007). Thus, the magnitude and change direction (e.g., increase or decrease) of annual litterfall production of forest stand greatly depend on their successional stages (Souza et al., 2019; Zhou et al., 2014). Moreover, the seasonal and annual periodicity in abiotic climatic variables such as rainfall and temperature leads to the variation in litterfall production at the forest community level. However, it is challenging to accurately evaluate the relationships between forest litterfall production and climatic conditions due to the large intra- and inter-annual variability of both litterfall and climatic conditions. Litterfall studies in the temperate zone have demonstrated that forests that experience seasonal changes in climate also experience seasonal changes in leaf flushing and litterfall (An et al., 2020; Li et al., 2010). Indeed, the evaluation of forest litterfall characteristics can be achieved with extensive within-site sampling over the long-term period, and the effect of climatic variability can also be assessed after isolating the seasonality of litterfall production patterns (Andivia et al., 2018; Kouki & Hokkanen, 1992). This will tremendously improve predictive models of global carbon dynamics and allow greater preparedness for the consequences of climate change.

Leaves are the active interface of carbon, energy, and water exchange between forest canopies and the atmosphere (Caritat et al., 2006). Thus, the changes in global climate including atmospheric CO₂ level, temperature, and precipitation patterns are expected to strongly influence litterfall production in forest ecosystems. Rising atmospheric CO₂ concentration generally stimulates photosynthesis and aboveground net primary productivity, leading to greater litterfall production in forest ecosystems (Liu et al., 2005). Temperature and moisture are external physical inputs that affect tree growth and leaf productivity (Allen et al., 2010; Neumann et al., 2017; Peng et al., 2011). But the effects of temperature and water on forest litterfall are not only dependent on the annual mean temperature and precipitation but also on the distribution of temperature and precipitation over the year and on a balanced supply of heat and water, especially in the growing season (Andivia et al., 2018; Liu et al., 2004). Moreover, some of the variability in forest litterfall production has been casually associated with extreme weather events such as severe drought, chilling, or winds (Lv et al., 2013; Staelens et al., 2003). Although these events undoubtedly cause substantial litterfall, there has been little quantification of the actual relationships between forest litterfall production and extreme weather fluctuations. Therefore, it is needed to investigate the effects of various climatic variables - single or in the combination of multiple factors - on forest litterfall production at the monthly and yearly scales, to better understand the process of litterfall production.

The mixed mature *Pinus koraiensis* forest (>200 years) is the representatively regional climax community in Changbai Mountains in northeastern China. This forest ecosystem functions as an important carbon sink

because of its high growth rate and its significant role in carbon sequestration (Fang et al., 2001). In recent decades, the Changbai Mountain region has been identified as a primary hotspot particularly vulnerable to the impacts of climate change. Scenarios for future climate change predict the increasing temperature and decreasing precipitation in Changbai Mountains (Dai et al., 2013; Zheng et al., 2017). Although seasonal and annual variation in litterfall biomass in Changbai Mountains has long been recognized, the roles of climatic factors influencing litterfall amount and seasonality are little known (Liu et al., 2009; Zhou et al., 2014). Here, we used 30 years of data of monthly and annually litterfall collected in mixed *P. koraiensis* old-growth forest, to determine the temporal trends (monthly and annual) on the production of various litterfall components and quantify the effects of climatic variables on different litterfall fraction production on both monthly and annual scales. We hypothesize that (a) the monthly litterfall production peaks in autumn and the annual litterfall production remains relatively stable along with the year in the climax forest; (b) in a relatively stable climax forest, climatic variables play a most important role in determining the litterfall production on both monthly and annual scales.

2. Materials and Methods

2.1. Study Area

The study site (42°24'N, 127°47'E) was located in the Changbai Mountain Nature Reserve in Jilin province, northeastern China. The Reserve has a typical temperate, continental climate, with windy springs, cool and short summers, foggy autumns, as well as long and cold winters. According to climate data (1981–2018) collected at 738 m above sea level, mean annual precipitation is about 708 mm, of which nearly 70%–80% falls during the growing season (May–October). The mean annual air temperature is 3.5 °C, with the highest and lowest monthly mean temperatures occurring in August (20.5 °C) and January (−16.5 °C), respectively. The soil in this area is developed from volcanic ash and classified as Eutric cambisol (FAO classification), with high organic matter in the surface layer. The mixed *P. koraiensis* old growth forest with broad-leaved trees distributes from 500 to 1,100 m above sea level. The mean canopy height and diameter at breast height are 18.6 m and 31.8 cm in 2015, respectively. The dominant tree species in the mixed forest were *P. koraiensis*, *Fraxinus mandschurica*, *Acer mono*, *Quercus mongolica*, and *Tilia amurensis*. The dominant shrub species were *Corylus mandshurica*, *Philadelphus schrenkii*, *Euonymus alatus*, and *Lonicera japonica*; the main herb species include *Anemone raddeana*, *A. cathayensis*, *Cyperus microiria*, and *Funaria officinalis*.

2.2. Sampling Method and Data Collection

Ten litterfall traps (1 × 1 m each) constructed of 1 mm mesh nylon net attached to a plastic frame were randomly located (a height of 1 m above ground surface) in a 10,000 m² (100 × 100 m) long-term forest research plot (42°24'N, 128°05'E, 740 m above sea level) within a mixed *P. koraiensis* old-growth forest on Changbai Mountain. The distance between any two litterfall traps was not less than 20 m. Litterfall was retrieved monthly during the growing season (May–October). The non-growing season litterfall (November–April) was collected in April. We classified the growing season into three periods as early- (May–June), mid- (July–August), and late-season (September–October). The litterfall was separated into leaves (foliar litterfall of *P. koraiensis* and broadleaf tree species), reproductive fraction and twigs (including twig and bark), and miscellaneous components were not recorded from 1981 to 2002. Since 2003, the litterfall collected was separated into five main components: leaves, twigs, bark, a reproductive fraction (catkins, bracts, flowers, and seeds), and a miscellaneous fraction (lichens, mosses, and unidentifiable fractions). The cones of *P. koraiensis* were not included in the reproductive fraction, because they were always picked by animals (such as squirrels) and local inhabitants to get the seeds as food. After separation of litterfall, each fraction was dried at 60 °C to a constant mass and weighed. The data from all litterfall traps were averaged to generate an estimate for each sampling time. Annual litterfall data are available from 1981 to 2018 (30 years, no data available for 1986, 1987, 1989, 1991, 1996, 1998, 1999, and 2000), and monthly litterfall data are available after 2003 (June–October in 2003 and April–October from 2004 to 2018) covering a period of 110 months. Mean monthly litterfall production in a year was summed to represent the litterfall production per year (2003–2018).

Climate data were obtained from the meteorological observation field (738 m above sea level; 1981–2018) of the Changbai Mountain forest ecosystems research station, Institute of Applied Ecology, Chinese Academy of Sciences. Climatic variables on the monthly scale included mean monthly evapotranspiration (MME, mm month^{-1}), mean monthly precipitation (MMP, mm), mean monthly temperature (MMT, $^{\circ}\text{C}$), mean monthly maximum temperature (MMT_{max} , $^{\circ}\text{C}$), mean monthly minimum temperature (MMT_{min} , $^{\circ}\text{C}$), mean monthly wind speed (MMW, m s^{-1}). Climatic variables on the annual scale are mean annual evapotranspiration (MAE, mm year^{-1}), mean annual precipitation (MAP, mm), mean monthly precipitation in May, August, and October (MMP_{may} , MMP_{aug} , and MMP_{oct} , mm), mean annual temperature (MAT, $^{\circ}\text{C}$), mean annual maximum temperature (MAT_{max} , $^{\circ}\text{C}$), mean annual minimum temperature (MAT_{min} , $^{\circ}\text{C}$), mean monthly temperature in May, August, and October (MMT_{may} , MMT_{aug} , and MMT_{oct} , $^{\circ}\text{C}$) and mean annual wind speed (MAW, m s^{-1}). In this study, the mean annual atmospheric CO_2 concentration (ppm) used was the global annual average of CO_2 level collected from the NOAA Earth System Research Laboratory (ESRL) network.

2.3. Data Analysis

We chose to fit generalized additive mixed models (GAMMs) to characterize temporal trends (intra- and inter-annual) of litterfall production (*gamm* function in the R package *mgcv*). GAMMs were appropriate for capturing the nonlinear nature of litterfall changes over time. For analysis of the monthly data, month and year were included as the fixed factors in the model, with a Gaussian distribution with an identity link. The seasonal and annual trends of litterfall production and climatic variables were removed using the *diff* function of the R package *forecast* (Rowland et al., 2018). Then the multimodel inference approach (MIA) was used to estimate the effect of each climatic factor on each litterfall fraction production. MIA provides more stable and reliable inference results based on a set of best models than the traditional statistical inference that makes inferences based on one single best model (Burnham & Anderson, 2002). For each fraction of litterfall production on the monthly basis, a generalized linear model was constructed with MME, MMP, MMT, MMT_{max} , MMT_{min} , and MMW as predictive variables. For each fraction of litterfall on the yearly basis, CO_2 , MAE, MAP, MMP_{may} , MMP_{aug} , MAT, MAT_{max} , MAT_{min} , MMT_{may} , MMT_{aug} , and MAW were included in the generalized linear model for predicting the annual litterfall production. The values of litterfall and climatic indices were standardized with the *range* method of *preProcess* function in the R package *caret*. We applied the variance inflation factor ($\text{VIF} < 10$) with the *vif* function to identify multicollinearity among the variables involved in the generalized linear model. Accordingly, MMT_{max} and MMT_{min} were retained in the generalized linear model (Figure S1). All possible combinations of models with various subsets of predictors were compared to determine the best-fit model, which had the lowest corrected Akaike Information Criterion (AICc; *dredge* function in the R package *MuMIn*) (Barton, 2013). A summed Akaike weight for each predictor variable was estimated from the subset of best models with AIC values of < 2 using the *importance* and *subset* function. Akaike weight could indicate the relative variable importance in predicting the response. The important explanatory variable was defined as a predictor with an Akaike weight of > 0.50 (Burnham & Anderson, 2002). Furthermore, we applied a linear mixed model to estimate the proportion of variance in leaf, reproductive, twig, bark, miscellaneous, and total litterfall production explained by sampling years, sampling months, and litterfall traps using the *lmer* function in the R package *lme4*. A generalized additive model was used to determine the relationships of annual leaf, reproductive, twig, and total litterfall production with the total basal area ($\text{m}^2 \text{ha}^{-1}$) of the mixed old-growth forest. We used one-way ANOVAs to explore differences in litterfall production between the growing season (May–October) and non-growing season (November–April).

3. Results

3.1. Patterns in Seasonal and Annual Dynamics of Litterfall Production

The relative abundance of each litterfall component showed strong seasonal variability over the period 2003–2018 (Figure 1a). Leaf litter formed the major fraction, representing $47 \pm 12\%$ (mean $\pm$ SE) of the total litterfall production between May and October, with a peak of 86% in October (Figure 1a). The fall of bark and twig production occurred mainly during the non-growing season (November–April), whereas the leaf litter occurred mainly during the growing season (May–October) (Figure S2). The peak of reproductive (33%) in July and miscellaneous litterfall production (24%) appeared in August, respectively (Figure 1a). On

Figure 1. Monthly (a) and annual (b) variation in the relative abundance of leaf litterfall, reproductive litterfall, twig litterfall, bark litterfall, miscellaneous litterfall production in a mixed mature *P. koraiensis* forest in Changbai Mountains. *Note.* the nongrowing season litterfall (November–April) was collected in April.

average, bark, twig, reproductive, and miscellaneous litterfall production accounted for $8 \pm 2\%$, $20 \pm 5\%$, $15 \pm 4\%$, and $14 \pm 3\%$ of the total litterfall production, respectively (Figure 1a). Moreover, there were annual fluctuations in the composition of litterfall production over the period 2003–2018, with increased trends in twig and bark litterfall production and a decreased trend in leaf litterfall production (Figure 1b).

The seasonal trend of the litterfall fractions was independent of the annual amplitude over the period 2003–2018 (Figure 2). The production of leaf and total litterfall exhibited a strong and similar seasonal pattern, with the highest levels observed in the late growing season (September to October) and lowest values in the early and middle growing season (Figures 2a and 2f). Reproductive litterfall production showed two distinct peaks occurring in July and September, respectively (Figure 2b). Twig and bark litterfall production sharply decreased from the early growing season and consistently remained at low levels during May–October (Figures 2c and 2d). In contrast, the two peaks of miscellaneous litterfall production occurred in the early and mid growing season, respectively (Figure 2e).

We observed that the annual leaf and total litterfall production showed an S-shaped increasing pattern over the period 2003–2018 (Figures 2a and 2f) and 1981–2018 (Figures 3a and 3d), with increasing stand age. Reproductive and twig litterfall production kept stable from 1981 to 2003, then increased and had a sharp peak occurred in the 2010s (Figures 2b, 2c, 3b and 3c). Furthermore, both bark and miscellaneous litterfall production exhibited a wavelike increasing tendency over the period 2003–2018 (Figures 2d and 2e). Compared to the large seasonal and annual variations of the litterfall production, less variation among traps was observed in this forest studied (Table S1).

3.2. Relationships Between Monthly Litterfall Production and Climatic Variables

There were diverse variables retained in the average best-fitting models for the six litterfall components, indicating contrasting drivers on the monthly litterfall production (Table 1). Both leaf and the total litterfall production were similarly positively associated with MMT_{max} , but negatively with MME, MMP, and MMT_{min} (Table 1). Reproductive litterfall production increased with MME, MMP, MMT_{max} , and MMT_{min} , but decreased with MMW. Twig and miscellaneous litterfall production decreased with MMT_{max} but increased with MME, MMP, MMT_{min} , and MMW. Bark litterfall production was positively correlated with MME, MMP, and MMT_{min} , but negatively correlated with MMT_{max} (Table 1).

The relative variable importance of predictors differed among litterfall components (Table 1). MME and MMT_{max} were the best predictors for leaf, twig, bark, and total litterfall production based on their relative importance. All models included MMP, but MMP was the most important factor determining the miscellaneous litterfall production. MMT_{min} was very important for predicting leaf, bark, and total litterfall

Figure 2. Trends of annual (2003–2018) and monthly (April–October) leaf litterfall (a), reproductive litterfall (b), twig litterfall (c), bark litterfall (d), miscellaneous litterfall (e), and total litterfall production (f) in a mixed mature *P. koraiensis* forest in Changbai Mountains. The total litterfall here includes leaf, reproductive, twig, bark, and miscellaneous litterfall.

production. Twig litterfall production was more susceptible to wind speed than the other litterfall fractions (Table 1).

3.3. Relationships Between Annual Litterfall Production and Climatic Variables

The best-fitting models for the annual leaf litterfall production included MAP, MMP_{may} , MMP_{oct} , MAT_{max} , MMT_{may} , MMT_{oct} , and MAW (Table 2). The MMP_{oct} and MMT_{may} were the best predictors based on their relative importance. The models that best predicted the annual reproductive litterfall production included MAP, MMP_{may} , MMP_{aug} , MMP_{oct} , MAT_{max} , MAT_{min} , and MMT_{may} . Additionally, MAP was included in

Figure 3. Trends of annual (1981–2018) leaf litterfall (a), reproductive litterfall (b), twig litterfall (c), and total litterfall production (d) in a mixed mature *Pinus koraiensis* forest in Changbai Mountain. Gray areas indicate 95% confidence intervals of generalized additive mixed models. Total litterfall here includes leaf, reproductive, and twig litterfall.

most of the models. The annual twig litterfall production was best fitted by models that included MAP, MAT, MAT_{max}, MMT_{may}, MMT_{oct}, and MAW as predictor variables. The annual total litterfall production was best fitted by models that included MAP, MMP_{may}, MMP_{oct}, MAT_{max}, and MMT_{oct} (Table 2). Both CO₂ and MAE had no significant effect on the six litterfall component production at the year level. Moreover, we

Table 1

Generalized Linear Model Coefficient Estimated From the Average Best-Fitting Models (Conditional Average), Predicting the Monthly Litterfall Production in a Mixed Mature *P. koraiensis* Forest in Changbai Mountains (June–October in 2003 and April–October From 2004 to 2018)

	Leaf litterfall	Reproductive litterfall	Twig litterfall	Bark litterfall	Miscellaneous litterfall	Total litterfall
MME	−0.96*** (1.00, 2)	0.04 (0.12, 1)	0.37** (1.00, 4)	0.32*** (1.00, 2)	0.14 (0.34, 3)	−0.90*** (1.00, 3)
MMP	−0.14 (0.45, 1)	0.04 (0.12, 1)	0.13 (0.47, 2)	0.04 (0.27, 1)	0.19 (0.85, 6)	−0.11 (0.28, 1)
MMT _{max}	1.46*** (1.00, 2)	0.10 (0.18, 1)	−0.65*** (1.00, 4)	−0.66*** (1.00, 2)	−0.19 (0.09, 1)	1.36*** (1.00, 3)
MMT _{min}	−0.72*** (1.00, 2)	0.02 (0.12, 1)	0.11 (0.38, 2)	0.14 (1.00, 2)	0.04 (0.09, 1)	−0.75*** (1.00, 3)
MMW	-	−0.09 (0.16, 1)	0.22* (1.00, 4)	-	0.18 (0.45, 3)	0.09 (0.22, 1)
Intercept	0.50	0.46	0.64	0.68	0.33	0.49

Note. Significant results are marked with asterisks (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Non-significant results are shown if they are retained in the model. The numbers in the bracket are the relative importance of explanatory variables in the best models and the number of the best models, respectively. Bold values are greater than 0.50, indicating important explanatory variables.

Abbreviations: MME, mean monthly evapotranspiration; MMP, mean monthly precipitation; MMT_{max}, mean monthly maximum temperature; MMT_{min}, mean monthly minimum temperature; MMW, mean monthly wind speed.

Table 2

Generalized Linear Model Coefficient Estimated From the Average Best-Fitting Models (Conditional Average), Predicting the Annual Litterfall Production in a Mixed Mature *P. koraiensis* Forest in Changbai Mountains (1981–2018)

	MAP	MMP _{may}	MMP _{aug}	MMP _{oct}	MAT	MAT _{max}	MAT _{min}	MMT _{may}	MMT _{oct}	MAW	Intercept
Leaf litterfall	−0.12 (0.08, 1)	−0.19 (0.17, 2)		−0.37** (1.00, 8)		−0.28 (0.30, 2)		0.30* (0.92, 7)	0.18 (0.24, 2)	0.18 (0.12, 1)	0.56
Reproductive litterfall	0.38 (0.67, 7)	−0.38 (0.11, 1)	0.32 (0.31, 3)	0.19 (0.15, 2)		0.26 (0.07, 1)	0.21 (0.07, 1)	−0.34 (0.21, 2)			0.33
Twig litterfall	−0.57*** (1.00, 2)				0.54*** (1.00, 2)	−0.62** (1.00, 2)		−0.20 (0.54, 2)	0.55*** (1.00, 2)	−0.34* (1.00, 2)	0.76
Total litterfall	−0.17 (0.14, 1)	−0.19 (0.29, 1)		−0.45** (1.00, 6)		−0.26 (0.15, 1)			0.32 (0.76, 4)		0.55

Note. Significant results are marked with asterisks (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Non-significant results are shown if they are retained in the model. The numbers in the bracket are the relative importance of explanatory variables in the best models and the number of the best models, respectively. Bold values are greater than 0.50, indicating important explanatory variables.

Abbreviations: MAP, mean annual precipitation; MMP_{may}, mean monthly precipitation in May; MMP_{aug}, mean monthly precipitation in August; MMP_{oct}, mean monthly precipitation in October; MAT, mean annual temperature; MAT_{max}, mean annual maximum temperature; MMT_{min}, mean annual minimum temperature; MMT_{may}, mean monthly temperature in May; MMT_{oct}, mean monthly temperature in October; MAW, mean annual wind speed.

observed that the annual leaf and total litterfall production non-linearly increased with the total basal area of the mixed old-growth forest (Figures S3a and S3d).

4. Discussion

4.1. Seasonal and Annual Dynamics of Litterfall Production and Its Components

Using our long-term data on litterfall dynamics, we observed that the six litterfall components (leaf, reproductive, twig, bark, and miscellaneous litterfall, and the total litterfall production) showed various seasonal dynamics patterns from May to October in a mixed mature *P. koraiensis* forest on Changbai Mountain. The bulk of leaf litterfall production occurred in autumn (September and October) in this study, this partly supports our first hypothesis and is consistent with results gained in most of the temperate forests in the northern hemisphere (Zhang et al., 2014). Total litterfall production also exhibited a similar seasonal pattern with a major peak in autumn, which is tightly determined by leaf litterfall production (approximately 43% of the total litterfall amount). The winter-deciduous habit of many broad-leaved tree species (such as *F. mandschurica*, *A. mono*, and *T. amurensis*) is responsible for the peak leaf litterfall during the late growing season in this mixed mature forest on Changbai Mountain. Leaves in temperate broadleaf forests experience natural senescence in autumn when conditions get unfavorable for the net primary production (e.g., colder temperature and less light) (Zhang et al., 2014). Although new needles of evergreen conifers (e.g., *P. koraiensis* in this mixed mature forest) are produced in spring and old needles are shed during the whole year, needle litterfall of *P. koraiensis* also demonstrate a distinctly seasonal pattern, reaching its maximum values in autumn (Li et al., 2010). Therefore, needles of evergreen conifer forests in the temperate biome perhaps experience similar natural senescence in autumn (Bray & Gorham, 1964; Jeong et al., 2009).

We found that the reproductive litterfall production was bimodal with peaking July and September in this mixed forest, which was inconsistent with the prediction in the first hypothesis. A previous study conducted in this area indicated that the flowering phenology among tree species is almost synchronous, with a flowering peak in May, and the average duration of flowering lasts about four weeks, thereafter, flowers largely drop as litterfall from June to July (Wang et al., 2014). Additionally, wind-dispersed tree species such as *F. mandschurica* complete their seed dispersal in summer (e.g., July), while seed rains of animal-dispersed tree species such as *Q. mongolica* generally appear in autumn (e.g., September) (An et al., 2020; Qian et al., 2019; Wang et al., 2014). Hence, the bimodal patterns of reproductive litterfall production in this study are partly attributed to the two contrasting spatial distributions of seed dispersal (wind-dispersed models vs. animal-dispersed models). Similarly, it is found that the mass of reproductive litterfall in a Brazilian tropical

dry forest was determined by the dispersal syndromes of the tree species (Souza et al., 2019). Our results showed that the overall contribution of reproductive parts to total litterfall production was ~15%, which is similar to the value of ~16% found in *Q. ilex* forest in the Mediterranean region (Bou et al., 2015). Globally, the contribution of reproductive parts to total litterfall production is dramatically discrepant across various forest types. For example, the values range from 3% to 23% in tropical and subtropical forests (Nakagawa et al., 2019; Rowland et al., 2018; Yhou et al., 2007) and from <1% to 22% in temperate and Mediterranean forests (Bou et al., 2015; Caritat et al., 2006; Jeong et al., 2009). Several previous studies suggest that tree age is the strongest predictor of seed productions (Davi et al., 2016; Pesendorfer et al., 2020; Viglas et al., 2013). Trees increase the carbon allocation to reproductive structures once the age of peak growth has been surpassed (Genet et al., 2009; Hirayama et al., 2008). Meanwhile, the proportion of flowers and fruit in total litterfall of the climax communities is much greater than those of earlier successional communities (Zhou et al., 2007). Thus, substantial investment in carbon allocation of trees to reproductive structures is beneficial for producing offspring in our temperate old-growth forest.

Although the woody litterfall (twigs and barks) production occurred mainly during the nongrowing season from November to April (Figure S2), during the growing season it had higher values in May and August (Figure 1a). The new branches are sprouting during early spring, which can increase the bark litterfall as they grow and increase their diameter. Like other litterfall fractions, the proportion of woody litterfall fractions within total litterfall intensively varied with season. This is very important as the fractional composition of litterfall directly determines which type of litter is added to the forest soil in every period of the year (Portillo-Estrada et al., 2013; Staelens et al., 2011). Nevertheless, the pattern of shedding of woody material from tree crowns is complicated by endogenous processes affecting the rate of senescence and abscission of twigs and by environmental factors such as wind activity in particular (Pook et al., 1997). In our study, bark accounted for 8% of the total litterfall production in this temperate forest on Changbai Mountain, however, the corresponding value is only 0.6% in a subtropical evergreen broadleaved forest (Zhou et al., 2007). Our results indicated that, except for leaves, the woody litterfalls such as bark and twig are not negligible, especially for the nongrowing season, and must be considered in future litterfall studies.

Our study indicated that leaf litterfall production significantly increased over the 30-year period from 1981 to 2018 in the mixed mature forest, a zonal climax forest on Changbai Mountain. Due to the dominance of the leaf litterfall component during the growing season, the total litterfall production showed an S-shaped increasing annual pattern in spite of various temporal trends of other litterfall components, and the litterfall production showed an S-shaped relationship with the total basal area, indicating a basal area-related litterfall production in the old-growth forest studied. Such an S-shaped pattern of litterfall production may also be supported by an S-shaped change in tree size, wood biomass, and forest floor depth found in the old-growth Douglas-fir/western hemlock forests (Spies, 1998; Spies & Franklin, 1988). Tree growth and biomass have a slow increasing phase at first, then a rapid increasing phase until reaching the maximum growth rate, followed by a decreasing phase (Nakagawa et al., 2019; Spies, 1998; Spies & Franklin, 1988). The present study, for the first time, revealed a basal area-related litterfall production pattern over a long-term period and suggests that, even in old-growth or climax forests, the litterfall production is not stable.

The annual mean total litterfall production of 4.57 Mg ha^{-1} (1981–2018) is within the range of 3.78 to 6.00 Mg ha^{-1} reported for temperate forests (Jia et al., 2017; Zhang et al., 2014), but higher than the values of 3.92 Mg ha^{-1} in 2008 (Yuan et al., 2010) and 4.02 Mg ha^{-1} from 1980 to 2007 (Li et al., 2010), and lower than the values of 4.90 Mg ha^{-1} in 2003/2004 (Liu et al., 2009) and 4.86 Mg ha^{-1} in 2011/2012 (Zhou et al., 2014) measured in the same forest. The various average annual litterfall production estimated in the same stand suggests the importance of long-term studies on litterfall production. A recent meta-analysis has revealed that most litterfall sampling duration is one year, and even the longest observation is 19 years only (Jia et al., 2017). For instance, tree twigs and bark are retained for years to decades, and short-term studies over periods of just a few years may fail to capture their actual production rates (Bhatti & Jassal, 2014). The litterfall production across a 30-years period in the present study showed high year-to-year variation and increased gradually as the forest aged. In contrast, many previous studies using a space-for-time substitution approach indicated that forest litterfall production significantly decreased or did not change with increased stand age in forests (Berg et al., 1999; Erkan et al., 2018; Starr et al., 2005). Therefore, our study suggests

that litterfall studies require long-term data involving all types of aboveground litterfall to better or fully understand the forest dynamics and carbon pathway of forest ecosystems under future climate changes.

4.2. Effects of Climatic Factors on Monthly and Annual Litterfall Production

It is well known that temperature is an important forcing factor affecting litterfall production in forest ecosystems (Berg & Meentemeyer, 2001; Caritat et al., 2006; Kitayama et al., 2020). Various empirical and regression models show that the forest litterfall is closely associated with mean annual temperature both at the global and regional scales (Shen et al., 2019). Here, our results indicate that both the minimum and maximum temperatures are very important for litterfall production than mean temperature, partly supporting our second hypothesis. This mixed mature forest on Changbai Mountain has a distinct seasonal climate characterized by low temperatures. Therefore, the minimum temperature may play a key role as a trigger for the initiation of leaf abscission in autumn (Allen et al., 2010; Neumann et al., 2017). We observed negative effects of minimum temperatures on monthly leaf and total litterfall production. Increasing minimum temperatures decrease litterfall production, with warm weather favoring meristem activity and photosynthesis through the expansion of the growing period (Körner, 2015). However, extremely high temperatures may cause physical damage to tree tissues and consequently lead to more litterfall production (Zhou et al., 2007), which are proved by the positive relationships of mean monthly maximum temperature with monthly leaf and total litterfall production. Unlike leaf litterfall, the twig litterfall production at the monthly and annual level significantly decreased with maximum temperature, indicating opposite sensitivities of leaf and twig litterfall to a higher temperature. Therefore, the influence of temperatures on litterfall production is addressed via minimum and maximum temperatures, which may be far beyond the normal limits for tree growth (Lv et al., 2013; Neumann et al., 2017). Furthermore, we found that local temperature conditions (such as the mean temperature during May and October) contribute to determining the annual change in leaf litterfall production. Warmer weather in spring has positive effects on forest leaf productivity (Körner, 2015), leading to higher leaf litterfall production. However, the mean temperature during August did not feature in all models, suggesting it is not responsible for the patterns of annual litterfall production. These results with the specific role of temperature on litterfall production will have important implications for studying forest carbon cycle processes.

We observed negative relationships of monthly and annual leaf and total litterfall production with mean monthly and annual precipitation, as well as mean precipitation during May and October. Many processes controlled by precipitation strongly influence litterfall production (Bhatti & Jassal, 2014; Liu et al., 2004). For example, drought stress due to decreasing precipitation, particularly during the summer months, induces to increase the leaf litterfall production to reduce leaf water demand and thus conserve water resources (Andivia et al., 2018; Bhatti & Jassal, 2014). Litterfall was 10% higher in plots with reduced water availability compared to control plots in a rainfall-exclusion experiment (Liu et al., 2015). The negative effect of high precipitation on litterfall production is possible due to a higher number of cloudy days, lower radiation, and lower photosynthesis, and thus trees should have more leaves (then less leaf litterfall) to maintain productivity (Liu et al., 2004). Furthermore, reproductive litterfall production increases with precipitation, this may be related to the survival strategy of trees, because the increase in soil water availability is beneficial for the germination of the seeds and the growth of seedlings (Bou et al., 2015). In contrast, lower precipitation during the flowering period in May probably results in a massive falling of wilted flowers as reproductive litterfall. These results indicate that precipitation, like temperature, is also a main forcing climatic variable for forest litterfall production in the Changbai Mountain region.

The forest litterfall production is affected by a complex mix of climatic variables (Andivia et al., 2018; Berg & Laskowski, 2005). Actual evapotranspiration is a valuable, information-rich, and unique predictor in predicting litterfall as it expresses the combined effect of energy and water on ecological processes (Meentemeyer et al., 1982; Shen et al., 2019). At the global and regional scale, actual evapotranspiration is the most significant independent variable in the regression equation of total forest litterfall (Shen et al., 2019). Actual evapotranspiration alone is a superior predictor and can explain as much as 64% of the variation in coniferous forest litterfall on a European scale (Berg & Meentemeyer, 2001). In this study, we observed that the monthly leaf and total litter production was negative, and the reproductive, twig, bark, and miscellaneous litterfall production was positively correlated with evapotranspiration, a combined factor of temperature

and precipitation. Temperature and precipitation show interaction on forest litterfall production, as higher temperature alone triggers litterfall, whereas higher precipitation alone reduces it (Liu et al., 2004; Zhou et al., 2007). The effects of a relative increase in temperature combined with a relative decline in precipitation will inevitably lead to relatively higher litterfall production (Erkan et al., 2018), which can be used to validate and/or parametrize litterfall dynamics in forest ecosystem models.

Wind is a mechanical factor triggering litterfall shedding (Bou et al., 2015; Jonard et al., 2006). In this study, we observed increasing monthly twig litterfall production with increasing wind speed. Falling twigs were positively related to wind speeds during summer, but negatively related to wind speed during autumn and winter in a Mediterranean evergreen *Q. ilex* forest (Bou et al., 2015). The monthly twig litterfall production was found to be negatively correlated with wind speeds for *Kandelia obovate*, but positively correlated with wind speed for *Sonneratia apetala* in Futian, Shenzhen, China (Liu et al., 2014). The frequency distribution of wind speeds, the prevailing wind direction, and the vertical wind profile potentially influence the annual variation in the litterfall among tree species within a forest stand (Jonard et al., 2006; Portillo-Estrada et al., 2013). Thus, strong winds can underlie the continuous source of woody material (e.g., dead twigs) observed in forest litterfall production throughout a year, but a sustained wind can have similar effects (An et al., 2020; Christensen, 1975). Neglecting the effect of wind on litterfall production can be a serious bias, especially in the temperate broadleaf and mixed forests with a period of intensive leaf shedding, leading to an open canopy layer and thus more susceptible structure to wind influence (Jonard et al., 2006; Zhao, 1996). Current models do not explicitly incorporate the effects of variation in wind speed on forest litterfall production (Staelens et al., 2003). Hence, understanding the role of winds in controlling litterfall dynamics is of paramount importance for insight into the dynamics of forest ecosystems.

Mean annual atmospheric CO₂ concentration had no effect on the variability of annual litterfall production in the mixed mature forest studied. Similarly, elevated CO₂ did not affect annual litterfall production of three *Populus* spp. (Cotrufo et al., 2005). Differently, needle (*Pinus taeda*) and deciduous (*Liquidambar styraciflua*, *A. rubrum*, *Cercis Canadensis*, and *Cornus florida*) leaf litterfall production are significantly increased by the elevated CO₂, with an increment ranging from 4% to 22% (Finzi & Schlesinger, 2002; Norby et al., 2002). Elevated CO₂ generally stimulates photosynthesis and net primary production in short-term fumigations, however, this initial stimulation may become suppressed by excess carbohydrate or because nutrient supply is reduced as nutrients are increasingly immobilized by larger quantities of reduced quality litter (Liu et al., 2005). Therefore, the mechanisms underlying the diverse response patterns of litterfall to increasing CO₂ concentration warrant further exploration in global forest ecosystems.

5. Conclusions

In this study, we analyzed data collected in a temperate mature forest across 30 years and demonstrated that various climatic factors, mainly temperature, precipitation, and wind resulted in considerable variations in seasonal and annual litterfall production. Moreover, we identified temperature extremes (minimum and maximum temperatures) and precipitation as the central drivers of variability in litterfall production in that forest. These results have important implications for forest carbon cycle and productivity models because most of the models use simplified algorithms to simulate the litterfall production process. Incorporating climatic variables in those models may increase the accuracy of model predictions under climate change.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

All data used in this study are available from: <https://doi.org/10.5061/dryad.gmsbcc2ng>

Acknowledgments

The authors thank Lufu Zhao, Fenghua Wang, and Fuxian Liu for their assistance in the field and laboratory. This research was funded by the Natural Science Foundation of China, grant numbers 41971052 and 31500354.

References

- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., et al. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259(4), 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>
- An, J. Y., Han, S. H., Youn, W. B., Lee, S. I., Rahman, A., Dao, H. T. T., et al. (2020). Comparison of litterfall production in three forest types in Jeju Island, South Korea. *Journal of Forestry Research*, 31, 945–952. <https://doi.org/10.1007/s11676-019-00929-6>
- Andivia, E., Bou, J., Fernández, M., Caritat, A., Alejano, R., Vilar, L., & Vázquez-Piqué, J. (2018). Assessing the relative role of climate on litterfall in Mediterranean cork oak forests. *iForest: Biogeosciences and Forestry*, 11(6), 786–793. <https://doi.org/10.3832/ifer2825-011>
- Barton, K. (2013). *Package 'MuMIn' Version 1.43*.
- Berg, B., Albrektson, A., Berg, M. P., Cortina, J., Johansson, M.-B., Gallardo, A., et al. (1999). Amounts of litter fall in some pine forests in a European transect, in particular Scots pine. *Annals of Forest Science*, 56(8), 625–639. <https://doi.org/10.1051/forest:19990801>
- Berg, B., & Laskowski, R. (2005). Litter fall. *Advances in Ecological Research*, 38, 19–71.
- Berg, B., & Meentemeyer, V. (2001). Litter fall in some European coniferous forests as dependent on climate: A synthesis. *Canadian Journal of Forest Research*, 31(2), 292–301. <https://doi.org/10.1139/cjfr-31-2-292>
- Bhatti, J. S., & Jassal, R. S. (2014). Long term aboveground litterfall production in boreal jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) stands along the Boreal Forest Transect Case Study in western central Canada. *Écoscience*, 21(3–4), 301–314. [https://doi.org/10.2980/21-\(3-4\)-3699](https://doi.org/10.2980/21-(3-4)-3699)
- Bou, J., Compte, A., & Vilar, L. (2015). Litterfall and growth dynamics relationship with the meteorological variability in three forests in the Montseny natural park. *Folia Forestalia Polonica, Series A*, 57, 145–159. <https://doi.org/10.1515/ffp-2015-0015>
- Bray, J. R., & Gorham, E. (1964). Litter production in forests of the world. *Advances in Ecological Research*, 2, 101–157. [https://doi.org/10.1016/s0065-2504\(08\)60331-1](https://doi.org/10.1016/s0065-2504(08)60331-1)
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. Springer.
- Caritat, A., García-Berthou, E., Lapeña, R., & Vilar, L. (2006). Litter production in a *Quercus suber* forest of Montseny (NE Spain) and its relationship to meteorological conditions. *Annals of Forest Science*, 63(7), 791–800. <https://doi.org/10.1051/forest:2006061>
- Christensen, O. (1975). Wood litter fall in relation to abscission, environmental factors, and the decomposition cycle in a danish oak forest. *Oikos*, 26(2), 187–195. <https://doi.org/10.2307/3543708>
- Cotrufo, M. F., De Angelis, P., & Polle, A. (2005). Leaf litter production and decomposition in a poplar short-rotation coppice exposed to free air CO₂ enrichment (POPFACE). *Global Change Biology*, 11(6), 971–982. <https://doi.org/10.1111/j.1365-2486.2005.00958.x>
- Dai, L., Jia, J., Yu, D., Lewis, B. J., Zhou, L., Zhou, W., et al. (2013). Effects of climate change on biomass carbon sequestration in old-growth forest ecosystems on Changbai Mountain in Northeast China. *Forest Ecology and Management*, 300, 106–116. <https://doi.org/10.1016/j.foreco.2012.06.046>
- Davi, H., Cailleret, M., Restoux, G., Amm, A., Pichot, C., & Fady, B. (2016). Disentangling the factors driving tree reproduction. *Ecosphere*, 7(9), e01389. <https://doi.org/10.1002/ecs2.1389>
- Erkan, N., Comez, A., Aydin, A. C., Denli, O., & Erkan, S. (2018). Litterfall in relation to stand parameters and climatic factors in *Pinus brutia* forests in Turkey. *Scandinavian Journal of Forest Research*, 33(4), 338–346. <https://doi.org/10.1080/02827581.2017.1406135>
- Fang, J. Y., Chen, A. P., Peng, C. H., Zhao, S. Q., & Ci, L. J. (2001). Changes in forest biomass carbon storage in China between 1949 and 1998. *Science*, 292(5525), 2320–2322. <https://doi.org/10.1126/science.1058629>
- Finzi, A. C., & Schlesinger, W. H. (2002). Species control variation in litter decomposition in a pine forest exposed to elevated CO₂. *Global Change Biology*, 8(12), 1217–1229. <https://doi.org/10.1046/j.1365-2486.2002.00551.x>
- Genet, H., Bréda, N., & Dufrêne, E. (2009). Age-related variation in carbon allocation at tree and stand scales in beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) using a chronosequence approach. *Tree Physiology*, 30(2), 177–192. <https://doi.org/10.1093/treephys/tpp105>
- Hirayama, D., Nanami, S., Itoh, A., & Yamakura, T. (2008). Individual resource allocation to vegetative growth and reproduction in subgenus Cyclobalanopsis (*Quercus*, Fagaceae) trees. *Ecological Research*, 23(2), 451–458. <https://doi.org/10.1007/s11284-007-0398-4>
- Jeong, J., Kim, C., An, H.-C., Cho, H.-S., & Choo, G.-C. (2009). A comparison of litterfall dynamics in three coniferous plantations of identical age under similar site conditions. *Journal of Ecology and Field Biology*, 32(2), 97–102. <https://doi.org/10.5141/jefb.2009.32.2.097>
- Jia, B., Xu, Z., Zhou, G., & Yin, X. (2017). Statistical characteristics of forest litterfall in China. *Science China Life Sciences*, 61(3), 358–360. <https://doi.org/10.1007/s11427-016-9143-x>
- Jonard, M., Andre, F., & Ponette, Q. (2006). Modeling leaf dispersal in mixed hardwood forests using a ballistic approach. *Ecology*, 87(9), 2306–2318. [https://doi.org/10.1890/0012-9658\(2006\)87\[2306:MLDIMH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2306:MLDIMH]2.0.CO;2)
- Kitayama, K., Ushio, M., & Aiba, S.-I. (2020). Temperature is a dominant driver of distinct annual seasonality of leaf litter production of equatorial tropical rain forests. *Journal of Ecology*, 109, 727–736. <https://doi.org/10.1111/1365-2745.13500>
- Körner, C. (2015). Paradigm shift in plant growth control. *Current Opinion in Plant Biology*, 25, 107–114. <https://doi.org/10.1016/j.pbi.2015.05.003>
- Kouki, J., & Hokkanen, T. (1992). Long-term needle litterfall of a Scots pine *Pinus sylvestris* stand: Relation to temperature factors. *Oecologia*, 89(2), 176–181. <https://doi.org/10.1007/BF00317216>
- Kucharik, C. J., Foley, J. A., Delire, C., Fisher, V. A., Coe, M. T., Lenters, J. D., et al. (2000). Testing the performance of a dynamic global ecosystem model: Water balance, carbon balance, and vegetation structure. *Global Biogeochemical Cycles*, 14(3), 795–825. <https://doi.org/10.1029/1999GB001138>
- Leff, J. W., Wieder, W. R., Taylor, P. G., Townsend, A. R., Nemergut, D. R., Grandy, A. S., & Cleveland, C. C. (2012). Experimental litterfall manipulation drives large and rapid changes in soil carbon cycling in a wet tropical forest. *Global Change Biology*, 18(9), 2969–2979. <https://doi.org/10.1111/j.1365-2486.2012.02749.x>
- Li, X., Hu, Y., Han, S., Liu, Y., & Zhang, Y. (2010). Litterfall and litter chemistry change over time in an old-growth temperate forest, north-eastern China. *Annals of Forest Science*, 67, 1–206. <https://doi.org/10.1051/forest/2009099>
- Liu, C., Han, S., & Lin, L. (2009). Dynamic characteristics of litterfalls in four forest types of Changbai Mountains, China. *Chinese Journal of Ecology*, 28(1), 7–11.
- Liu, C., King, J. S., & Giardina, C. P. (2005). Effects of elevated concentrations of atmospheric CO₂ and tropospheric O₃ on leaf litter production and chemistry in trembling aspen and paper birch communities. *Tree Physiology*, 25(12), 1511–1522. <https://doi.org/10.1093/treephys/25.12.1511>
- Liu, C., Li, F., Yang, Q., Tam, N. F., Liao, W., & Zan, Q. (2014). Long-term differences in annual litter production between alien (*Sonneratia apetala*) and native (*Kandelia obovata*) mangrove species in Futian, Shenzhen, China. *Marine Pollution Bulletin*, 85(2), 747–753. <https://doi.org/10.1016/j.marpolbul.2014.04.047>

- Liu, C., Ogaya, R., Barbeta, A., Yang, X., & Peñuelas, J. (2015). Contrasting impacts of continuous moderate drought and episodic severe droughts on the aboveground-biomass increment and litterfall of three coexisting Mediterranean woody species. *Global Change Biology*, 21(11), 4196–4209. <https://doi.org/10.1111/gcb.13029>
- Liu, C., Westman, C. J., Berg, B., Kutsch, W., Wang, G. Z., Man, R., & Ilvesniemi, H. (2004). Variation in litterfall-climate relationships between coniferous and broadleaf forests in Eurasia. *Global Ecology and Biogeography*, 13(2), 105–114. <https://doi.org/10.1111/j.1466-882X.2004.00072.x>
- Lu, G. H., Zhou, G. S., & Wang, X. Y. (2013). Factors controlling litterfall production of forest in China. *Advanced Materials Research*, 726, 4248–4251. <https://doi.org/10.4028/www.scientific.net/AMR.726-731.4248>
- Meentemeyer, V., Box, E., & Thompson, R. (1982). World patterns and amounts of terrestrial plant litter production. *BioScience*, 32(2), 125–128. <https://doi.org/10.2307/1308565>
- Nakagawa, M., Ushio, M., Kume, T., & Nakashizuka, T. (2019). Seasonal and long-term patterns in litterfall in a Bornean tropical rainforest. *Ecological Research*, 34(1), 31–39. <https://doi.org/10.1111/1440-1703.1003>
- Neumann, M., Mues, V., Moreno, A., Hasenauer, H., & Seidl, R. (2017). Climate variability drives recent tree mortality in Europe. *Global Change Biology*, 23(11), 4788–4797. <https://doi.org/10.1111/gcb.13724>
- Norby, R. J., Hanson, P. J., O'Neill, E. G., Tschaplinski, T. J., Weltzin, J. F., Hansen, R. A., et al. (2002). Net primary productivity of a CO₂-enriched deciduous forest and the implications for carbon storage. *Ecological Applications*, 12(5), 1261–1266. <https://doi.org/10.2307/3099969>
- Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W., et al. (2011). A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change*, 1(9), 467–471. <https://doi.org/10.1038/nclimate1293>
- Pesendorfer, M. B., Bogdziewicz, M., Szymkowiak, J., Borowski, Z., Kantorowicz, W., Espelta, J. M., & Fernández-Martínez, M. (2020). Investigating the relationship between climate, stand age, and temporal trends in masting behavior of European forest trees. *Global Change Biology*, 26(3), 1654–1667. <https://doi.org/10.1111/gcb.14945>
- Pook, E., Gill, A., & Moore, P. (1997). Long-term variation of litter fall, canopy leaf area and flowering in a Eucalyptus maculata forest on the south coast of New South Wales. *Australian Journal of Botany*, 45(5), 737–755. <https://doi.org/10.1071/BT95063>
- Portillo-Estrada, M., Korhonen, J. F., Pihlatie, M., Pumpanen, J., Frumau, A. K., Morillas, L., et al. (2013). Inter- and intra-annual variations in canopy fine litterfall and carbon and nitrogen inputs to the forest floor in two European coniferous forests. *Annals of Forest Science*, 70(4), 367–379. <https://doi.org/10.1007/s13595-013-0273-0>
- Qian, D., Kuang, X., Wang, X., Lin, F., Yuan, Z., Ye, J., & Hao, Z. (2019). Spatio-temporal dynamics of woody plants seed rains in broad-leaved Korean pine mixed forest in Changbai Mountains from 2006 to 2017, China. *Journal of Applied Ecology*, 30(5), 1487–1493. <https://doi.org/10.13287/j.1001-9332.201905.012>
- Rowland, L., da Costa, A. C., Oliveira, A. A., Almeida, S. S., Ferreira, L. V., Malhi, Y., et al. (2018). Shock and stabilization following long-term drought in tropical forest from 15 years of litterfall dynamics. *Journal of Ecology*, 106(4), 1673–1682. <https://doi.org/10.1111/1365-2745.12931>
- Ryan, M. G., & Law, B. E. (2005). Interpreting, measuring, and modeling soil respiration. *Biogeochemistry*, 73(1), 3–27. <https://doi.org/10.1007/s10533-004-5167-7>
- Shen, G., Chen, D., Wu, Y., Liu, L., & Liu, C. (2019). Spatial patterns and estimates of global forest litterfall. *Ecosphere*, 10(2), e02587. <https://doi.org/10.1002/ecs2.2587>
- Souza, S. R., Veloso, M. D. M., Espírito-Santo, M. M., Silva, J. O., Sánchez-Azofeifa, A., Souza e Brito, B. G., & Fernandes, G. W. (2019). Litterfall dynamics along a successional gradient in a Brazilian tropical dry forest. *Forest Ecosystems*, 6(1), 35. <https://doi.org/10.1186/s40663-019-0194-y>
- Spies, T. A. (1998). Forest structure: A key to the ecosystem. *Northwest Science*, 72(2), 34–39.
- Spies, T. A., & Franklin, J. (1988). Old growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. *Natural Areas Journal*, 8(3), 190–201.
- Staelens, J., Nachtergale, L., De Schrijver, A., Vanhellefont, M., Wuyts, K., & Verheyen, K. (2011). Spatio-temporal litterfall dynamics in a 60-year-old mixed deciduous forest. *Annals of Forest Science*, 68(1), 89–98. <https://doi.org/10.1007/s13595-011-0010-5>
- Staelens, J., Nachtergale, L., Luyssaert, S., & Lust, N. (2003). A model of wind-influenced leaf litterfall in a mixed hardwood forest. *Canadian Journal of Forest Research*, 33(2), 201–209. <https://doi.org/10.1139/X02-174>
- Starr, M., Saarsalmi, A., Hokkanen, T., Merilä, P., & Helmsaari, H.-S. (2005). Models of litterfall production for Scots pine (*Pinus sylvestris* L.) in Finland using stand, site and climate factors. *Forest Ecology and Management*, 205, 215–225. <https://doi.org/10.1016/j.foreco.2004.10.047>
- Viglas, J. N., Brown, C. D., & Johnstone, J. F. (2013). Age and size effects on seed productivity of northern black spruce. *Canadian Journal of Forest Research*, 43(6), 534–543. <https://doi.org/10.1139/cjfr-2013-0022>
- Wang, Y., Shi, S., Lin, F., Yuan, Z., Ye, J., Wang, X., & Hao, Z. (2014). Reproductive traits and their correlation among woody plants in a broadleaf-Korean pine (*Pinus koraiensis*) mixed forest in Northeast China. *Chinese Science Bulletin*, 59(24), 2407–2415. <https://doi.org/10.1360/N972014-00278>
- Yuan, Z. Q., Li, B. H., Bai, X. J., Lin, F., Shi, S., Ye, J., et al. (2010). Composition and seasonal dynamics of litter falls in a broad-leaved Korean pine (*Pinus koraiensis*) mixed forest in Changbai Mountains, Northeast China. *Chinese Journal of Applied Ecology*, 21(9), 2171–2178.
- Zhang, H., Yuan, W., Dong, W., & Liu, S. (2014). Seasonal patterns of litterfall in forest ecosystem worldwide. *Ecological Complexity*, 20, 240–247. <https://doi.org/10.1016/j.ecocom.2014.01.003>
- Zhao, X. (1996). Effect of fallen tree on natural regeneration in Korean pine-deciduous mixed forest of Changbai Mountain. *Journal of Jilin Forestry University*, 11(4), 200–204.
- Zheng, J., Guo, R., Li, D., Zhang, J., & Han, S. (2017). Nitrogen addition, drought and mixture effects on litter decomposition and nitrogen immobilization in a temperate forest. *Plant and Soil*, 416(1–2), 165–179. <https://doi.org/10.1007/s11104-017-3202-4>
- Zhou, G., Guan, L., Wei, X., Zhang, D., Zhang, Q., Yan, J., et al. (2007). Litterfall production along successional and altitudinal gradients of subtropical monsoon evergreen broadleaved forests in Guangdong, China. *Plant Ecology*, 188(1), 77–89. <https://doi.org/10.1007/s11258-006-9149-9>
- Zhou, Y., Su, J. Q., Janssens, I. A., Zhou, G. S., & Xiao, C. W. (2014). Fine root and litterfall dynamics of three Korean pine (*Pinus koraiensis*) forests along an altitudinal gradient. *Plant and Soil*, 374, 19–32. <https://doi.org/10.1007/s11104-013-1816-8>
- Zhu, X., Zou, X., Lu, E., Deng, Y., Luo, Y., Chen, H., & Liu, W. (2021). Litterfall biomass and nutrient cycling in karst and nearby non-karst forests in tropical China: A 10-year comparison. *The Science of the Total Environment*, 758, 143619. <https://doi.org/10.1016/j.scitotenv.2020.143619>