Temperature and precipitation diversely control seasonal and annual dynamics of litterfall in a temperate mixed mature forest, revealed by long-term data analysis

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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

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 – 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 on the role of climatic factors controlling forest litterfall amount and seasonality in temperate mixed mature
forests. This insight is 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 the 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 through 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 stands 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 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., 2019; 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 the 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 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 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 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 (I) the monthly litterfall production peaks in autumn and the annual litterfall production remains relatively stable along with the year in the climax forest; (II) 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). Mean annual air temperature is 3.5 °C, with the highest and lowest monthly mean temperature occurring in August (20.5 °C) and January (-16.5 °C), respectively. 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 1100 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 m × 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 10000 m² (100 m × 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, reproductive fraction (catkins, bracts,
flowers and seeds) and 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
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

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 of 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, °C), mean monthly maximum temperature (MMT_{max}, °C), mean monthly
minimum temperature (MMT_{min}, °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, °C), mean annual maximum temperature (MAT_{max}, °C), mean annual
minimum temperature (MMT_{min}, °C), mean monthly temperature in May, August and
October (MMT_{may}, MMT_{aug} and MMT_{oct}, °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 non-linear 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 diff function of 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 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$\text{max}$, MMT$_{\text{min}}$ and MMW as predictive variables. For each fraction of litterfall on the yearly basis, CO$_2$, MAE, MAP, MMP$_{\text{may}}$, MMP$_{\text{aug}}$, MAT, MAT$_{\text{max}}$, MAT$_{\text{min}}$, MMT$_{\text{may}}$, MMT$_{\text{aug}}$ 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 range method of preProcess function in the R package caret. We applied the variance inflation factor (VIF < 10) with vif function to identify multicollinearity among the variables involved in the generalized linear model. Accordingly, MMT$_{\text{max}}$ and MMT$_{\text{min}}$ were retained in the generalized linear model (Fig. 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 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 lmer function in the R package lme4.
Generalized additive model was used to determine the relationships of annual leaf, reproductive, twig and total litterfall production with the total basal area (m² ha⁻¹) of the mixed old-growth forest. We used one-way ANOVAs to explore differences in litterfall production between 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 (Fig. 1a). Leaf litter formed the major fraction, representing 47 ± 12% (mean ± SE) of the total litterfall production between May and October, with a peak of 86% in October (Fig. 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) (Fig. S2). The peak of reproductive (33%) in July and miscellaneous litterfall production (24%) appeared in August, respectively (Fig. 1a). On average, bark, twig, reproductive and miscellaneous litterfall production accounted for 8 ± 2%, 20 ± 5%, 15 ± 4% and 14 ± 3% of the total litterfall production, respectively (Fig. 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 (Fig. 1b).
Fig. 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 non-growing season litterfall (Nov.-Apr.) was collected in April.
The seasonal trend of the litterfall fractions was independent of the annual amplitude over the period 2003 – 2018 (Fig. 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 (Fig. 2a, f). Reproductive litterfall production showed two distinct peaks occurring in July and September, respectively (Fig. 2b). Twig and bark litterfall production sharply decreased from the early growing season and consistently remained at low levels during May – October (Fig. 2c, d). In contrast, the two peaks of miscellaneous litterfall production occurred in the early and mid growing season, respectively (Fig. 2e).
Fig. 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 \textit{P. koraiensis} forest in Changbai Mountains. The total litterfall here includes leaf, reproductive, twig, bark and miscellaneous litterfall.
We observed that the annual leaf and total litterfall production showed an S-shaped increasing pattern over the period 2003 – 2018 (Fig. 2a, f) and 1981 – 2018 (Fig. 3a, d), with increasing stand age. Reproductive and twig litterfall production kept stable from 1981 to 2003, then increased and had a sharp peak occurred in 2010s (Figs. 2b, c and 3b, c). Furthermore, both bark and miscellaneous litterfall production exhibited a wavelike increasing tendency over the period 2003 – 2018 (Fig. 2d, e).

Compared to the large seasonal and annual variations of the litterfall production, less variation among traps was observed in this forest studied (Table S1).
Fig. 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 modes. Total litterfall here includes leaf, reproductive and twig litterfall.
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 was similarly positively associated with $\text{MMT}_{\text{max}}$, but negatively with $\text{MME}$, $\text{MMP}$ and $\text{MMT}_{\text{min}}$ (Table 1). Reproductive litterfall production increased with $\text{MME}$, $\text{MMP}$, $\text{MMT}_{\text{max}}$ and $\text{MMT}_{\text{min}}$, but decreased with $\text{MMW}$. Twig and miscellaneous litterfall production decreased with $\text{MMT}_{\text{max}}$, but increased with $\text{MME}$, $\text{MMP}$, $\text{MMT}_{\text{min}}$ and $\text{MMW}$. Bark litterfall production was positively correlated with $\text{MME}$, $\text{MMP}$ and $\text{MMT}_{\text{min}}$, but negatively correlated with $\text{MMT}_{\text{max}}$ (Table 1).
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 – 2018).

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.

<table>
<thead>
<tr>
<th></th>
<th>Leaf litterfall</th>
<th>Reproductive litterfall</th>
<th>Twig litterfall</th>
<th>Bark litterfall</th>
<th>Miscellaneous litterfall</th>
<th>Total litterfall</th>
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</thead>
<tbody>
<tr>
<td>MME</td>
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<td>0.04</td>
<td><strong>0.37</strong></td>
<td>-0.32***</td>
<td>0.14</td>
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<td>0.10</td>
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<td><strong>-0.66</strong>*</td>
<td>-0.19</td>
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<td>(0.18, 1)</td>
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<td>MMW</td>
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<td>Intercept</td>
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<td>0.68</td>
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</table>

MME, mean monthly evapotranspiration; MMP, mean monthly precipitation; MMTmax, mean monthly maximum temperature; MMTmin, mean monthly minimum temperature; MMW, mean monthly wind speed.
The relative variable importance of predictors differed among litterfall components (Table 1). MME and MMTmax were the best predictors for leaf, twig, bark and the total litterfall production based on their relative importance. All models included MMP, but MMP was the most important factor determining the miscellaneous litterfall production. MMTmin was very important for predicting leaf, bark and total 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, MMPmar, MMPoct, Mmax, MMar, MMAX, M Mont and MAW (Table 2). The MMPoct and MMar were the best predictors based on their relative importance. The models that best predicted the annual reproductive litterfall production included MAP, MMPmar, MMPaug, MMPoct, Mmax, MMin, and MMar. Additionally, MAP was included in most of the models. The annual twig litterfall production was best fitted by models that included MAP, M, Mmax, MMPmar, MMPoct and MAW as predictor variables. The annual total litterfall production was best fitted by models that included MAP, MMPmar, MMPoct, Mmax and MMPoct (Table 2). Both CO2 and MAE had no significant effect on the six litterfall component production at the year level. Moreover, we observed that the annual leaf and total litterfall production non-linearly increased with the total basal area of the mixed old-growth forest (Fig. S3a, d).
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). 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.

<table>
<thead>
<tr>
<th></th>
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<td>-0.45**</td>
<td>-0.26</td>
<td>0.32</td>
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MAP, mean annual precipitation; MMPMay, mean monthly precipitation in May; MMPAug, mean monthly precipitation in August; MMPOct, mean monthly precipitation in October; MAT, mean annual temperature; MATMax, mean annual maximum temperature; MATMin, mean annual minimum temperature; MMTMay, mean monthly temperature in May; MMTOct, mean monthly temperature in October; MAW, mean annual wind speed.
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 similarly 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., 2019; 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- versus 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; Zhou 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 flower and fruit in total litterfall of the climax communities is much greater than those of earlier successional communities (Zhou et al., 2007). Thus, a 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 non-growing season from November to April (Fig. S2), during the growing season it had higher values in May and August (Fig. 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 non-growing 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 changes 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 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 Mg ha\(^{-1}\) 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 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, Björn 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, B. & 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 scale (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, extreme 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 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 of 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 possibly 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 the productivity (Liu et al., 2004). Furthermore, reproductive litterfall production increases with precipitation, this may
be related to 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 Changbai Mountain region.

The forest litterfall production is affected by a complex mix of climatic variables (Andivia et al., 2018; Berg, Björn & 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, B. & Meentemeyer 2001). In this study, we observed that the monthly leaf and total litter production was negatively, 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 an 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 relative increase in temperature combined with 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 with 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., 2019; Christensen 1975). Neglecting the effect of wind on litterfall production can be a serious bias, especially in temperate broadleaf and mixed forests with a period of intensive leaf shedding, leading to 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 stiraciflua, A. rubrum, Cercis Canadensis* and *Cornus florida*) leaf litterfall production is
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 litterfall production process. Incorporating climatic variables in those
models may increase the accuracy of model predictions under climate change.

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collected the litterfall; C.W. and X. Z. wrote the first draft of the manuscript and M.-
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season litterfall (Nov.-Apr.) was collected in April.

Fig. 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
Fig. 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 modes. Total litterfall here includes leaf, reproductive and twig litterfall.