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Inter-annual litterfall variation in *Abies georgei* var. *smithii* forests of Southeastern Tibet

Inter-annuelle Streufallvariation in *Abies georgei* var. *smithii* Wäldern im Südosten Tibets

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Keywords: *Sejila Mountain, Forrest's fir, Abies chengii, Forest gap, Litter annual production, Plant organs, Seasonal dynamics, Subalpine forest, nutrients, carbon*

Schlüsselbegriffe: *Sejila Mountain, Forrest's Tanne, Abies chengii, Bestandeslücken, Baumkomponenten, Saisonalität, Subalpine Wälder, Nährstoffe, Kohlenstoff*

Abstract

Since litterfall is an important process in high-altitude forest ecosystems, we measured over three years the litterfall amount and composition in five habitats (i.e., closed canopy forest, forest gaps of three sizes, and logged forest) in an *Abies georgei* var. *smithii* forest in Sejila Mountain, southeastern Tibet. The annual litterfall ranged between 2.08 Mg ha^{-1} year^{-1} and 2.35 Mg ha^{-1} year^{-1} with an average of 2.21 Mg ha^{-1} year^{-1}, is thus relatively stable and lower than litterfall in other dark coniferous forest types in the same region. Approximately 86.3 % of litterfall is composed of needles and twigs, with needles being the dominant component. Seasonal litterfall exhibited a single peak (about 20 % of the total litterfall) from October to November every year. The period August-September produced with about 4 % the least litterfall. The an-

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nual litterfall dynamic was mainly determined by the biological characteristics of *A. georgei* var. *smithii*. Significant differences in litterfall were evident in the five different habitats with the highest amount of litterfall occuring in the small forest gap. Tree regeneration and shrub distribution apparently lead to changes in litterfall distribution in closed forest, compared to logged forest and different gap sizes.

Zusammenfassung

Da Streufall ein wichtiger Prozess in Bergwäldern ist, haben wir über einen Zeitraum von drei Jahren die Streufallmenge und deren Zusammensetzung an fünf Standorten (geschlossener Bestand, drei unterschiedlich große Bestandeslücken und ein geschlägerter Bestand) in einem *Abies georgei* var. *smithii* Wald in den Seijila Bergen von Südost Tibet gemessen. Der jährliche Streufall variierte von 2.08 Mg ha^{-1} $year^{-1}$ bis 2.35 Mg ha^{-1} $year^{-1}$ mit einem Mittelwert von 2.21 Mg ha^{-1} $year^{-1}$; somit ist der Streufall von *A. georgei* var. *smithii* relativ stabil und geringer als der Streufall in anderen dunklen Nadelwäldern in dieser Region. 86.3 % der Streufallmenge sind Nadeln und Zweige, wobei Nadeln der Hauptbestandteil sind. Die saisonale Verteilung zeigt einen Streufallpeak (etwa 20 % der jährlichen Streufallmenge) für jedes Jahr zwischen Oktober und November. Zwischen August und September wurde mit 4 % die geringste Streufallmenge gemessen. Die jährliche Streufalldynamik wurde beeinflusst durch die Besonderheiten von *A. georgei* var. *smithii*. Wir konnten signifikante Unterschiede in der Streufallmenge zwischen den fünf untersuchten Standorten feststellen, wobei der höchste Streufall in der kleinsten Bestandeslücke gemessen wurde. Verjüngung und Sträucher bewirken scheinbar Veränderungen in der Streufallverteilung zwischen geschlossenen, lückigen und geschlägerten Beständen.

1. Introduction

Litterfall, in addition to fine root turnover, is the major source of matter and energy for decomposing organisms in terrestrial ecosystems. Plant litterfall is correlated with primary production and plays a crucial role in stabilizing the ecosystem functions (e.g., Wang 1989; Maguire 1994; Witkamp 1963; Berg *et al.*, 2001). As soil microbial decomposition of litterfall releases CO_2 to the atmosphere, studies of litterfall and its decomposition receive increasing attention in the context of global changes. Forest litterfall is expected to increase with global warming, particularly in temperate and cold regions, where temperature increase is expected to be larger than in tropical and subtropical regions (Delucia *et al.* 1999). Understanding the dynamic processes of accumulation and decomposition of litter is crucial to understand the structure and function of forest ecosystems temperate and cold zones (Peng *et al.* 2002).

Abies georgei var. *smithii* (synonyms *Abies forrestii Creib* var. *smithii* (Trav. Lab. Forest. Toulouse 1 (2, 1): 177, 1929); *Abies delavayi* var. *smithii* (Monogr. 143. t. 8B. 1971), FOC I, 1999) forests are the most widespread and well-preserved primary forests in southeastern Tibet. These forests represent the zonal vegetation and climax community in subalpine zones of southeastern Tibet and play an essential role in maintaining biodiversity of the high-altitude valleys of the Brahmaputra river basin. Previous studies of litterfall in subalpine coniferous forests have been carried out mostly in closed canopy forests, as researchers hold the view that the canopy forest is the most representative habitat (Ye, 2016; Wu, 2014; NFGA, 2012). However, using closed canopy stands as reference may lead to substantial biases, as it ignores the impact of heterogeneous stand structure, including natural gaps and logging, on litterfall distribution. *Abies georgei* var. *smithii* forests frequently exhibit gaps and open patches as the result of tree death due to natural causes and/or human intervention. These gaps are also important for natural forest regeneration. The regeneration and changes in tree density in gaps may change the amount, composition and distribution of litterfall in gaps compared to closed canopies.

In this study, we investigated five different habitat types of *A. georgei* var. *smithii* forests, to better understand the litterfall production and nutrient circulation of this important forest ecosystem. The purpose is to provide a scientific basis for long-term ecological research on carbon cycling and energy conversion in subalpine dark coniferous forest ecosystems in southeastern Tibet.

2. Material and Methods

2.1 Overview of the research area

The sampling sites are located on the eastern slopes of Sejila Mountain at an elevation of about 3800 m.a.s.l. (29° 48′ N, 94° 49′ E, Fig. 1). These sampling sites are part of long-term fixed standard plots of the National Forest Ecosystem Observation & Research Station of Nyingchi Tibet (http://lzf.cern.ac.cn). The dominant tree species in this region is *Abies georgei* var. *smithii*. Meteorological observations at Nyingchi Ecological Research Station show annual temperature of 3.5 °C. The mean temperature in the warmest month (July) is 11.2 °C and in the coldest month (January) it is -4.1 °C. The annual precipitation sum is 1095 mm. Summer precipitation from June to September accounts for 75 % – 82 % of the annual total. The annual average evaporation is 544 mm, and the annual average relative humidity is 83 %. The annual number of sunshine hours is 1150 h with an average annual percentage of sunshine of 26 % (Xu *et al.* 2010; Luo *et al.* 2014).

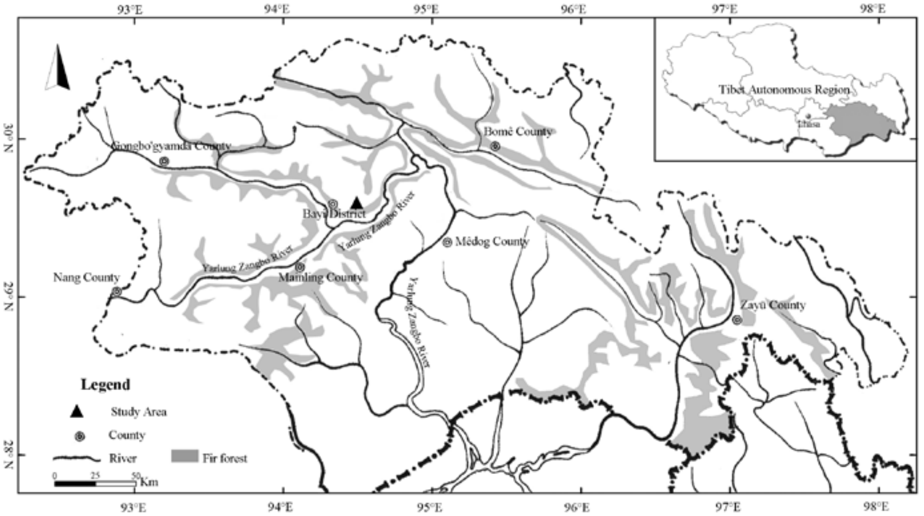

Figure 1: Location of study area in southeast Tibet.

Abbildung 1: Lage des Untersuchungsgebietes im Südosten Tibets.

Abies georgei var. *smithii* is a shade-tolerant tree species under cool and cold climates. The low demand for light is especially pronounced in the seedling stage. This species often forms pure forests in valleys, shaded or semi-shaded slopes in subalpine and alpine regions. *Abies georgei* var. *smithii* is also known to form coniferous mixed forests with spruce, larch, hemlock, pine and broad-leaved species. The *A. georgei* var. *smithii* coniferous forest in sub-alpine region of the southeast Tibet is commonly found at altitudes between 3100 and 4380 m and represent about 30 % forest area in this region. The average age of the assessed trees was about 200 years, their average height 31.9 m, and average diameter at breast height (DBH) 49.7 cm. Natural regenerating trees (with height of 1.5 – 20 m) under closed canopy have density of 196 ha^{-1} and an average DBH is 5.6 cm. The density of naturally regenerated saplings (tree height 0.2 – 1.5 m) is 369 ha^{-1} and their average root collar diameter (DRC) is 2.5 cm. In comparison, in forest gaps, the density of naturally regenerated saplings (with height of 0.2 – 1.5 m) is higher with 470 ha^{-1} and an average DRC is 3.1 cm and the density of naturally regenerated trees (with height of 1.5 – 20 m) is 246 ha^{-1} with an average DBH of 6.8 cm.

In our study region, 5.2 ha forest has been logged about 25 years ago in 1990. 8 trees per hectare with tree height between 25 – 30 m were left as mother trees. Saplings with density of 62 ha^{-1} (average DRC 1.4 cm) and trees with height of 1.5 – 20 m of 43 ha^{-1} (average DBH of 6.2 cm) were found in this logged area.

Shrub layer was composed of three species of honeysuckle (*Lonicera* spp.) and three species of rhododendron (*Rhododendron hirtipes*, *R. uvarifolium*, and *R. oreotrephes*) and *Rosa omeiensis*, *Sorbus rehderiana*, *Artemisia desertorum*, *Berberis franchetiana Schneid* var., and *Rubus biflorus*. All shrub species were found in gaps, while only five appeared in the closed canopy forest.

The herb layer plants mainly consisted of *Impatiens nyimana*, *Cacalia pentaloba*, *Aster albescens*, *Iris bulleyana*, *Primula florimdae*, *Polyonatum cirrhifolium*, *Streptopus simplex*, *Hemiphragma heterophyllum*, *Polygonum polystachyum*, *Ainsliaea latifolia*, and *Epilobium sikkimense*. The vine layer plant is *Smilax menispermoidea*.

This forest is characterized by poorly developed acid brown soils with mild humification process.

2.2 Sampling sites

A series of litterfall traps were placed in five different habitat types: closed canopy forest, small gap, middle gap, large gap, and logged forest. 30 × 30 m square sampling plots were set under closed canopy and logged forest. In contrast, elliptical sampling plots with consistent size were used in the three gaps. The area of small gaps was smaller than 100 m^2, middle gaps were sized 100 – 300 m^2 and large gaps were bigger than 300 m^2. In total, 15 plots were established with three replications in each of the five habitat types (Table 1).

Table 1: Description of sampling plot setup.

Tabelle 1: Beschreibung der Probeflächen.

Habitat	Description	Sample plot shape	Number of sample plots	Number of litter traps	Area (m^2)
Closed canopy forest	Natural primary forest, canopy density 0.6-0.8	Rectangle	3	27	900
Small gap	Formed by natural tree death	Approximately Ellipse	3	27	75-90
Middle gap	Formed by natural tree death	Ellipse	3	27	157-210
Large gap	Formed by natural tree death	Ellipse	3	27	320-370
Logged forest	Logged ~25 years ago, now regenerating naturally	Rectangle	3	27	900

We divided rectangular plots into 36 grids, and placed nine litter traps equidistantly between each grid point (Fig. 2B). For elliptical plots, nine litter traps were placed along short and long axis (Fig. 2A). 54 traps were set in six sampling plots of closed canopy forests and logged forests and 81 traps were set in nine plots of the three gap types. The litter traps were made of a 40-mesh nylon nets and 100 cm × 10 cm × 2 cm wooden slats and thus each trap collected litter for an area of 1.0 m^2. Traps were placed at a height of 20 cm above ground.

From May 2013 to May 2016, litter was collected regularly every month. Since it was difficult to collect litter in winter during snow cover from late December to March, litter accumulated during this period was collected in March and we thus made 10 collections per year.

The collected litter was sorted into components: needles, branch, bark, flowers, cone (including seminiferous scales, bract scales and cone axis), epiphytic (including usnea, moss and lichen) and clastics (too small to identify further). After oven-drying to constant weight at 80 °C, all components were weighted on an electronic scale accurate to 0.01 gram. The average annual litterfall of each habitat type was calculated by upscaling the collected litterfall amount to Mg ha^{-1} $year^{-1}$. We used the monthly average litterfall (December-March pooled) to explore seasonal variations.

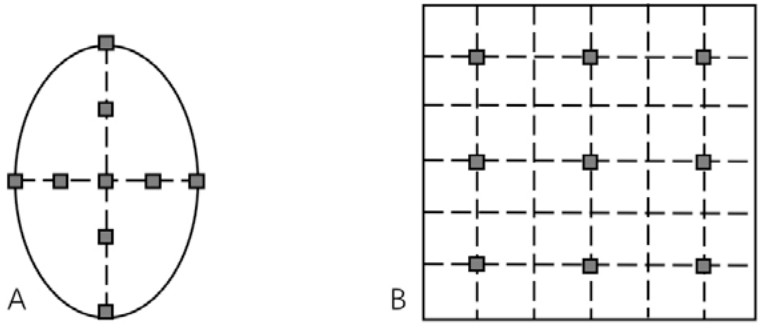

Figure 2: Placement of litterfall traps in elliptic plots (A) and rectangular plots (B).

Abbildung 2: Positionierung der Streufall-Sammler in elliptischen (A) und rechteckigen Flächen (B).

2.3 Statistics

One-way ANOVA was used to study the significance of data differences in litterfall among different habitats. LSD (Least-Significant Difference) was used to make multiple comparisons between litterfall in the five different habitat types.

3. Results

3.1 Annual litterfall by year and habitat

The annual litterfall of *Abies georgei* var. *smithii* was 2.08 to 2.35 Mg ha^{-1} $year^{-1}$ over three years, the average litterfall was 2.21 Mg ha^{-1} $year^{-1}$, and the coefficient of variation was 6 %. There was no significant difference in annual litterfall between different years ($p > 0.05$). The five habitats can be ordered based on the annual litterfall as: small gap (3.31 Mg ha^{-1} $year^{-1}$) > closed canopy forest (2.73 Mg ha^{-1} $year^{-1}$) > middle gap (1.92 Mg ha^{-1} $year^{-1}$) > large gap (1.82 Mg ha^{-1} $year^{-1}$) > logged forest (1.27 Mg ha^{-1} $year^{-1}$, Table 2).

The litterfall in the gap habitats were significantly different compared to other habitats. Only between the middle gap and large gap there was no significant difference. The analysis of the regeneration of shrubs and saplings (Table 3) indicated, that litterfall was negatively correlated with sapling and shrub coverage in the five habitats with a correlation coefficient of -0.94.

Table 2: Litterfall by year and habitats (mean ± standard deviation) in Abies georgei var. smithii forests (Mg ha^{-1} year^{-1}). Different lowercase letters for the same parameter in the same column indicate significant differences among different years and habitats at $p < 0.05$. Period is from May to April of the following year.

Tabelle 2: Streufall pro Jahr und Habitat (Mittelwert ± Standardabweichung) für *Abies georgei* var. *smithii* Wälder (Mg ha^{-1} year^{-1}). Unterschiedliche Buchstaben zeigen signifikante Unterschiede an mit $p < 0.05$. Messperiode ist von Mai bis April des darauffolgenden Jahres.

Period	Small gap	Middle gap	Large gap	Closed canopy forest	Logged forest	Annual average
2013–2014	3.58	2.17	1.97	2.66	1.36	2.35 ± 0.83a
2014–2015	3.13	1.72	1.69	2.75	1.14	2.08 ± 0.82a
2015–2016	3.21	1.86	1.80	2.79	1.31	2.19 ± 0.78a
Average	3.31 ± 0.24A	1.92 ± 0.23B	1.82 ± 0.14B	2.73 ± 0.07C	1.27 ± 0.12D	2.21 ± 0.81

Table 3: Comparison of litterfall and coverage by shrubs and saplings in different habitats.

Tabelle 3: Vergleich von Streufall und Deckungsgrad von Sträuchern und Verjüngung in den untersuchten Habitaten.

Habitat	Average litterfall (Mg ha^{-1} year^{-1})	Coverage shrubs and saplings (%)	Coverage (%)	
			Shrubs	Saplings
Closed canopy forest	2.73	18	8	10
Small gap	3.31	14	9	5
Middle gap	1.92	33	20	13
Large gap	1.82	47	27	20
Logged forest	1.27	69	49	20

3.2 Annual variation of litterfall components

The litterfall components in decreasing order were needles (1.35 Mg ha^{-1} year^{-1}) > branches (0.55 Mg ha^{-1} year^{-1}) > cones (0.11 Mg ha^{-1} year-*1*) > epiphytes (0.07 Mg ha^{-1} year^{-1}) > clastics (0.05 Mg ha^{-1} year^{-1}) > bark (0.04 Mg ha^{-1} year^{-1}) > flowers (0.03 Mg ha^{-1} year^{-1}) (Fig. 3). Among the seven components, needles accounted for 61.3 % of the total litterfall, followed by branches (25.0 %). All other components accounted for 13.7 % of the total litterfall produced. Thus, needles and branches were the most important components of litterfall in the studied *A. georgei* var. *smithii* forests. Needle and branch litterfall differed significantly between each year ($p < 0.01$), while there were no significant difference in the litterfall of other components in different years ($p > 0.05$).

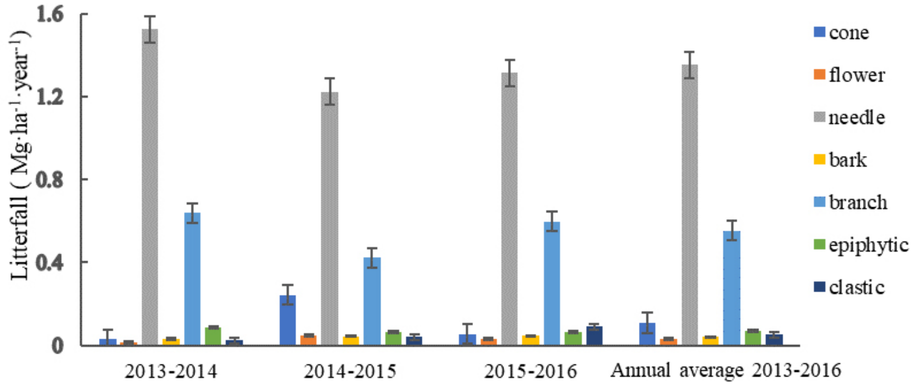

Figure 3: Annual litterfall components of the Abies georgei var. smithii forests, using average values from the five studied habitats.

Abbildung 3: Streufallkomponenten pro Jahr in Wäldern mit *Abies georgei* var. *smithii* (Mittelwert der fünf untersuchten Habitate).

3.3 Monthly dynamics of litterfall by components

Because of the large differences in litterfall by components, we did a more detailed analysis of their seasonal litterfall dynamics. Monthly variation of litterfall by component of litterfall in the *A. georgei* var. *smithii* forest are shown in Fig. 4.

The peak litterfall period is from October to November with 0.43 Mg ha^{-1} of litterfall was produced. Litterfall fluctuates after November decreasing to 0.09 Mg ha^{-1} from August to September, when the next litterfall peak starts. This pattern appears to be typical for the dynamic litterfall in *A. georgei* var. *smithii* forests.

Among the components, needle litterfall was produced at a higher rate than other components, with a maximum of 0.35 Mg ha^{-1} and a minimum of 0.03 Mg ha^{-1}. Dynamic changes in needle litterfall were similar to those in total amount, which indicated that needles were not only the most important contributor to litterfall in absolute terms, but also determined the litterfall dynamic.

Branch litterfall was different from needle litterfall with less annual variation. Two small peaks (0.09 and 0.08 Mg ha^{-1}) were evident in March – April and July – August.

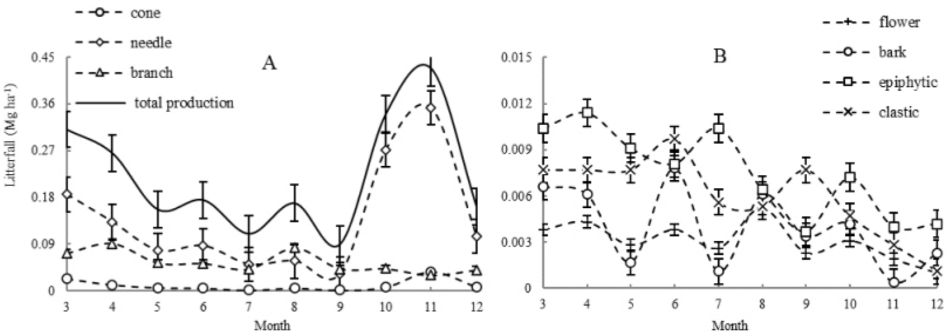

Figure 4: Monthly litterfall of cones, needles, branch, and the monthly total litterfall (A) and litterfall of flowers, barks, epiphytes and clastics (B).

Abbildung 4: Monatswerte des Streufalls von Zapfen, Nadeln, Ästen und vom Gesamtstreufall (A) und Streufall von Blüten, Rinden, Flechten und Fragmenten (B).

4. Discussion

4.1 Comparison of litterfall between this study and other coniferous forests in China, Europe and worldwide

Our 3-year study showed that annual litterfall of *Abies georgei* var. *smithii* forests in southeastern Tibet is much lower than that of temperate coniferous forests and boreal coniferous forests in China (Zhang, *et al.*, 2014). The annual litterfall is similar to that of *Pinus sylvestris* in northern Europe (Portillo-Estrada, *et al.*, 2013), but lower than that of *A. borisii-regis* in northern Greece (Kavvadias, *et al.*, 2001) and *Pseudotsuga menziesii* in Western Europe (Portillo-Estrada, *et al.*, 2013). It is also lower than the litterfall of coniferous European forests (Neumann, *et al.*, 2018). The annual litterfall of *A. georgei* var. *smithii* forests is lower than *Picea likiangensis* var. *linzhiensis* forests (Wang et al., 1998), which is located in the same geographical area. Our results are also lower compared to *P. schrenkiana* forests in Tianshan region (Liu *et al.*, 2014), spruce–fir forests in the Lesser Khingan Mountains of Heilongjiang (Hou *et al.*, 2013), *A. fabri* forests in Mount Gongga (Luo *et al.*, 2003) and *A. fabri* forests in Shennongjia Mountain (Chun *et al.*, 2009; Cui *et al.*, 2017). Similar amount of litterfall was observed in the eastern part of Qinghai-Tibet plateau (Fu, *et al.*, 2017). We summarized the available data on litterfall of conifer forests in Table 4.

The average litterfall of different components is relatively stable, which appears to be a key characteristics of old-growth *A. georgei* var. *smithii* forests. High altitude areas are sensitive to global climate changes. Some researchers predict that forest biomass will increase with the increasing temperature in high-altitude areas, and that litterfall might increase correspondingly (Delucia *et al.*, 1999; Peng *et al.*, 2002). Our study indicates that there has been no significant litterfall change between years no increasing trend, indicating currently no obvious change of litterfall amount over our observation period. *A. georgei* var. *smithii* forests can be categorized as old growth forest forests with low litterfall production. This result is consistent with a European study on *Picea abies* and *Picea sitchensis* (Hansen, *et al.*, 2009).

Table 4: Comparison of litterfall observations of fir and other coniferous forests in China, Europe and worldwide (Mg ha^{-1} year^{-1}).

Tabelle 4: Vergleich der Ergebnise dieser Studie mit der Literatur zu Tannen- und anderen Nadelwäldern in China, Europa und weltweit (Mg ha^{-1} year^{-1}).

Region	Forest Types	Litterfall	Source
China	*Abies georgei* var. *smithii*	2.21	This study
	Picea likiangensis var. *linzhiensis*	3.84	Wang et al., 1998
	Spruce–fir forest in eastern Qinghai-Tibet Plateau	2.38	Fu et al., 2017
	Picea schrenkiana in Tianshan	2.62	Liu et al., 2014
	Spruce–fir forest in Xiao Hinggan Mountains	3.44	Hou et al., 2013
	Abies fabri in Mount Gongga	2.81	Luo et al., 2003
	Abies fragesii in Shennongjia Mountain	5.7~6.22	Cui et al., 2017
Europe	*Pinus sylvestris* in northern Europe	2.86	Portillo-Estrada et al., 2013
	Abies borisii-regis in northern Greece	2.51	Kavvadias et al., 2001
	Pseudotsuga menziesii in Western Europe	4.34	Portillo-Estrada et al., 2013
	Coniferous forests in Europe	3.22~4.65	Neumann et al., 2018
World	Temperate coniferous forests	4.7~6.0	Zhang et al., 2014

4.2 Annual litterfall of different components

Among the seven studied litterfall components, needles and branch are in absolute terms the most important components. Despite annual variations of epiphyte fall, litterfall of other components remained stable between different years. This indicates that annual litterfall of *A. georgei* var. *smithii* forests is relatively stable, which was also observed in other studies on fir forests in China.

4.3 Seasonal dynamics of litterfall

There is controversy about seasonal dynamics in litterfall of spruce and fir forests. Some scientists reported that monthly dynamic trend of spruce and fir forest litterfall is not significant (Zhang et al·, 2014), while others support that there are significant fluctuations of the monthly litterfall of spruce and fir forest (Bray, et al·, 1964). Litterfall in A· georgei var. smithii is driven by the biological characteristics of this tree species. The regularity of litterfall seasonality suggest a strong link to seasonal meteorological conditions. Among the components of litterfall, needle litterfall was produced at a significantly higher rate than other components, with a maximum value of 0.35 Mg ha^{-1} and a minimum value of 0.03 Mg ha^{-1}. Dynamic in needle fall are similar to those of total litterfall, which indicates that needle are not only the most important contributor to litterfall, but also drives the seasonal dynamics. Branch litterfall had less seasonal variation compared to needle litterfall. Two small peaks of branch litterfall (0.09 and 0.08 Mg ha^{-1}) were evident in March – April and July – August. Other components were produced all year round with no obvious regularity and at low rates.

4.4 Differences in litterfall between different habitats

Forest gaps are heterogeneous features formed by disturbances and are common in forest ecosystems (Dusan, *et al.*, 2007). Gaps in subalpine dark coniferous forests modify habitat conditions, species composition, biodiversity, structure, function, regeneration and succession dynamics of forest communities (Luo, *et al.*, 2014; Oakley, *et al.*, 2006; Xue, *et al.*, 2013). We found that the subalpine dark coniferous forest represented by *A. georgei* var. *smithii* can be categorized as old growth forest. There are significant differences in litterfall between old-growth forests and gaps. The amount of litterfall in the small gap habitat is higher than in closed canopy forest and also higher than in middle gaps, large gaps and logged forest, which indicates that litterfall distribution pattern is affected by gap size. This result is different from the conclusion that litterfall of closed canopy forest is greater than gap in *Abies faxoniana* Rehd. primary forest in western Sichuan, China. The statistical analysis shows that the gap size is correlated to tree regeneration and shrub coverage in the studied habitats. There are fewer saplings and shrubs in small gaps and closed canopy forest habitat, while there are more shrubs and saplings in middle to large gaps and the regeneration density is higher (Luo *et al.*, 2002). Sheltering effect of the canopy of shrubs and saplings cause the distribution of litterfall to become more uneven, which appears to be an important reason for the difference in the litterfall in different habitats. This is supported by clear inverse relationships between litterfall of different habitats and understory tree regeneration and shrub density.

4.5 Synthesis

This study reveals that dynamics of litterfall production in *A. georgei* var. *smithii* forests exhibits a single peak (about 20 % of the total litterfall) from October to November every year. The period from August to September produces the least (only 4 %) amount of litterfall. Significant differences were evident in litterfall of some components, with needles dominating both annual and seasonal litterfall. The tree species regeneration and shrub distribution appears to be important for changes in litterfall distributions across different habitats.

Subalpine dark coniferous forests are the most important component of Tibetan forest resources. As the climax community and typical representative of alpine mountainous vegetation, it plays a crucial role in the study of several ecological concepts, in terms structural characteristics, forest functions, understand8ing the effects of forest management in response to climate change, restoration and conservation of degraded forests. Previous studies about litterfall in Southeast Tibet alpine dark coniferous forests have mainly focused on the accumulation, nutrients and decomposition of spruce litterfall. There is a lack of research on litterfall production and dynamic process. This paper expands our understanding of the litterfall production, seasonal and annual dynamics for *A. georgei* var. *smithii* forests and its spatial heterogeneity, closing an important knowledge gap fills in high-altitude forest ecosystems in Tibet.

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