

茂兰喀斯特森林主要演替群落的凋落物动态

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摘 要 对茂兰喀斯特森林3种主要演替群落——喀斯特原生乔木林、次生林和灌木林的凋落物数量、组成特征及季节动态变化进行了为期27个月的观测研究。结果表明, 茂兰喀斯特原生乔木林、次生林和灌木林的年平均凋落物量分别为4.503、3.505和2.912 t·hm⁻²; 年总凋落物的叶、枝、花果和其他的比例分别为64.72%、14.60%、12.33%、8.35%; 74.28%、7.43%、10.88%、7.41%和75.94%、8.56%、12.93%、2.57%, 叶凋落物量占总凋落物量的64.72%–75.94%; 茂兰喀斯特森林3种演替群落凋落物的月动态变化规律均为双峰型, 峰值分别出现在生长季早期3–5月和休眠期10–12月。

关键词 喀斯特森林, 凋落物, 凋落节律, 茂兰, 演替群落

Litter dynamics of major successional communities in Maolan karst forest of China

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Abstract

Aims Litter is a key in nutrient cycling and energy flow of forest ecosystems. Our objective was to study the functions of karst forest litter by analyzing litter dynamics.

Methods Litter samples were collected monthly from karst primary forest, secondary forest and shrubland in our Maolan karst study area from October 2006 to December 2008. We divided the samples into leaves, branches, flowers and fruit, and others and weighed each after drying to constant weight at 80 °C.

Important findings The annual mean litter productions of primary forest, secondary forest and shrubland in the Maolan karst study area were 4.503, 3.505 and 2.912 t·hm⁻², respectively. The proportions of leaves, branches, flowers and fruits, and others for karst primary forest were 64.72%, 14.60%, 12.33% and 8.35%, respectively, while for karst secondary forest were 74.28%, 7.43%, 10.88% and 7.41%, respectively, and for karst shrubland were 75.94%, 8.56%, 12.93% and 2.57%, respectively. Therefore, leaves dominated litter. The monthly litterfall production dynamics for each community exhibited a bimodel distribution, with peaks early in the growing season and at dormancy.

Key words karst forest, litter, litter-fall dynamics, Maolan, succession community

凋落物是森林生态系统的重要组成部分, 是林地有机质的主要物质库和维持土壤肥力的基础, 是生态系统内物质循环的中心环节(Bray & Gorham, 1964; 王凤友, 1989; 骆宗诗等, 2007)。Chapin等(2002)的研究表明, 多数生态系统中植物所吸收的养分, 90%以上的氮和磷及60%以上的矿质元素都来自于植被凋落残体归还给土壤的养分再循环。森林凋落物作为连接植被与土壤两大系统的“纽带”, 一直是森林生态学、森林水文学、森林土壤学、生

物地球化学及环境化学等学科的重要研究内容(吴承祯等, 2000)。

近年来, 相关研究人员将森林凋落物放在全球气候变暖大背景下来进行研究, 非常重视凋落物在碳循环和营养元素循环中所起的作用、凋落物分解和土壤微生物活动释放的CO₂对温室效应的贡献(吴雅琼等, 2007)及全球气候变暖对凋落物动态的影响等(彭少麟和刘强, 2002; 宋新章等, 2008)。尽管有关凋落物的研究较多, 但对茂兰喀斯特植被凋

落物的研究较少(钱正敏等, 2009; 魏鲁明等, 2009), 且研究植被类型单一, 凋落物收集年限短而凋落节律无重复性, 缺乏与不同植被类型的比较。本研究主要针对这种现状, 拟通过对贵州茂兰国家级自然保护区喀斯特演替序列中3种主要群落类型进行为期27个月的凋落物量动态研究, 并与国内主要森林植被做对比分析, 来探讨茂兰喀斯特主要演替植被的凋落物产量、组成特征、季节动态变化及其与森林结构和物质循环的关系, 为阐明喀斯特地区物质循环的生物地球化学过程提供科学依据, 对喀斯特林分的改造和森林的优化经营亦有重要参考价值。

1 研究区概况和研究方法

1.1 研究区和样地环境概况

研究区在贵州省黔南布依族苗族自治州荔波县境内, 位于茂兰国家自然保护区的喀斯特原始森林核心区内, 该区是目前世界上同纬度地区残存下来的仅有的、原生性强、相对稳定的喀斯特森林生态系统, 也是喀斯特区原生性森林分布面积最大的

地区(周政贤, 1987)。选取的喀斯特原生乔木林是该地带的顶级森林群落, 喀斯特次生林是处于演替中间阶段的森林群落, 而灌木林是演替初级阶段的群落。群落植被概况见表1, 植被树种主要是一些适应性强的乡土种, 以耐旱、喜钙类型为主(钱正敏等, 2009)。研究区土壤主要为石灰土和零星分布的硅质土, 土层浅薄且不连续, 岩石渗漏性强, 土体持水量较低, 地表水缺乏, 临时性干旱频繁。区内年平均气温18.3 °C, 7月平均气温26.4 °C, 1月平均气温8.3 °C, ≥ 10 °C积温5 767.9 °C; 年平均降水量1 752 mm, 集中分布于5–10月, 夏季半年(5–9月)的降水量多达1 420 mm, 占全年总降水量的81%; 年平均相对湿度83%, 全年日照时数1 272.8 h, 日照率29%, 属于中亚热带季风湿润气候区(周政贤, 1987; 朱守谦, 1997)。研究期间拉桥观测站的月平均降水量、大气相对湿度和气温见图1。

1.2 研究方法

2006年9月在茂兰核心区拉桥小流域选取喀斯特原生乔木林、次生林和灌木林3种植被演替群落,

表1 演替群落植被基本概况

Table 1 Basic features of vegetation in successional communities

植被类型 Vegetation type	坡度 Slope	坡向 Slope aspect	位置 Location	植被特征 Vegetation characteristics	优势种 Dominant species
喀斯特原生乔木林 Karst primary arboreal forest	30°–40°	Northeast	25°18'05"– 25°18'16" N, 107°57'10"– 107°57'40" E	层次结构比较完整, 乔木层、灌木层和草本层之间分化清晰, 以乔木层为主, 高10–20 m, 乔木层覆盖率达80%以上; 灌木层高3–8 m, 盖度5%–10%; 地表层有地衣苔藓着生, 林下覆盖有3–5 cm厚的枯枝落叶层。 The stand structure was well integral and hierarchic, which could be clearly divided into tree layer, shrub layer and herb layer, and structure was dominated by tree layer. The mean tree height and coverage of tree layer were 10–20 m and more than 80%, respectively. The height of shrub layer with coverage of 5%–10% was 3–8 m, some lichens and mosses grew on the ground, the thickness of litter layer was 3–5 cm under forest.	圆果化香树、短萼海桐、小果润楠、青檀、光叶海桐、丝栗栲 <i>Platycarya longipes</i> , <i>Pittosporum brevicalyx</i> , <i>Machilus microcarpa</i> , <i>Pteroceltis tatarinowii</i> , <i>Pittosporum glabratum</i> , <i>Castanopsis fargesii</i>
喀斯特次生林 Karst secondary forest	30°–40°	Southwest	25°18'35"– 25°18'50" N, 107°56'45"– 107°57'00" E	林分层次结构分化明显, 乔木层、灌木层比较发达, 高5–12 m, 乔木层覆盖率达80%以上; 灌木层高2–3 m, 盖度10%左右, 地表有少量藤刺、蕨类、地衣苔藓等分布, 林下枯枝落叶层厚1–2 cm。 The stand structure was well hierarchic, of which tree layer and shrub layer were matured. The mean tree height and coverage of tree layer were 5–12 m and more than 80%, respectively. The height of shrub layer with coverage of 10% was 2–3 m, The land was covered by a small amount of thorns, ferns, lichens and mosses, the thickness of litter layer was 1–2 cm under forest.	云贵鹅耳枥、青冈、丝栗栲、马尾松、香叶树、十大功劳 <i>Carpinus pubescens</i> , <i>Cyclobalanopsis glauca</i> , <i>Castanopsis fargesii</i> , <i>Pinus massoniana</i> , <i>Lindera communis</i> , <i>Mahonia fortunei</i>
喀斯特灌木林 Karst shrubland	20°–30°	Northeast	25°18'20"– 25°18'35" N, 107°56'10"– 107°56'25" E	林分垂直结构单一, 无或有少量乔木, 主要以灌木层为主, 高度2–4 m, 覆盖率达80%以上, 林下覆盖的枯枝落叶层厚约1–2 cm。 The stand vertical structure was simple with a small amount of or no tree layer, which was dominated by shrub layer. The mean tree height and coverage of shrub layer were 2–4 m and more than 80%, respectively. The thickness of litter layer was 1–2 cm under forest.	南天竹、圆果化香树、香叶树、荔波鹅耳枥、齿叶黄皮、多脉青冈 <i>Nandina domestica</i> , <i>Platycarya longipes</i> , <i>Lindera communis</i> , <i>Carpinus lipoensis</i> , <i>Clausena dumiana</i> , <i>Cyclobalanopsis multiervis</i>

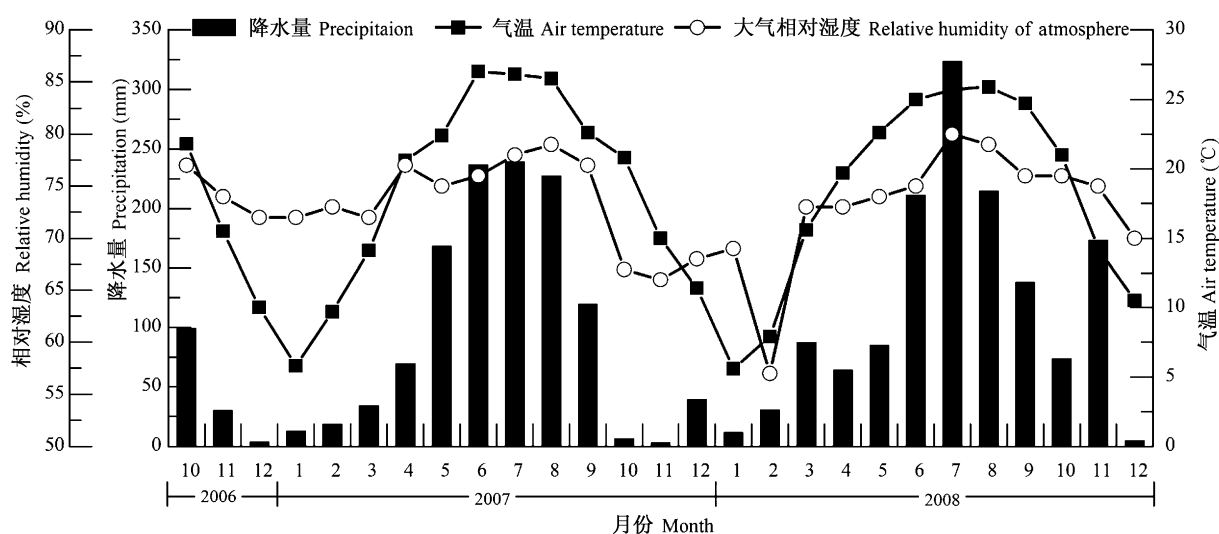


图1 拉桥观测站月平均降水量、大气相对湿度和气温的变化。

Fig. 1 Monthly variation of rainfall, relative humidity of atmosphere and air temperature in the Laqiao observation station.

按照随机加局部控制的原则并兼顾重复性, 考虑样地密度、样地最小面积、坡向和坡位等因素, 一共布置9个10 m × 10 m灌木林样地、9个20 m × 30 m原生乔木林样地和4个20 m × 30 m次生林样地。凋落物的测定采用直接收集测定法(王凤友, 1989), 在设置的每个样地内按照“梅花形”五点法布置5个凋落物收集器, 收集器由孔径为0.2 mm × 0.2 mm的尼龙网制成, 接收面积1.0 m × 1.0 m, 放置于离地面50 cm的高处。从2006年10月起, 每月月底收集凋落物1次, 2008年12月底结束收集, 为期27个月。

将凋落物分成树叶、枝、落花落果和其他等组成, 树叶又分成常绿树叶和落叶树叶两种。将各分组的凋落物于80 °C烘干至恒重后分别称重, 最后计算出各类凋落物量。试验样地附近有一气象观测站, 记录常规气象指标, 其月平均降水量和气温等用于分析凋落物的月动态特征。

2 结果

2.1 凋落物的总凋落量

喀斯特植被演替系列因林分组成、人为干扰以及演替阶段的不同, 其凋落物的年总凋落物量表现出一定的差异。27个月的观测结果表明(图2), 喀斯特原生乔木林的年总凋落物量为4.002–5.004 t·hm⁻², 年平均凋落物量4.503 t·hm⁻², 变异系数为16%; 次生林的年总凋落物量为3.239–3.771 t·hm⁻², 年平均凋落物量3.505 t·hm⁻², 变异系数为11%; 灌

木林的年总凋落物量为2.815–3.009 t·hm⁻², 年平均凋落物量2.912 t·hm⁻², 变异系数为5%。年平均凋落物量表现为喀斯特原生乔木林>喀斯特次生林>喀斯特灌木林。

方差分析的结果表明, 3种不同喀斯特植被类型的月平均凋落物量差异极显著($F = 5.890$, $p = 0.004 < 0.01$), LSD 多重比较的结果是原生乔木林的月平均凋落物量(370.54 kg·hm⁻²)显著高于次生林(296.21 kg·hm⁻²) ($p = 0.034 < 0.05$), 极显著高于灌木林(254.13 kg·hm⁻²) ($p = 0.001 < 0.01$), 而次生林和灌木林的月平均凋落物量之间无显著差异($p = 0.224 > 0.05$)。

2.2 凋落物的组成

叶凋落物是凋落物的主体, 喀斯特原生乔木林、次生林和灌木林的叶凋落物量占总凋落物量的比例分别是64.72%、74.28%和75.94%, 所占比例表现为喀斯特原生林<次生林<灌木林。叶凋落物以常绿树叶为主, 其中次生林常绿树叶凋落最多, 占叶凋落物量的65.00%; 枝凋落物量以原生乔木林最多, 占总凋落物量的14.60%, 灌木林次之, 为8.56%, 次生林最少, 占7.43%; 3种植被类型的花果凋落物量相差不大, 占总凋落物量的10.88%–12.93%; 凋落物中其他成分较少, 占2.57%–8.35%。

2.3 凋落物的凋落节律

3种植被类型的凋落物动态具有明显的季节性, 其凋落总量、叶、枝、花果和其他组分的月凋落变

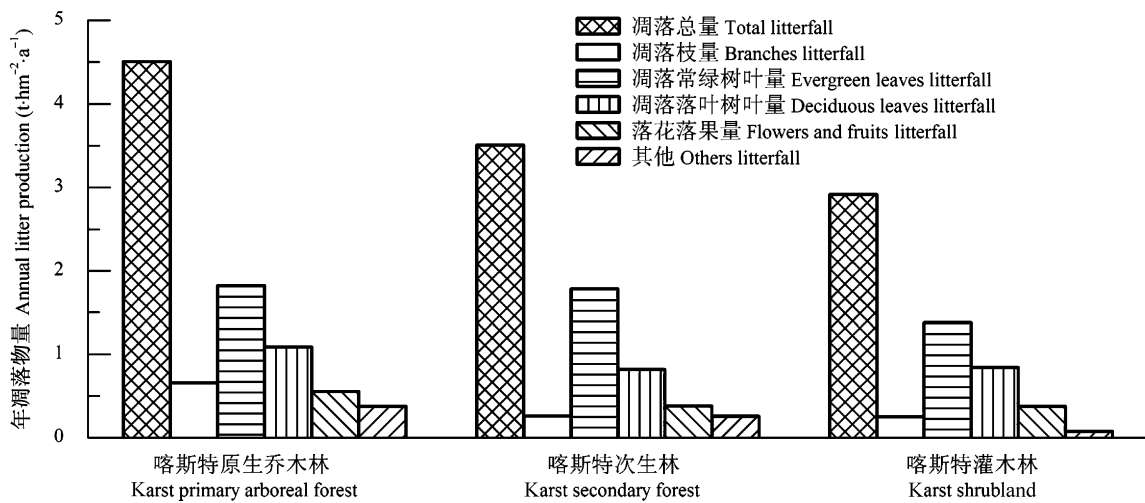


图2 不同演替群落的年凋落物量。
Fig. 2 Annual litter production in different successional communities.

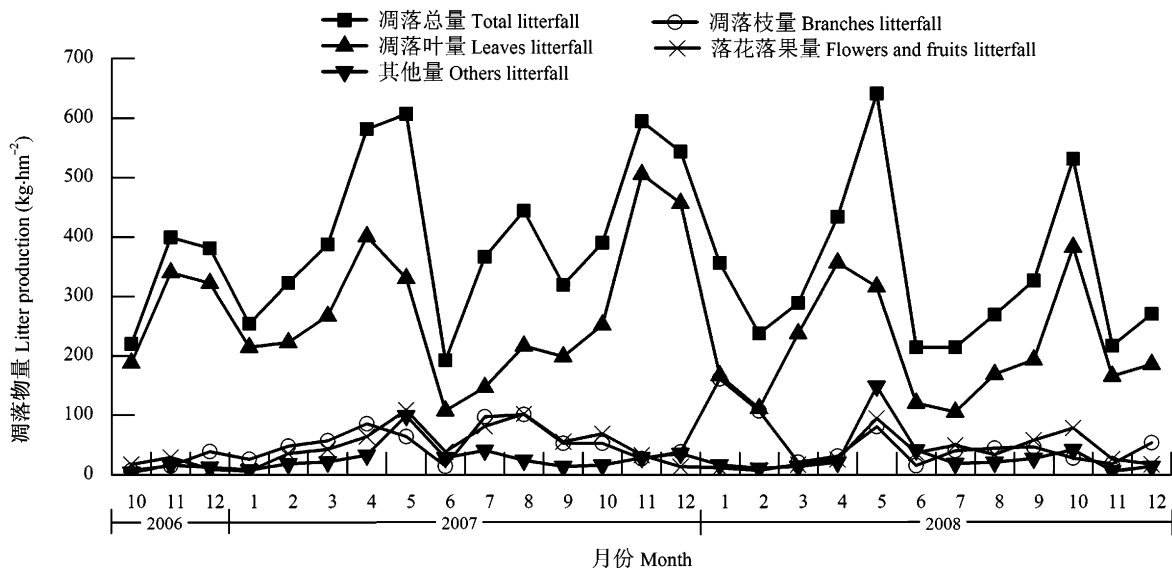


图3 喀斯特原生乔木林凋落物的月动态。
Fig. 3 Monthly dynamics of litterfall in karst primary arboreal forest.

化见图3–5。结果显示，各植被类型叶凋落物量的月变化趋势与凋落物总量的趋势一致，枝和其他凋落物量的月变化波动不规则，花果凋落物量的变化与其物候现象相一致。

喀斯特原生乔木林的凋落物总量和叶凋落物量的凋落节律为双峰型，第1次峰值一般出现在生长季前期(3–5月)，第2次峰值出现在10–12月，凋落物总量和叶凋落物量在第1次凋落高峰时分别占全

年凋落物量的32.78%和33.14%，第2次凋落高峰时分别占28.01%和32.91%。其中第1次凋落高峰时的叶凋落物以常绿树种落叶为主，占该峰值总落叶量的86.34%。凋落枝量在27个月中呈不规则变化。2008年1月凋落枝量达到峰值(160.86 kg·hm⁻²)，是月平均值(50.93 kg·hm⁻²)的3.16倍，2月的也达平均值的2.11倍，远高于2007年1月(25.87 kg·hm⁻²)和2月(47.71 kg·hm⁻²)的值，该异常可能与2008年1月中旬

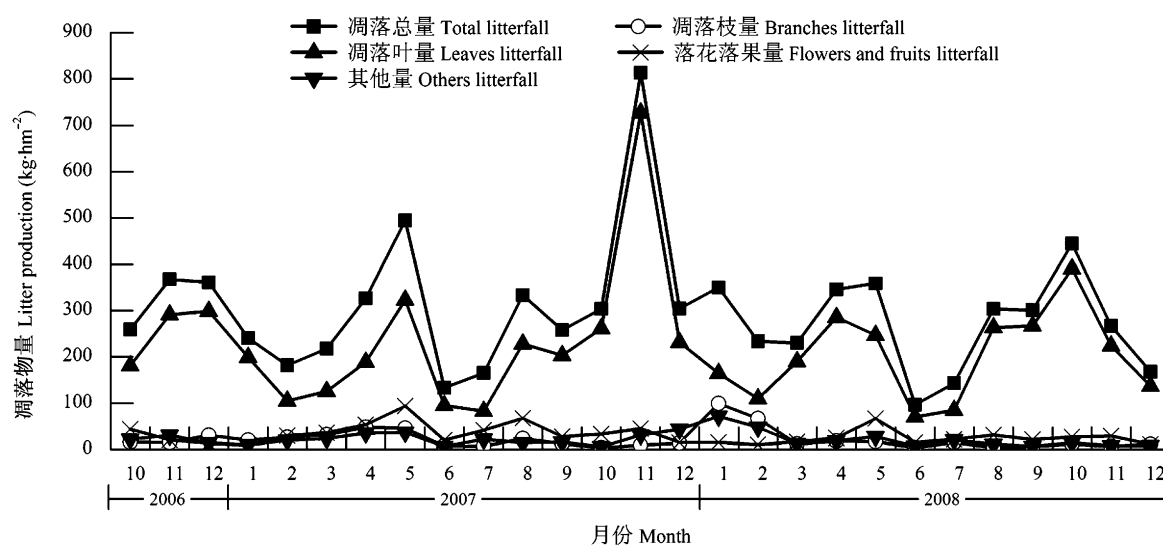


图4 喀斯特次生林凋落物的月动态。
Fig. 4 Monthly dynamics of litterfall in karst secondary forest.

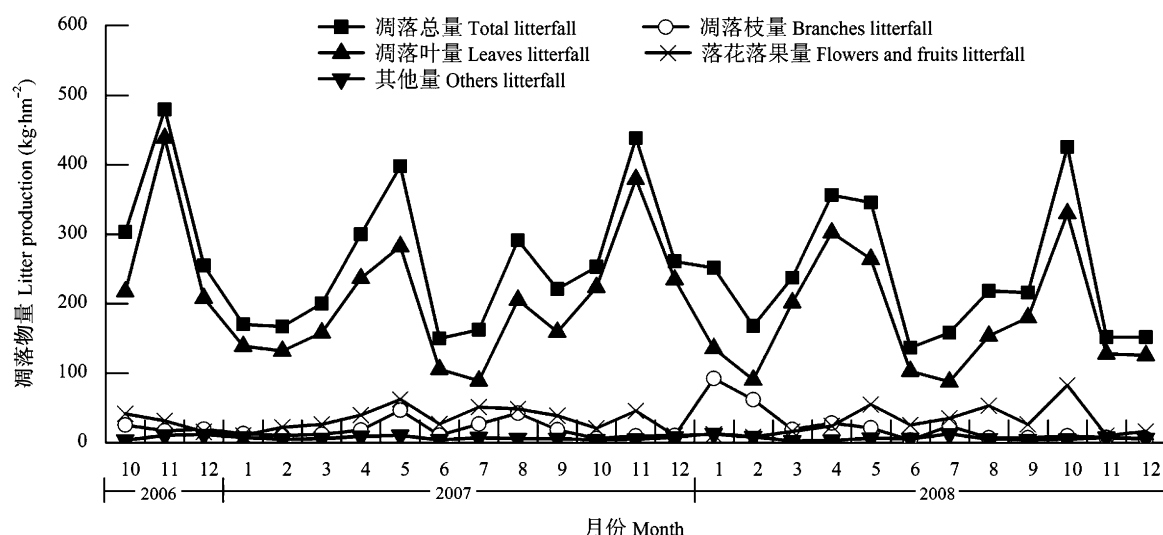


图5 喀斯特灌木林凋落物的月动态。
Fig. 5 Monthly dynamics of litterfall in karst shrubland.

至2月初的凝冻天气导致枝条大量折断凋落有关。其他量只在5月出现1个峰值。花果凋落物量在5月和10月稍多是与其物候现象相一致的, 分别占全年花和果实凋落物量的18.68%和13.86%。

由青冈(*Cyclobalanopsis glauca*)和丝栗栲(*Castanopsis fargesii*)组成的喀斯特次生林的凋落节律为双峰型, 第1次峰值出现在生长季前期(4-5月), 此时凋落物总量和叶凋落物量占全年凋落物量的比

例分别为21.76%和20.16%, 第2次峰值出现在10-12月, 此时凋落物总量和叶凋落物量占全年凋落物的比例分别为32.41%和37.49%。其中第1次凋落高峰时的叶凋落物中常绿树种落叶占绝大部分, 是该峰值总落叶量的99.03%, 而第2次凋落高峰时的叶凋落物中落叶树种落叶占该峰值总落叶量的48.48%, 常绿树种落叶占51.52%, 即常绿和落叶约各占1/2。凋落枝量的月平均值只有21.59 kg·hm⁻², 低于原生

乔木林的凋落量,且月变化波动不规则。2008年1月和2月凋落枝量出现峰值,分别为99.34和66.22 kg·hm⁻²,是月平均值的4.60倍和3.07倍,可能与2008年1月中旬至2月初的凝冻天气有关。其他量波动平缓且无明显峰值。花果只在5月出现1个峰值,占全年花和果实凋落物量的21.30%。

由齿叶黄皮(*Clausena dunniana*)、香叶树(*Lindera communis*)和园果化香(*Platycarya longipes*)幼树组成的喀斯特灌木林的凋落节律亦为双峰型,第1次峰值出现在生长季前期(3–5月),第2次峰值出现在10–12月,凋落物总量和叶凋落物量在第1次凋落高峰时占全年凋落物量的比例分别为31.59%和32.74%,在第2次凋落高峰时分别占28.76%和31.75%。其中第1次凋落高峰时的叶凋落物以常绿树种落叶为主,占该峰值总落叶量的94.42%,而第2次凋落高峰时以落叶树种落叶为主,占该峰值的

60.50%。凋落枝量在27个月中无明显变化规律。2008年1月中旬至2月初的凝冻天气对灌木林也有较大影响,2008年1月的凋落枝量达到峰值(92.06 kg·hm⁻²),为月平均值(20.78 kg·hm⁻²)的4.43倍,2月的凋落枝量也达到月平均值的2.95倍,远高于2007年1月(12.54 kg·hm⁻²)和2月(9.68 kg·hm⁻²)。其他量波动很平缓且无明显峰值。花果凋落物量分别在5月和10月出现峰值,分别占全年花和果实凋落物量的15.39%和14.00%。

3 讨论

3.1 凋落物的总凋落量比较

凋落物是森林生态系统生物量的重要组成部分,是森林生态系统功能的体现,其凋落量受地带性、森林结构、气候条件、植被类型和林木的生理特征等一系列因素影响(表2)。

表2 中国气候带主要森林凋落物量的分布格局

Table 2 Distribution patterns of litterfall in main forests of climate zones in China

气候带 Climate zone	类型 Type	凋落物量 Litterfall (t·hm ⁻² ·a ⁻¹)	凋落叶比例 leaf litterfall- rate (%)	文献 Reference
热带 Tropical zone	红树林 Mangrove forest	12.545–13.882	64.3–79.9	Lin <i>et al.</i> , 1990; Zhang & Chen, 2003
	季雨林 Monsoon forest	8.244–11.290	55.3–65.6	Zheng <i>et al.</i> , 1990; Wu <i>et al.</i> , 1994
南亚热带 Southern subtropical zone	人工阔叶林 Artificial broad-leaved forest	5.541–10.433	61.4–87.5	Zou <i>et al.</i> , 2006; Lu <i>et al.</i> , 2008
	常绿阔叶林 Evergreen broad-leaved forest	4.630–8.840	51.0–81.3	Wang <i>et al.</i> , 1996; Hou <i>et al.</i> , 1998; Yan <i>et al.</i> , 2001; Guan <i>et al.</i> , 2004
	针阔混交林 Coniferous and broad-leaved mixed forest	8.500	67.0	Zhang <i>et al.</i> , 2000
	灌木林 Shrubbery	4.773	69.2	Guan & Chen, 1998
中亚热带 Central subtropical zone	人工阔叶林 Artificial broad-leaved forest	7.318–9.538	65.3–72.0	Yang <i>et al.</i> , 2003, 2004
	常绿阔叶林 Evergreen broad-leaved forest	6.770–13.030	41.1–70.2	Liu <i>et al.</i> , 1995; Katagiri <i>et al.</i> , 2001; Yang <i>et al.</i> , 2003; Yan <i>et al.</i> , 2008
	次生常绿阔叶林 Secondary evergreen broad-leaved forest	6.870–11.700	42.3–57.7	Wu, 2006; Yan <i>et al.</i> , 2008
	针阔混交林 Coniferous and broad-leaved mixed forest	7.123–8.390	56.9–61.9	Lin & Fan, 2005; Yan <i>et al.</i> , 2008
	灌木林 Shrubbery	6.380	77.7	Yan <i>et al.</i> , 2008
	滇桂喀斯特原生林 Karst primary forest in Guangxi and Yunnan	1.834–4.058	78.0–83.6	Zeng <i>et al.</i> , 2010
	滇桂喀斯特次生林 Karst secondary forest in Guangxi and Yunnan	1.979–3.510	76.3–95.3	Liu & Duan, 2004; Wu <i>et al.</i> , 2007; Zeng <i>et al.</i> , 2010
	北亚热带 Northern subtropical zone	人工针阔混交林 Artificial coniferous and broad-leaved mixed forest	3.610–4.689	33.7–72.1
温带 Temperate zone	针阔混交林 Coniferous and broad-leaved mixed forest	4.689–5.701	55.5–79.7	Luo <i>et al.</i> , 2007; Wu <i>et al.</i> , 2009
	人工针叶林 Artificial coniferous forest	3.714	91.9	Chen <i>et al.</i> , 1998
	落叶阔叶林 Deciduous broad-leaved forest	2.883–3.130	64.8–76.0	Zhang <i>et al.</i> , 2008; Liu <i>et al.</i> , 2009
	针阔混交林 Coniferous and broad-leaved mixed forest	4.146–4.902	60.3–74.0	Zhang <i>et al.</i> , 2008; Liu <i>et al.</i> , 2009
	常绿针叶林 Evergreen coniferous forest	2.472	54.0	Zhang <i>et al.</i> , 2008
	落叶针叶林 Deciduous coniferous forest	2.337	73.0	Zhang <i>et al.</i> , 2008

由于植被类型和生境条件的不同,即使是同一气候带,其凋落物量也有很大差异。茂兰喀斯特3种植被类型的年平均凋落物量低于中亚热带常绿阔叶林(6.770–13.030 t·hm⁻²·a⁻¹) (刘文耀等, 1995; Katagiri *et al.*, 2001; 杨玉盛等, 2003; 阎恩荣等, 2008)和次生常绿阔叶林(6.870–11.700 t·hm⁻²·a⁻¹) (吴擢溪, 2006; 阎恩荣等, 2008), 低于针阔混交林(7.123–8.390 t·hm⁻²·a⁻¹) (林德喜和樊后保, 2005; 阎恩荣等, 2008)和人工阔叶林(7.318–9.538 t·hm⁻²·a⁻¹) (杨玉盛等, 2003, 2004), 甚至低于亚热带灌木林(6.380 t·hm⁻²·a⁻¹) (阎恩荣等, 2008)。茂兰喀斯特植被的凋落物量仅为同一地带性常绿阔叶林的30%左右, 反映了非地带性因素对森林凋落物量的影响。茂兰喀斯特土层浅薄且贫瘠缺水的生境条件形成了生物量较低的特殊山地喀斯特植被类型, 且常绿树种为该区森林植被的主体, 落叶树种所占比例较小, 进一步导致了喀斯特区域较低的凋落物量。

在相同气候带和相似喀斯特生境条件下, 茂兰喀斯特原生林和次生林的年凋落物量高于滇桂喀斯特原生林(1.834–4.058 t·hm⁻²·a⁻¹)和次生林(1.979–3.510 t·hm⁻²·a⁻¹) (刘曦和段昌群, 2004; 吴毅等, 2007; 曾昭霞等, 2010)。该现象可能是由于滇桂喀斯特森林属于偏干性森林类型, 且植被的人为干扰严重, 而茂兰喀斯特森林属于偏湿性森林, 组成结构复杂, 且植被人为干扰程度较低, 物种类型多样, 因而凋落物量高于滇桂喀斯特区森林。但总体而言, 喀斯特地区植被的凋落物量较常态地貌同气候区的林型低。

3.2 凋落物叶凋落量的比较

王凤友(1989)综述世界上大量有关凋落物的研究后认为, 叶凋落量占凋落物总量的60%–80%。本研究中茂兰喀斯特演替群落3种植被类型的落叶量占总凋落物量的64.7%–75.9%, 在该范围之内, 体现了落叶在喀斯特森林生态系统的凋落物归还中的关键地位。

茂兰喀斯特演替群落3种植被类型的落叶量占总凋落物量的比例低于滇桂喀斯特原生林(78.0%–83.6%)和次生林(76.3%–95.3%) (刘曦和段昌群, 2004; 吴毅等, 2007; 曾昭霞等, 2010), 亦低于中亚热带灌木林(77.7%) (阎恩荣等, 2008), 但高于中亚热带常绿阔叶林(41.1%–70.2%) (刘文耀等, 1995; Katagiri *et al.*, 2001; 杨玉盛等, 2003; 阎恩荣等,

2008)、次生常绿阔叶林(42.3%–57.7%) (吴擢溪, 2006; 阎恩荣等, 2008)和针阔混交林(56.9%–61.9%) (林德喜和樊后保, 2005; 阎恩荣等, 2008)。在亚热带成熟群落中, 植物种类组成多样, 结构层次相对复杂, 木质残体碎屑的凋落来源更为丰富, 凋落物量相对较多, 落叶量占总凋落物量的比例较小; 在亚热带喀斯特退化群落中, 植被高度低, 群落结构趋于简单化, 返还的凋落物数量也相应下降, 落叶量占总凋落物量的比例较大, 说明茂兰喀斯特森林的群落结构较滇桂喀斯特群落更稳定、更成熟, 但比中亚热带常绿阔叶林群落要简单。

3.3 凋落物的凋落节律及对气候因子的响应

凋落物的季节动态与森林植物自身的生物学特性和当地气候条件的变化有密切关系。茂兰喀斯特森林3种演替群落的季节动态均为双峰型, 5月和10–12月达到两个最大峰值, 其中前者峰值的叶凋落物以常绿树种为主, 而后者峰值的叶凋落物以落叶树种为主。因为春季大量常绿树种一次性换叶, 凋落量急增, 形成第1个凋落峰值, 而10–12月正是落叶树种的落叶季节, 此时叶凋落物量急增, 形成总凋落物量的第2次峰值。

茂兰喀斯特森林与大多数亚热带阔叶树种凋落物的季节节律(4月与12月出现峰值) (王凤友, 1989; 杨玉盛等, 2003; 官丽莉等, 2004; 阎恩荣等, 2008)不一致, 应该与研究区雨季时间为5–10月, 降水主要集中在6–8月有关(图1)。喀斯特森林植物为了适应喀斯特地区降水集中、缺水少土等特殊自然环境, 减少水分丢失, 缩短了其生理生长周期。同时, 喀斯特植被的月平均凋落物量与月平均降水量之间呈线性负相关关系($r = -0.295$, $p = 0.007 < 0.05$), 而与月平均气温之间无线性相关关系($r = -0.003$, $p = 0.985$), 说明茂兰喀斯特森林的凋落节律主要受水分控制, 而其他亚热带阔叶林主要受温度控制。另外, 喀斯特森林凋落物总量在5月出现峰值后, 在6月出现低谷, 这与邹碧等(2006)的研究结果相似, 即一段时间的大量落叶后, 跟着是一个少落叶时期。

4 结论

1)茂兰喀斯特原生乔木林、次生林和灌木林凋落物的年平均凋落量分别为4.503、3.505和2.912 t·hm⁻², 茂兰喀斯特地区的凋落物量较常态地貌同

气候区植被低。

2) 茂兰喀斯特森林演替群落的叶凋落物量占总凋落物量的64.72%–75.94%，森林群落结构较中亚热带常绿阔叶林群落简单。

3) 茂兰喀斯特森林3种演替群落凋落物的季节动态均为双峰型，峰值分别出现在生长季早期和休眠期，与当地的植被特性和水分状况密切相关。

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参考文献

- Bray JR, Gorham E (1964). Litter production in forests of the world. In: Cragg JB ed. *Advances in Ecological Research*. Academic Press, New York. 101–157.
- Chapin FS III, Matson PA, Mooney HA (2002). *Principles of Terrestrial Ecosystem Ecology*. Springer-Verlag, New York.
- Chen LX (陈立新), Chen XW (陈祥伟), Duan WB (段文标) (1998). Larch litter and soil fertility. *Chinese Journal of Applied Ecology* (应用生态学报), 9, 581–586. (in Chinese with English abstract)
- Guan DS (管东生), Chen YJ (陈玉娟) (1998). Litterfall and the nutrients return of *Rhodomyrtus tomentosa* shrubland in Hong Kong. *Rural Eco-Environment* (农村生态环境), 14(2), 24–28. (in Chinese with English abstract)
- Guan LL (官丽莉), Zhou GY (周国逸), Zhang DQ (张德强), Liu JX (刘菊秀), Zhang QM (张倩媚) (2004). Twenty years of litter fall dynamics in subtropical evergreen broad-leaved forests at the Dinghushan Forest Ecosystem Research Station. *Acta Phytoecologica Sinica* (植物生态学报), 28, 449–456. (in Chinese with English abstract)
- Hou Y (侯庸), Wang BS (王伯荪), Zhang HD (张宏达), Li MG (李鸣光) (1998). The litterfall of the south subtropical evergreen broad-leaved forest in Heishiding Nature Reserve. *Ecologic Science* (生态科学), 17(2), 14–18. (in Chinese with English abstract)
- Katagiri S, Li CH (李昌华), Kawaguchi H, Nagayama Y (2001). Nutrients return of litterfall of a natural evergreen broad-leaved forest in southern China. *Resources Science* (资源科学), 23(A), 58–67. (in Chinese with English abstract)
- Lin DX (林德喜), Fan HB (樊后保) (2005). Changes in amount, nutrient contents and turnover time of forest litter after interplanting hardwood species under Masson pine stand. *Scientia Silvae Sinicae* (林业科学), 41(6), 7–15. (in Chinese with English abstract)
- Lin P (林鹏), Lu CY (卢昌义), Wang GL (王恭礼), Chen HX (陈焕雄) (1990). Study on dynamics of litter fall of *Bru-guiera sexangula* mangrove in Hainan Island, China. *Acta Phytoecologica et Geobotanica Sinica* (植物生态学与地植物学学报), 14, 69–74. (in Chinese with English abstract)
- Liu WY (刘文耀), Xie SC (谢寿昌), Xie KJ (谢克金), Yang GP (杨国平) (1995). Preliminary studies on the litterfall and coarse woody debris in mid-mountain humid evergreen broad-leaved forest in Ailao Mountains. *Acta Botanica Sinica* (植物学报), 37, 807–814. (in Chinese with English abstract)
- Liu X (刘曦), Duan CQ (段昌群) (2004). Research on characteristics of secondary semi-humid evergreen broad-leaved forest in Samachang area. *Yunnan Environmental Science* (云南环境科学), 23(A01), 53–56. (in Chinese with English abstract)
- Liu Y (刘颖), Han SJ (韩士杰), Lin L (林鹿) (2009). Dynamics characteristics of litterfalls in four forest types of Changbai Mountains, China. *Chinese Journal of Ecology* (生态学杂志), 28, 7–11. (in Chinese with English abstract)
- Long CL (龙翠玲) (2009). Study on dynamic pattern of species diversity in gaps of karst forest in Maolan Natural Reserve, Guizhou Province. *Journal of Mountain Science* (山地学报), 27, 278–284. (in Chinese with English abstract)
- Lu LH (卢立华), Jia HY (贾宏炎), He RM (何日明), Li JL (李吉良), Qin SY (覃书源) (2008). A preliminary study on litter falls of six kinds of plantations in the tropical south Asia. *Forest Research* (林业科学研究), 21, 346–352. (in Chinese with English abstract)
- Luo ZS (骆宗诗), Xiang CH (向成华), Mu CL (慕长龙) (2007). The litterfall of major forests in Guansi River Watershed in Mianyang City, Sichuan Province. *Acta Ecologica Sinica* (生态学报), 27, 1772–1781. (in Chinese with English abstract)
- Peng SL (彭少麟), Liu Q (刘强) (2002). The dynamics of forest litter and its responses to global warming. *Acta Ecologica Sinica* (生态学报), 22, 1534–1544. (in Chinese with English abstract)
- Qian ZM (钱正敏), Ran JC (冉景丞), Rong L (容丽), Lan HB

- (兰洪波), Shen QX (申秋秀), Linghu KH (令狐克红) (2009). Dynamic study on forest litter amount in Maolan karst forest. *Journal of Anhui Agricultural Sciences* (安徽农业科学), 37, 3485–3487, 3523. (in Chinese with English abstract)
- Song XZ (宋新章), Jiang H (江洪), Zhang HL (张慧玲), Yu SQ (余树全), Zhou GM (周国模), Ma YD (马元丹), Scott XC (2008). A review on the effects of global environment change on litter decomposition. *Acta Ecologica Sinica* (生态学报), 28, 4414–4423. (in Chinese with English abstract)
- Wang FY (王凤友) (1989). Review on the study of forest litterfall. *Advance in Ecology* (生态学进展), 6(2), 82–89. (in Chinese with English abstract)
- Wang LM (王良睦), Shao C (邵成), Zheng WJ (郑文教), Lin P (林鹏) (1996). Studies on litter fall and residues in the subtropical rain forest in Hexi of Fujian. *Journal of Xiamen University (Natural Science)* (厦门大学学报(自然科学版)), 35, 795–800. (in Chinese with English abstract)
- Wei LM (魏鲁明), Yu DL (余登利), Chen ZR (陈正仁) (2009). Study on the dynamic variation of litter falls in Maolan karst forest. *Journal of Nanjing Forestry University (Natural Science Edition)* (南京林业大学学报(自然科学版)), 33(3), 31–34. (in Chinese with English abstract)
- Wu CZ (吴承祯), Hong W (洪伟), Jiang ZL (姜志林), Zheng FH (郑发辉) (2000). Advances in research of forest litterfall in China. *Acta Agriculturae Universitatis Jiangxiensis* (江西农业大学学报), 22, 405–410. (in Chinese with English abstract)
- Wu XX (吴雪仙), Chen LW (陈林武), Xiang CH (向成华), Zhang FH (张发会), Mu CL (慕长龙) (2009). Litter production and nutrient return in three kinds of plantations in the upper reaches of the Jialing River. *Journal of Sichuan Forestry Science and Technology* (四川林业科技), 30(3), 12–17. (in Chinese with English abstract)
- Wu Y (吴毅), Liu WY (刘文耀), Shen YX (沈有信), Cui JW (崔建武), Li YH (李玉辉), Liu LH (刘伦辉) (2007). Dynamics of litterfall and litter on forest floor of natural forest and plantation in Stone Forest World Geological Park. *Journal of Mountain Science* (山地学报), 25, 317–325. (in Chinese with English abstract)
- Wu YQ (吴雅琼), Liu GH (刘国华), Fu BJ (傅伯杰), Guo YH (郭玉华) (2007). Soil CO₂ efflux of forest ecosystem in China: distribution and controlling factors. *Acta Ecologica Sinica* (生态学报), 27, 2126–2135. (in Chinese with English abstract)
- Wu ZM (吴仲民), Lu JP (卢俊培), Du ZH (杜志鹤) (1994). Litter production and storage in the natural and regenerated tropical montane rain forests at Jianfengling, Hainan Island. *Acta Phytoecologica Sinica* (植物生态学报), 18, 306–313. (in Chinese with English abstract)
- Wu ZX (吴擢溪) (2006). Amount, component, and seasonal pattern of litterfall in secondary evergreen broadleaved forest. *Journal of Mountain Science* (山地学报), 24, 215–221. (in Chinese with English abstract)
- Yan ER (阎恩荣), Wang XH (王希华), Zhou W (周武) (2008). Characteristics of litterfall in relation to soil nutrients in mature and degraded evergreen broad-leaved forests of Tiantong, East China. *Journal of Plant Ecology (Chinese Version)* (植物生态学报), 32, 1–12. (in Chinese with English abstract)
- Yan JH (闫俊华), Zhou GY (周国逸), Tang XL (唐旭利), Zhang DQ (张德强) (2001). Characteristics of litter and its contained water in three succession communities in Dinghushan Mountain. *Chinese Journal of Applied Ecology* (应用生态学报), 12, 509–512. (in Chinese with English abstract)
- Yang YS (杨玉盛), Chen YX (陈银秀), He ZM (何宗明), Guo JF (郭剑芬), Liu CH (刘春华) (2004). Comparatively study on litter properties between plantations of *Fokienia hodginsii* and *Cunninghamia lanceolata*. *Scientia Silvae Sinicae* (林业科学), 40(1), 2–10. (in Chinese with English abstract)
- Yang YS, Lin P, Guo JF, Lin RY, Chen GS, He ZM, Xie JS (2003). Litter production, nutrient return and leaf-litter decomposition in natural and monoculture plantation forests of *Castanopsis kawakamii* in subtropical China. *Acta Ecologica Sinica* (生态学报), 23, 1278–1289.
- Zeng ZX (曾昭霞), Liu XL (刘孝利), Wang KL (王克林), Zeng FP (曾馥平), Song TQ (宋同清), Song XJ (宋希娟) (2010). Comparison of litterfall and nutrients return properties of primary and secondary forest ecosystems, the karst region of Northwest Guangxi. *Ecology and Environmental Sciences* (生态环境学报), 19, 146–151. (in Chinese with English abstract)
- Zhang DQ (张德强), Ye WH (叶万辉), Yu QF (余清发), Kong GH (孔国辉), Zhang YC (张佑倡) (2000). The litter-fall of representative forests of successional series in Dinghushan. *Acta Ecologica Sinica* (生态学报), 20,

- 938–944. (in Chinese with English abstract)
- Zhang QM (张乔民), Chen YF (陈永福) (2003). Production and seasonal change pattern of litter fall of *Rhizophora apiculata* in Sanya River mangroves, Hainan Island. *Acta Ecologica Sinica* (生态学报), 23, 1977–1983. (in Chinese with English abstract)
- Zhang XP (张新平), Wang XP (王襄平), Zhu B (朱彪), Zong ZJ (宗占江), Peng CH (彭长辉), Fang JY (方精云) (2008). Litter fall production in relation to environmental factors in northeast China's forests. *Journal of Plant Ecology (Chinese Version)* (植物生态学报), 32, 1031–1040. (in Chinese with English abstract)
- Zheng Z (郑征), Liu LH (刘伦辉), He AJ (和爱军), Jing GF (荆桂芬) (1990). Litterfall and leaf consumption by animals in humid seasonal rain forest in Xishuangbanna, China. *Acta Botanica Sinica* (植物学报), 32, 551–557. (in Chinese with English abstract)
- Zhou ZX (周政贤) (1987). *Scientific Survey of the Maolan Karst Forest* (茂兰喀斯特森林科学考察集). Guizhou People's Press, Guiyang. 1–23. (in Chinese)
- Zhu SQ (朱守谦) (1997). *Ecological Study of Karst Forest (II)* (喀斯特森林生态研究(II)). Guizhou Science and Technology Press, Guiyang. 33–167. (in Chinese)
- Zou B (邹碧), Li ZA (李志安), Ding YZ (丁永祯), Tan WN (谭万能) (2006). Litterfall of common plantations in south subtropical China. *Acta Ecologica Sinica* (生态学报), 26, 715–721. (in Chinese with English abstract)

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