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ORIGINAL PAPER

Litterfall production along successional and altitudinal gradients of subtropical monsoon evergreen broadleaved forests in Guangdong, China

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Abstract Evaluation of litterfall production is important for understanding nutrient cycling, forest growth, successional pathways, and interactions with environmental variables in forest ecosystems. Litterfall was intensively studied during the period of 1982–2001 in two subtropical monsoon vegetation gradients in the Dinghushan Biosphere Reserve, Guangdong Province, China. The two gradients include: (1) a successional gradient composed of pine forest (PF), mixed pine and broadleaved forest (MF) and monsoon evergreen broadleaved forest (BF), and (2) an altitudinal gradient composed of Baiyunci ravine rain forest (BRF), Qingyunci ravine rain forest (QRF), BF and mountainous evergreen broadleaved forest (MMF). Mean annual litterfall production was 356, 861 and 849 g m^{-2} for PF, MF and BF of the successional gradient, and 1016, 1061, 849 and 489 g m^{-2} for BRF, QRF, BF and MMF of the altitudinal gradient, respectively. As expected, mean annual litterfall of the pioneer forest PF was the lowest, but rapidly increased over the observation period while those in other forests were relatively stable, confirming that forest litterfall production is closely related to successional stages and growth patterns. Leaf proportions of total litterfall in PF, MF, BF, BRF, QRF and MMF were 76.4%, 68.4%, 56.8%, 55.7%, 57.6% and 69.2%, respectively, which were consistent with the results from studies in other evergreen broadleaved forests. Our analysis on litterfall monthly distributions indicated that litterfall production was much higher during the period of April to September compared to other months for all studied forest types. Although there were significant impacts of some climate variables (maximum and effective temperatures) on litterfall production in some of the studied forests, the mechanisms of how climate factors (temperature and rainfall) interactively affect litterfall await further study.

Keywords Dinghushan natural reserve · Litterfall production · Litterfall components · Forest succession · Altitudinal gradient

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Introduction

Litterfall production is related to environmental factors (Finer 1996; Florence and Lamb 1975; Kozlowski et al. 1990; Hart et al. 1992), the vegetation biomass and plant community composition (Pedersen and Hansen 1999; Hosking 2003). Because litterfall production reflects the interactions between biological heredity of trees and the influence of environmental fluctuations, litterfall production can be perceived as an indicator of forest condition (Pedersen and Hansen 1999). Evaluation of litterfall production is also important for understanding nutrient cycling, carbon fluxes and disturbance ecology. For example, significant accumulation or reduction of litterfall amount in some forest communities can cause changes in frequencies of wildfire disturbance (Edmonds et al. 2000).

The main emphasis in earlier litterfall studies was placed on the amount, composition (Chandler 1943; Viro 1955) and distribution (Kittredge 1948) (summarized by Pedersen and Hansen 1999). More recently, this literature has shifted to evaluating the ecological role of litterfall in nutrient cycling in forests (Bringmark 1977; Waring and Schlesinger 1985; Stevens et al. 1989; Haase 1999; Gordon et al. 2000; Zimmermann et al. 2002) and its interactions with biotic and non-biotic variables (Prescott et al. 2000; Cárcamo et al. 2000; Trofymow et al. 2002; Prescott et al. 2004). This shift is important for understanding litterfall production patterns along forest development stages and environmental gradients. For example, based on numerous studies in litter production from world forests, Bray and Gorham (1964) and Albrektson (1988) found that annual litterfall production increased rapidly during stand development until canopy closure, and then remained relatively constant over a long period of time before decreased in old stands. In another study Xiao et al. (1998) used data on litterfall and its relationship to environmental variables to calibrate the Terrestrial Ecosystem Model for assessing the sensitivity of net ecosystem production of the terrestrial biosphere to transient changes in atmospheric CO_2 concentrations and climate.

The subtropical monsoon evergreen broadleaved forest is important in Guangdong, China because of its high biodiversity and its significant role in watershed protection. This regional climax forest exhibits large variations along successional (temporal scale) and altitudinal (spatial scale) gradients. Unfortunately, these forests were severely affected by large-scale deforestation and land use changes in the 1960's and 1970's. In order to restore the damaged environment, a large-scale reforestation program was launched in the mid 1980's in Guangdong province. Successful implementation of this 10-year reforestation program has created various types of pine plantations. Concern has been expressed that there may be important differences in ecological function between these plantations and the regional climax forests (Lu and Liu 1988; personal communication with Dr. Shaolin Peng from Zhongshan University, China). This highlights an important need to conduct scientific research to examine the ecological differences between these plantations and the climax forests, and between various climax forests along environmental gradients. As mentioned previously, litterfall production is a useful indicator of forest condition and function. By assessing the differences in litterfall production between vegetation types, we may gain important insights into differences in ecological function between various forest communities. Such information is needed to understand how well we have achieved forest restoration objectives and for guiding future reforestation planning.

In this study, we tested the following research hypotheses: (1) litterfall production increases along the successional series but decreases along the altitudinal gradient of the subtropical monsoon evergreen broadleaved forest; (2) trends in litterfall components (leaf, twig, flower, etc.) exist along the successional and altitudinal gradients; and (3) environmental variables (temperature, precipitation, etc.) significantly contribute to litterfall production. The Dinghushan Biosphere Reserve provides an ideal location for this research because various forest types that are in different successional stages as a result of fire disturbance and harvesting are present in a relatively small area, controlled by similar environmental factors. In addition, the forest types are distributed along altitudinal gradients, and in contrast to most literature which report litterfall production over a period of <5 years, data for the Dinghushan Biosphere Reserve is available for more than 15 consecutive years.

Materials and methods

Study sites

The Dinghushan Biosphere Reserve (112°30′39″ E to 112°33′41″ E, 23°09′21″ N to 23°11′30″ N) is located in the mid part of Guangdong province in Southern China, about 84 km from Guangzhou city and with an area of 1133 ha. The elevation ranges from 10 to 1,000 m above sea level.

The Dinghushan Biosphere Reserve has a typical subtropical monsoon climate, with an annual average precipitation of 1,927 mm, of which nearly 80% falls in the wet season (from April to September) and 20% in the dry season (from October to March). The annual mean temperature is 21.4°C and relative humidity is 80%.

Due to the geographic location and its diverse vegetation types, the Reserve is called an ‘‘oasis of the Tropic of Cancer.’’ Key vegetation types include pine forest, mixed pine and broadleaved forest and monsoon evergreen broadleaved forest at similar altitudes. In addition, river-bank forest, ravine rain forest, lowland evergreen broadleaved forest, mountainous evergreen broadleaved forest and shrub-grasslands are present along an altitudinal gradient. In the Reserve, a total of 1,843 plant species, 267 families, and 877 genera have been identified and documented (Peng and Zhang 1995).

In this paper, six dominant vegetation types including pine forest (PF), mixed forest (MF), monsoon evergreen broadleaved forest (BF), Baiyunci ravine rainforest (BRF), Qingyunci ravine rainforest (QRF) and mountainous evergreen broadleaved forest (MMF) were studied. A detailed description of key species compositions is presented in Table 1. These six communities are divided into successional and altitudinal gradients (Table 1).

PF, MF and BF are located at the elevations of 150–300 m at sea level and belong to different natural successional stages, from the pioneer community PF to the regional climax vegetation BF. PF was seeded in 1956, and has not been disturbed by humans for more than 40 years. Its species composition has changed greatly with the natural immigration of many broadleaved species. MF also existed for more than 40 years, and originated from PF created by natural successional processes. If sufficient time is allowed, MF will become BF. BF has been well protected for more than 400 years in the study area. This natural successional process from PF to MF to BF can be reversed if degraded disturbance (deforestation or fire) takes place.

The ravine rainforests (BRF and QRF), BF and MMF are all climax communities occurring at various elevations. These communities are undisturbed, except for QRF. Both BRF and QRF forests are located in the core area of the Reserve. While the BRF is intact, the QRF has been heavily disturbed by recreational activities. The elevations of the ravine rainforests (BRF and QRF), BF and MMF are <50 m, 150–300 m and 500–800 m at sea level, respectively.

Data collection

Fifteen litterfall traps of 1 m^2 were placed randomly at each of the study plots ranging from 1 to 2 ha in size. The distance between litterfall traps was approximately 15 m. The traps were made of plastic net that allowed throughfall to percolate easily but retained litter particles. Usually, the traps were located at a height of 50 cm aboveground, but in some cases where understory shrubs were tall, they were placed higher than 50 cm. Litterfall was collected once a month. The collection periods are shown in Table 1.

After air-drying, the litterfall was subdivided into leaf (separated into broadleaves and needles for PF and MF, respectively), branch, bark, flower and fruit categories. The unidentified fine litter particles were added to flower and fruit category. All litterfall components were then dried at 65° to constant for weighting.

Climatic data (rainfall and temperature) were obtained from a weather station at the Dinghushan

Table 1 Characteristics of the studied forests in subtropical monsoon evergreen broadleaved forests in Guangdong, China

Series	Successional series (similar altitude)			Altitudinal gradient (all climax forests)			
Site code	PF	MF	BF	BRF	QRF	BF***	MMF
Forest type	Pine forest	Mixed forest	Monsoon evergreen broadleaved forest	Ravine rainforest located in Baiyunci	Ravine rainforest located in Qingyunci		Mountainous evergreen broadleaved forest
Dominant tree species	*Pinus massoniana.* Regeneration species: *Rhodomyrtus tomentosa*, *Dicranopteris dichotoma*	*Schima superba*, *Castanopsis chinensis*, *Craibiodendron kwangtungense etc*.s	*Castanopsis chinensis*, *Cryptocarya chinensis*, *Cryptocarya concinna*, *Erythrophleum fordii etc.*	*Ficus nervosa*, *Ficus variegata var. chlorocarpa*, *Caryota ochlandra*, *Canarium album*, *Ormosia fordiana etc.*			*Lithocarpus hancei*, *Engelhardtia fengelii*, *Machilus breviflora*
Succession stage	Pioneer community	Transition community	Regional climax	Topographical climax	Topographical climax		Topographical climax
*Approx. age of dominant trees (year)	50	50	400	300	300		About 100
*Tree coverage	70–80%	80–90%	80–90%	70–90%	70–90%		80–90%
*Basal area (cm^2/m^2)	n.a.	41.06	3.57	18.8	22.3		29.54
*Soil types	Lateritic red soil	Lateritic red soil	Lateritic red soil	Lateritic red soil	Lateritic red soil		Yellow soil
*Total *N* (%)	n.a.	2.30	1.67	1.43	1.48		2.22
**Soil pH	3.92	3.86	3.97	n. a.	4.07		4.11
Human interference	No	No	No	No	Yes, due to location in the tourism area		No
Elevation (m)	150–300	150–300	150–300	< 50	< 50		500–800
Litterfall data availability	Jan., 1994–Dec., 2001	Jan., 1982-Dec., 2001 (no data from Jan., 1983 to Dec., 1991)	Jan., 1981-Dec., 2001 (no data from Jan., 1992 to Dec.,1993)	Jul., 1996–Dec., 2001	Apr., 1996–Dec., 2001		Apr., 1996–Dec., 2001

*From Wang et al. (1982); **from Liu et al. (2002); ***BF in the altitudinal gradient is the same as BF in the successional series

Forest Ecosystem Research Station, part of the Chinese Ecosystem Research Network (CERN). The weather station was located in a low-density pine forest at an elevation of roughly 100 m and within 1 km of the six study communities. Weather data were recorded by an automatic aerograph and collected manually every day.

The selected temperature variables included monthly maximum temperature (14.3–35.5°), average temperature (10.8–30.7°) and minimum temperature (7.5–27.2°) during the period of 1981–2001. The minimum effective temperature for plants in the Reserve is 15° (Peng and Zhang 1995; Zhang and Ding 1996; Yi et al. 1994), which was used to calculate the total effective temperature in a period as follows:

$$\mathrm{ETS} = \begin{cases} \sum_{i=1}^{n}(T_i - 15), & T_i \geq 15 \\ 0, & T_i. \end{cases} \quad (1)$$

where, ETS—cumulative effective temperature (°C); T_i—daily average air temperature(°C); and n—number of days per period. In this study, n is number of days of the month.

Statistical analysis

Homogeneity of variances and normality of distributions of data sets were checked. Data that were not homogeneous were logarithmically transformed prior to analysis. Using the SAS GLM procedure, analysis of variance (ANOVA) was performed on litterfall production data sets (monthly and annually) for determining the statistical difference between forest types in both the successional and altitudinal gradients. To compare the trend slopes of annual litterfall production between the studied forests, a linear regression model with dummy variables was used (Draper and Smith 1998).

In order to test the relationship between monthly litterfall production series and associated monthly climatic variables (maximum temperature, mean temperature, minimum temperature, effective temperature and rainfall), time series analyses were conducted using STATISTICA. Because the series may be auto-correlated, the direct cross-correlation may give a misleading indication of the relationship (Wei and Davidson 1998; Jassby and Power 1990). Therefore, a pre-whitening process is conducted before the data are cross-correlated. For the pre-whitening process we used the Autoregressive Integrated Moving Average (ARIMA) model for input series to reduce the residuals to white noise (eliminating auto-correlation). The residual series are then cross-correlated for litterfall series and associated climatic variable series.

Results

Litterfall production

Successional series

The mean annual litterfall production was 356 ± 149, 861 ± 94, and 849 ± 120 g m^{-2} for PF, MF and BF, respectively, for the study periods shown in Table 1. The average annual litterfall production in PF was significantly lower ($P < 0.001$) than that in MF and BF, which clearly demonstrated that the early pioneer pine forests have less litterfall production most likely due to its earlier development stage and lower total biomass accumulation. However, the difference in annual litterfall production between MF and BF was not statistically significant, indicating that both MF and BF have similar capacities of litterfall production despite their different successional stages. The amounts of annual litterfall production in MF and BF are consistent with the results from Finer (1996).

The difference in litterfall production dynamics between the vegetation communities in the successional series is presented in Fig. 1 (A and B). PF had the lowest annual litterfall production, but had an increased rate of litterfall production over time and large annual variation due to its rapid development as a pioneer community after 1990 (Fig. 1A). However, both MF and BF showed slightly decreasing trends. The year-to-year variation in litterfall production of MF and BF communities was much less compared with those in PF, which demonstrated that MF and BF were in relatively stable stages. The linear trend slopes between MF and BF were not significantly different, but both were significantly higher ($P < 0.001$) than that for PF. The mean monthly litterfall productions were 36.54 ± 14.04, 70.72 ± 22.53 and 70.55 ± 26.57 g m^{-2} for PF, MF and BF, respectively, of which the amount in April to September accounted for 56.7%, 64.5% and 63.7% of the annual total (Fig. 1B) for the three forests, respectively.

Altitudinal gradient

Annual litterfall production for BRF, QRF and MMF were relatively constant, with no apparent trend existing during the study period (Fig. 2A). Similarly, linear trend slopes among these three forests were not significantly different (Fig. 2A). This clearly demonstrates that when forest communities reach climax through successional pathways, their litterfall production remains relatively constant.

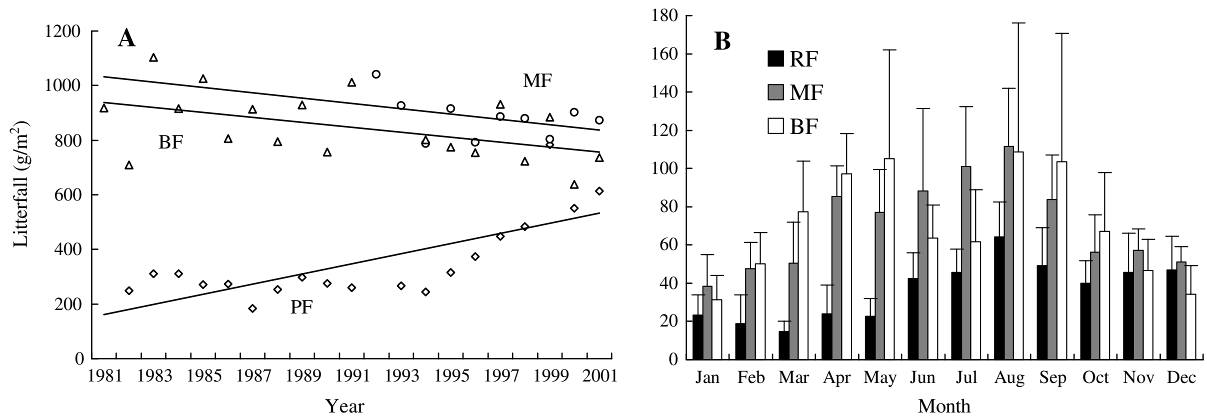

Fig. 1 Average annual (**A**) and monthly (**B**) litterfall of three forest communities of a successional series PF, MF and BF (see Table 1 for more detailed information on three forest sites)

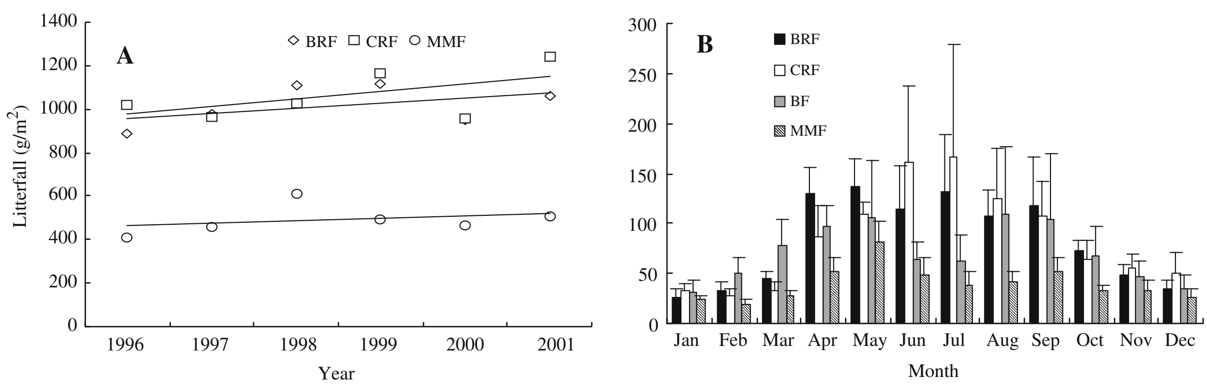

Fig. 2 Average annual (**A**) and monthly (**B**) variation in the amounts of litterfall (g/m^2) in four forest communities of an altitudinal gradient BRF, QRF, BF and MMF (see Table 1 for more detailed information on four forest sites)

The mean annual litterfall productions were 1,016 ± 84, 1,061 ± 105, 849 ± 120 and 489 ± 61 g m^{-2} for BRF, QRF, BF and MMF, respectively. Litterfall production from the ravine rainforest (BRF and QRF) and evergreen broadleaved forest (BF) were significantly higher than that from the high elevation MMF ($P < 0.001$), which suggests that altitude plays an important role in litterfall production. With increased elevation, the amount of annual litterfall production gradually decreased in the order of the ravine rainforest (BRF and QRF) > BF > MMF.

The mean monthly litterfall productions were 83.50 ± 41.91, 84.66 ± 46.71, 70.55 ± 26.57 and 39.56 ± 16.30 g m^{-2} for BRF, QRF, BF and MMF, respectively, over the period 1981–2001 (Fig. 2B). The litterfall production in the wet and hot season (April–September) amounted to 73.9%, 74.2%, 63.7% and 65.8% of the annual total, respectively. These litterfall monthly distribution patterns in the altitudinal series appeared similar to those in the successional series.

Components of litterfall

The proportion of flower and fruit in litterfall of the climax communities BF, BRF and QRF were much greater than those of earlier successional communities (PF and MF) and mountainous MMF ($P < 0.05$) (Table 2). The proportions of both broad leaves and branches increased with successional series from PF to MF to BF whereas the needle and bark components decreased significantly with the natural successional process from PF, MF to BF (Table 2). These changes in

Table 2 Litterfall components (%) of the six studied forests in subtropical monsoon evergreen broadleaved forests in Guangdong, China

Communities	PF	MF	BF	BRF	QRF	MMF
Flower and fruit	14.0(4.0)a	12.9(1.8)ab	22.6(4.4)c	18.6(2.7)d	21.1(4.9)cd	9.8(2.4)b
Broad leaves	10.6(6.6)a	45.3(3.8)b	56.8(7.0)b	55.7(1.7)b	57.6(7.8)b	69.2(5.2)b
Needle leaves	65.8(8.6)a	23.1(5.3)b	0	0	0	0
Branch	8.6(4.6)a	16.1(3.4)b	20.7(6.9)c	25.0(3.3)c	21.5(4.3)bc	20.7(5.1)bc
Bark	5.8(1.6)a	3.7(0.6)b	0.6(0.1)c	0.9(0.3)d	0.5(0.2)c	0.4(0.1)c

Note: Standard error of the mean is shown in parentheses. Means with the same letter within a row are not significantly different ($P>0.05$) from each other

litterfall components reflected the significant shift of key plant species over successional stages.

Over the altitudinal gradient, the percentages of litterfall components were found to be similar in BRF, QRF and BF, which were 18.6–22.6% for flower and fruit, 55.7–57.6% for broad leaves, 20.7–25.0% for branch and 0.6–0.9% for bark components.

The monthly distribution of litterfall components (Fig. 3) showed larger amounts of litterfall for each component during April–September, which is similar to the monthly distribution of total litterfall (Figs. 1 and 2). However, the greatest amounts of total litterfall normally occurred between June and August, depending on the type of forest, while the highest litterfall for the major broad leaves took place in April or May for the majority of the studied forests.

The effects of climate variables on litterfall production

Air temperature, particularly maximum temperature and effective temperature, can be important variables for influencing litterfall production for some types of the studied forests (Table 3). Maximum temperature had a significant positive effect on litterfall production for the BRF, QRF and MMF, while effective temperature significantly ($P<0.05$) influenced litterfall production in MF, BRF and MMF. However, mean temperature only influenced litterfall production of MMF, and minimum temperature had no significant effect on litterfall production for any of the studied forests. These results demonstrate that different forests responded to air temperature differently in terms of litterfall production. Rainfall was a significant variable for BF, BRF and MMF ($P<0.05$), but not for the other forest types.

When comparing litterfall production between the studied forests, it appears that MMF was more sensitive to climatic variables than other forest types. Except for minimum temperature, all other selected climatic variables significantly influenced litterfall production in MMF. By contrast, no climatic variables had significant effects on litterfall production in PF, and only one variable affected litterfall production in MF, BF and QRF.

Discussion

Litterfall production and its components

Average annual litterfall production in the monsoon evergreen broadleaved forest (regional climax) of the Dinghushan Biosphere Reserve during 1981–2001 was 849 ± 120 g m^{-2} (57% for leaf, 21% for branch, 23% for flower and fruit and 0.6% for bark). These results are consistent with other studies on the same vegetation type in the southern part of the subtropics in Guangdong, China (Tu et al. 1993; Weng et al. 1993), which reported that average annual litterfall amounts for 1982–1986 and 1983–1990 were 916 ± 146 g m^{-2} (55% for leaf, 20% for twig and 25% for miscellany) and 906 ± 119 g m^{-2} (53% for leaf, 21% for twig and 26% for flower and fruit), respectively. Chen et al. (1992) reported that the litterfall of under-developed monsoon evergreen broad-leaved forests in Heishiding, located 100 km from the Reserve, was 523 g m^{-2} (68% for leaf, 16% for twig, 11% for flower and

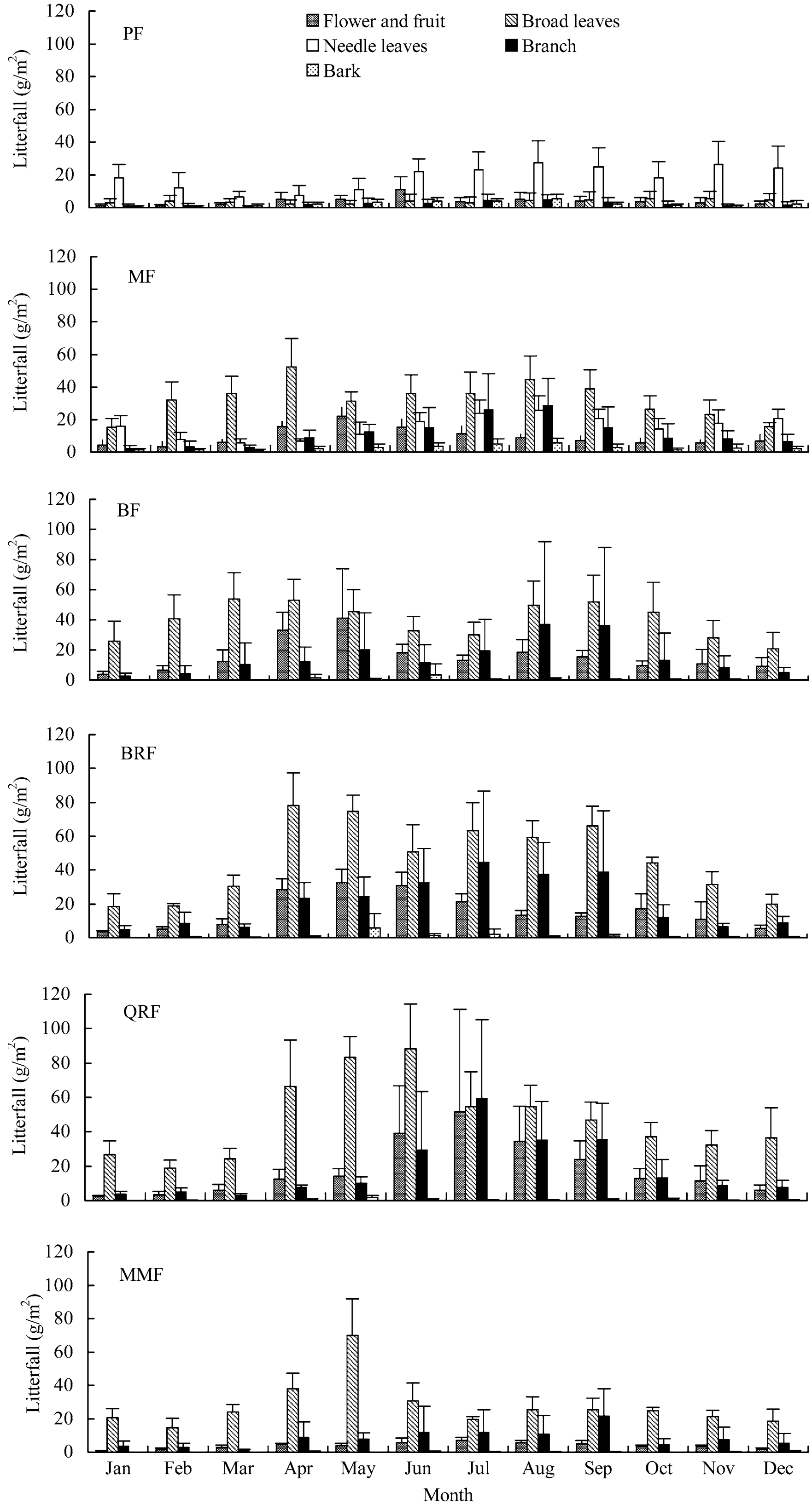

Fig. 3 Monthly distribution of each litterfall component in the six communities (unit: g/m^2) (see Table 1 for more detailed information on six forest sites)

Table 3 The effects of climatic variables on the amount of monthly litterfall through time series analysis in subtropical monsoon evergreen broadleaved forests in Guangdong, China

Forest	Litterfall (g/m^2)	Max. temperature (°C)		Mean temperature (°C)		Minimum temperature (°C)		Effective temperature (°C)		Rainfall (mm)	
	ARIMA*	ARIMA	Correlation** ($P < 0.05$)	ARIMA	Correlation ($p < 0.05$)	ARIMA	Correlation ($P < 0.05$)	ARIMA	Correlation ($P < 0.05$)	ARIMA	Correlation ($P < 0.05$)
PF	$(0,1,1)(0,0,1)^{12}$	$(0,1,1)(0,0,1)^{12}$	n.s.	$(0,1,1)(0,0,1)^{12}$	n.s.	$(0,1,1)(0,0,1)^{12}$	n.s.	$(0,1,1)(0,0,1)^{12}$	n.s.	$(0,1,1)(0,0,1)^{12}$	n.s.
MF	$(1,1,1)(0,0,1)^{12}$	$(0,1,0)(0,0,1)^{12}$	n.s.	$(0,1,0)(0,0,1)^{12}$	n.s.	$(0,1,0)(0,0,1)^{12}$	n.s.	$(0,1,0)(0,0,1)^{12}$	Significant, 0.23, lag 0	$(0,1,0)(0,0,1)^{12}$	n.s.
BF	$(1,1,1)(0,0,1)^{12}$	$(0,1,1)(0,0,1)^{12}$	n.s.	$(0,1,1)(0,0,1)^{12}$	n.s.	$(0,1,1)(0,0,1)^{12}$	n.s.	$(0,1,1)(0,0,1)^{12}$	n.s.	$(0,1,1)(0,0,1)^{12}$	Significant, 0.18, lag 0
BRF	$(0,1,0)(0,0,1)^{12}$	$(0,1,0)(0,0,1)^{12}$	Significant, 0.36, lag 0	$(0,1,0)(1,0,0)^{12}$	n.s.	$(0,1,0)(1,0,0)^{12}$	n.s.	$(0,1,0)(1,0,0)^{12}$	Significant, 0.30, lag 0	$(0,1,0)(1,0,0)^{12}$	Significant, 0.29, lag 0
QRF	$(0,1,0)(1,0,0)^{12}$	$(0,1,0)(1,0,0)^{12}$	Significant, 0.33, lag 0	$(0,1,0)(1,0,0)^{12}$	n.s.	$(0,1,0)(1,0,0)^{12}$	n.s.	$(0,1,0)(1,0,0)^{12}$	n.s.	$(0,1,0)(1,0,0)^{12}$	n.s.
MMF	$(0,1,1)(1,0,0)^{12}$	$(0,1,0)(1,0,0)^{12}$	Significant, 0.30, lag 0	$(0,1,0)(1,0,0)^{12}$	Significant, 0.28, lag 0	$(0,1,0)(1,0,0)^{12}$	n.s.	$(0,1,0)(1,0,0)^{12}$	Significant, 0.39, lag 0	$(0,1,0)(1,0,0)^{12}$	Significant, 0.38, lag 0

*ARIMA—Autoregressive Integrated Moving Average model

**Cross correlation between litterfal and each of the climate variables. n.s. indicates no significant correlation. When there is a significant correlation, correlation co-efficiency and lag number is given fruit and 5% for trash), which was much less than the developed monsoon forests indicated above. This suggests that litterfall production amounts could largely reflect successional stages. Weng et al. (1993) also reported the average annual litterfall production (1983–1990) from a coniferous forest stand was 270 ± 42 g m^{-2} (65% for leaf, 12% for twig and 23% for flower and fruit), less than that in PF from this study. However, this coniferous stand was 18 years younger than the PF stands in our study.

Our results from the Dinghushan Biosphere Reserve are consistent with studies in other tropical and subtropical forests in terms of annual litterfall production (Table 4). The proportion of leaf to total litterfall in this study was relatively low compared to those in other types of world forests, but comparable to similar vegetation types in neighboring areas (Tu et al. 1993).

The proportions of flower and fruit in litterfall of the climax communities BF, BRF and QRF were much greater than those of earlier successional communities (PF and MF) and the mountainous MMF (Table 2). This may be due to the fact that the PF, MF and MMF communities were composed of more young plants. In the altitudinal gradient, similar percentages of litterfall components in all three climax forest types (BRF, QRF and BF) might reflect that the structure and environment of the three communities were relatively stable and similar to each other. However, litterfall in MMF showed a relatively lower percentage of flower and fruit, and a higher percentage of broad leaves, which is unique in the altitudinal gradient.

Litterfall production and climatic variables

Our study indicated that litterfall production in five of the six studied communities were not significantly affected by rainfall. This might be due to precipitation not being a limiting factor in the Dinghushan Biosphere Reserve. In fact, rainfall only controls the vegetation growth and hence the

Table 4 Comparison of litterfall production and its components in various forest types of the world

Geographical location	Forest type	Annual litterfall	Component	Reference
Not defined	Tropical rainforest	1100 g m^{-2}	/	Bray and Gorham 1964
	Temperate deciduous broad-leaved forest	550 g m^{-2}	/	
77°15′ E, 8°29′ N	several dominant species in tropical forests	563–865 g m^{-2}	73–81% leaf 12–21% woody 3–9% reproductive	Sundarapandian et al. (1999)
108°55′ E, 18°37′ N	Mountainous rain forest	770 g m^{-2}	70.7% leaf 21.3% branch 8% trash	Lu et al. (1988)
	Semi-deciduous monsoon forest	970 g m^{-2}	76.4% leaf 17.5% branch 6.1% trash	
82°15′ W, 29°47′ N	cypress (*Taxodium ascendens*) plantation	324 g m^{-2}	/	Liu et al. (1997)
	Slash pine (*Pinus elliottii*) plantation	359 g m^{-2}	/	
22°53′ E, 41°06′ N 22°32′ E, 40°23′ N 21°25′ E, 39°30′ N 22°30′ E, 39°50′ N	Maritime pine (*Pinus pinaster*) Black pine (*Pinus nigra*) Fir (*Abies borisiiregis*) beech (*Fagus silvatica*)	400–142 g m^{-2}, in the order: beech>fir>black pine> maritime pine	/	Kavvadias et al. (2001)
Located in south Jutland, Denmark	Norway spruce (*Picea abies*) stand	342 g m^{-2}	Up to 90% leaf	Pedersen and Hansen (1999)
	Sitka spruce (*Picea sitchensis*) stand	352 g m^{-2}		
	Beech (*Fagus sylvatica*) stand	311 g m^{-2}		
20°50′ E, 62°14′ N	*Pinus sylvestris* L. stand	200 g m^{-2}	74% leaf	Finer (1996)

litterfall production through increasing soil water content and atmospheric humidity. In studying needle litterfall prediction models for even-aged natural shortleaf pine (*Pinus echinata*) stands, Huebschmann et al. (1999) expected lagged precipitation to be a statistically significant variable, but found the contrary due to adequate precipitation during the study period. Together with our findings this suggests that precipitation or lagged precipitation would have no statistically significant effects on litterfall production for the stands where there is no shortage of water supply.

Our results clearly show that litterfall production amounts were higher in April to September than in other months for all studied forest communities. These results seem consistent with temperature patterns in the study area, which may indicate the importance of air temperature in influencing litterfall production. However, our analysis suggested that only monthly maximum and effective temperature had significant effects on litterfall production in three of the six studied forests, and explained only 25–40% of the variation. Other climatic variables such as monthly mean and minimum temperatures and rainfall were not responsible for the patterns of monthly litterfall production for the majority of the studied forests. This demonstrates that climatic variables were not as important as initially expected. We speculate that the relatively high litterfall rates during April–September may be associated with frequent storms occurring during this period, which may cause more physical breakage to plant tissues (leaves and branches). Another possible cause is that extreme high temperatures in summer may cause physical damage to these plant tissues and consequently lead to more litterfall production. As such, our results indicate that maximum temperature was a more important factor than other temperature variables. Further studies are needed to investigate the mechanisms of litterfall production in evergreen broadleaved forests in the study area before solid conclusions can be drawn.

Nevertheless, higher litterfall amounts in summer clearly indicate that temperature plays an important role in litterfall production in the study area. It is expected that increases in summer temperature due to climate change will increase litterfall production, which will lead to changes in carbon fluxes associated with litterfall and wildfire disturbance frequency.

Monthly litterfall patterns

The monthly litterfall production pattern is mainly controlled by community characteristics and environmental factors (Huebschmann et al. 1999; Sundarapandian and Swamy 1999; Lu and Liu 1988; Kavvadias et al. 2001; Pedersen and Hansen 1999). Finer (1996) reported that litterfall in September was 41% of the annual total due to high effective temperature totals. Our results show that litterfall production amounts were much higher in hot and wet months (from April to September) than the rest of year for all studied forests, which is also consistent with studies of similar vegetation types and nearby areas (Chen et al. 1992; Tu et al. 1993; Weng et al. 1993).

Monthly litterfall production in BF community showed two apparent maximum values in May and August and minimum values in June to July ($P < 0.001$) (Fig. 1B). Other similar studies from monsoon evergreen broadleaved forests demonstrated the same pattern (Lu and Liu 1988; Tu et al. 1993). Thus, the pattern of monthly litterfall distribution stated above is likely the general phenomenon of litterfall deposition in the regional vegetation such as BF in the Reserve.

Conclusions

The differences in litterfall production (monthly and annually) and dynamics between PF, MF and BF of the successional series demonstrate that litterfall production closely corresponds to forest succession stages. Annual litterfall production doubled from the pioneer forest PF to the climax forest BF. In contrast, the climax forests along the altitudinal gradient generally had a relatively stable annual litterfall production over time. The climax forest types BRF and QRF at lower elevations (<50 m at sea level) produced litterfall about two times as great as the climax forest MMF at higher elevations (500–800 m). The percentage of leaf litterfall ranges from 56% to 76%, and was the most important component of total litterfall production in all studied forest types. Our results also show that air temperature (especially maximum and effective temperatures) was an important environmental variable in affecting litterfall production in the studied communities.

Based on the findings of this research we conclude that the magnitude of litterfall production and associated ecological function of plantation forests cannot reach the levels of the regional climax forests in the first 40–50 years in Guangdong, China. This rejects the notion that in terms of litterfall production, the harvesting of late successional series or climax forests can be easily restored by plantations of pioneer species. The relatively stable litterfall production in all studied climax forests clearly shows their ecological equilibrium states. Finally, the significant role of temperature in litterfall production may have important implications for studying carbon cycle processes as litterfall represents an important carbon flux in forest ecosystems.

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