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高山森林林窗对凋落叶分解的影响

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摘要: 林窗对降水和光照等环境条件的再分配以及分解者群落的影响可能深刻作用于森林凋落物分解过程, 但有关高山森林林窗大小对凋落物分解的影响尚无研究报道。采用凋落物分解袋法, 研究了川西高山森林不同大小林窗对非生长季节和生长季节红桦 (*Betula albo-sinensis*) 和岷江冷杉 (*Abies faxoniana*) 凋落叶质量损失的影响。结果显示, 经过一年的分解, 不同生境下红桦和岷江冷杉凋落叶分别分解了 27.25%—30.12% 和 27.04%—27.96%, 其中非生长季节占 53.83%—60.18% 和 50.23%—59.09%。林窗对红桦和岷江冷杉凋落叶质量损失的影响因物种不同而呈现季节差异。总体上, 林窗加快了岷江冷杉凋落叶的分解而延缓了红桦凋落叶的分解。与郁闭林下相比, 林窗显著增加了 2 种凋落叶非生长季节的质量损失速率, 显著降低了生长季节 2 种凋落叶的质量损失速率; 2 种凋落叶质量损失速率在非生长季节随林窗面积增大而加快, 在生长季节随林窗面积增大而减慢。林窗显著影响了初冻期、深冻期和融化期岷江冷杉凋落叶的质量损失率, 但对红桦凋落叶质量损失率影响不显著。可见, 高山森林凋落物分解过程受到林窗的显著影响, 并且阔叶和针叶凋落叶在非生长季节和生长季节响应应具有明显差异。

关键词: 林窗; 凋落物分解; 质量损失; 非生长季节; 针叶林; 高寒地区

Effects of gap sizes on foliar litter decomposition in alpine forests

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Abstract: Forest gaps are one of the most normal interferences in primary forest ecosystems, and they play an important role in not only aboveground processes but also belowground processes. However, many studies have paid more attention to the effects of forest gaps on aboveground processes. Increasing evidence has demonstrated that forest gaps have a strong effect on mass loss and carbon and nutrient release in litter by redistributing precipitation, light, and other environmental factors. At high latitudes and altitudes, litter decomposition due to forest gaps may be more complex because of seasonal snow cover and freeze-thaw cycles. Theoretically, interception of rainfall and snowfall in the winter by the canopy and canopy shading may cause the hydrothermal dynamics on the forest floor to vary with respect to gap sizes and critical periods. Currently, little information is available on the effects of gap sizes on litter decomposition at different critical periods. In order to understand the effects of forest gaps on litter decomposition in forest ecosystems at high altitudes, litterbags with red birch (*Betula albosinensis*) and Minjiang fir (*Abies faxoniana*) foliar litter were incubated on the forest floor in small, medium,

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and large gaps and the adjacent closed canopy from November 21, 2011 to October 29, 2012. Then, the litterbags were sampled at the periods of onset of soil freezing (OF), soil deep-freezing (DF), soil thawing (TP), early growth (EP), mid-growth (MP), and late growth (LP), and the mass loss was calculated. After a year of litter decomposition, red birch and Minjiang foliar litter lost 27.25—30.12% and 27.04—27.96% mass, respectively. The mass loss of red birch and Minjiang fir foliar litter in the non-growing season accounted for 53.8—60.18% and 50.23—59.09% of the total mass loss, respectively. Gap sizes have strong effects on the mass loss of Minjiang fir and red birch foliar litter, depending on tree species and sampling periods. Forest gaps accelerated the litter decomposition of Minjiang fir, but slowed down the litter decomposition of red birch. Regardless of tree species, forest gaps significantly accelerated the rates of mass loss of foliar litter in the non-growing season ($P < 0.05$), but significantly lowered them in the growing season ($P < 0.05$). The rates of mass loss of foliar litter increased with gap sizes in the non-growing season, but decreased with gap sizes in the growing season. Moreover, the rates of mass loss of Minjiang fir foliar litter in the periods of OF, DF, and TP increased significantly with gap sizes ($P < 0.05$), but the effects on red birch foliar litter were not significant ($P > 0.05$). In addition, the contribution of litter mass loss at different critical periods to a year of mass loss was in the order of DF > MP > OF > EP > LP > TP. Mass loss of red birch foliar litter in the non-growing season accounted for 60.18%, 54.46%, 55.34%, and 53.83% of the one-year mass loss in large gaps, middle gaps, small gaps, and closed canopy, respectively; similarly, the contributions of mass loss of Minjiang fir foliar litter to the one-year mass loss in the non-growing season were 59.09%, 54.37%, 52.22%, and 50.23%, respectively. These results suggest that forest gaps accelerated the mass loss of foliar litter in the snow-cover season, but slowed down the mass loss in the growing season. The responses of litter decomposition to gap sizes in the snow-cover season were different from those in the growing season, implying that gap sizes could have strong effects on litter decomposition at different critical periods in the coniferous forest ecosystem of alpine regions.

Key Words: forest gap; litter decomposition; mass loss; non-growing season; coniferous forest; alpine region

林窗 (forest gap) 是川西高山森林生态系统普遍存在的干扰形式^[1]。与郁闭林下相比,林窗改变了林内水热条件(光照、温度、降水)和分解者群落结构^[2],可能对凋落物分解过程具有强烈影响。在高寒森林生态系统,不同大小的林窗内冬季雪被厚度和持续时间的变异可能深刻作用于凋落物分解^[3-4]。一方面,林窗内雪被的绝热保温作用能使土壤微生物维持相对较高的活性^[5];另一方面,郁闭林冠下由于缺乏雪被覆盖,微生物活性受低温和冻结作用抑制^[6]。因而,林窗可能促进冬季凋落叶分解,并且不同大小林窗对雪被厚度和冻融循环格局的改变也可能不同程度地作用于凋落叶分解^[7-8]。与此相反,尽管生长季节适宜的温湿度条件更有利于凋落物分解,但林窗内相对更高的光照强度和光辐射效率^[9]可导致凋落物地表温度升高^[10],水分蒸发增加^[11],进而影响土壤微生物活性和土壤动物活动能力^[12]。因此,相比于郁闭林下,林窗可能抑制生长季节凋落叶分解。这意味着,林窗对高寒森林生态系统不同季节凋落物的分解具有截然不同的影响,但迄今的研究一直缺乏相应的关注,这极大地限制了对高寒森林地下生态过程的认识。

川西高山森林在调节区域气候、涵养水源、保育生物多样性等方面具有突出的战略地位。前期研究表明,林窗是川西高山森林群落最主要的自然更新方式^[13],影响凋落物分解的生物和非生物因素与林窗密切相关^[14]。因此,我们假设,林窗能显著影响川西高山森林凋落叶分解过程,在冬季促进凋落叶分解,在生长季节制约凋落叶分解;且阔叶和针叶凋落叶对林窗的响应不同。为验证上述假设,本研究采用凋落物分解袋法,以区域内代表性针叶树种岷江冷杉 (*Abies faxoniana*) 和阔叶树种红桦 (*Betula albo-sinensis*) 凋落叶为研究对象,研究林窗面积大小对针、阔树种凋落叶在非生长季节和生长季节分解的影响,以期深入认识高寒森林生态系统物质循环过程提供科学依据。

1 材料与方 法

1.1 研究区域与样地概况

研究区域位于四川省理县毕棚沟自然保护区(31°14′—31°19′ N,102°53′—102°57′ E, 2458—4619 m *a.s.l.*),地处青藏高原东缘与四川盆地的过渡带。年平均气温 2—4℃,最高气温 23℃ (7 月),最低温度为-18℃ (1 月),年降水量约 850 mm。该区域冬季具有明显的季节性雪被覆盖和冻融过程,雪被厚度达 50 cm,冻融时间长达约 120 d^[3]。区域内典型植被为岷江冷杉(*A. faxoniana*)、红桦(*B. albo-sinensis*)和川西云杉(*Picea balfouriana*)。土壤为发育于坡积物上的雏形土,基本理化性质见杨玉莲等^[15]。

表 1 样地内不同林窗的面积、形成木、边界木和形成方式

Table 1 The areas, species of gap maker and border and gap formation types of sampled site

林窗类型 Types of gap	林窗面积 /(m ²) Area of gap	形成木 Species of gap maker	边界木 Species of gap border	形成方式 Gap formation types
大林窗 Large gap	255.16~290.41	岷江冷杉 <i>Abies faxoniana</i>	岷江冷杉 <i>Abies faxoniana</i> 、 红桦 <i>Betula albo-sinensis</i>	折干 Beakage at trunk
中林窗 Intermediate gap	153.36~176.43			
小林窗 Small gap	38.25~46.58			

基于前期研究,在海拔 3598m 原始岷江冷杉林内设置 1 hm²样地(坡向 NE 38°,坡度 24°)。乔木层岷江冷杉占据绝对优势,其次是红桦,伴生少量野樱桃(*P. tatsienensis*);灌木主要有高山杜鹃(*Rhododendron delavayi*)、三颗针(*Berberis sargentiana*)和绢毛蔷薇(*Rosa sericea*)等;草本以铁线莲(*Clematis*)、苔草(*Carex*)和羊茅(*Festuca*)等为主,林窗内草本盖度约 85%。按照林窗面积大小在样地内分别选取大林窗(large gap, LG)、中林窗(intermediate gap, IG)和小林窗(small gap, SG)各 3 个。同时,在岷江冷杉郁闭林下(the closed canopy, CC)设置 3 个 10 m×10 m 的样方作为对照。然后调查林窗的基本性质(表 1),并进行整理和清除工作。

1.2 凋落物分解试验

2011 年秋季搜集岷江冷杉和红桦新鲜凋落叶,室温下自然风干,称取 10 g 风干凋落叶装入分解袋(大小为 20 cm×20 cm,贴地面孔径 0.50 mm,上表面孔径 1 mm),于 2011 年 11 月埋设于样地,分解试验为期 1 年,共埋设分解袋 1440 袋=每次取样(10)×林窗(4)×3(重复)×2(物种)×6 次。同时,采用纽扣式温度记录器(iButton DS1923-F5, Maxim/Dallas Semiconductor, Sunnyvale, USA)记录空气和各林窗下调落袋内温度,设定每 2 h 记录一次温度数据。此外,采用钢尺测量各海拔林窗及林下雪被厚度。各林窗温度和雪被变化见图 1、图 2 和表 2。

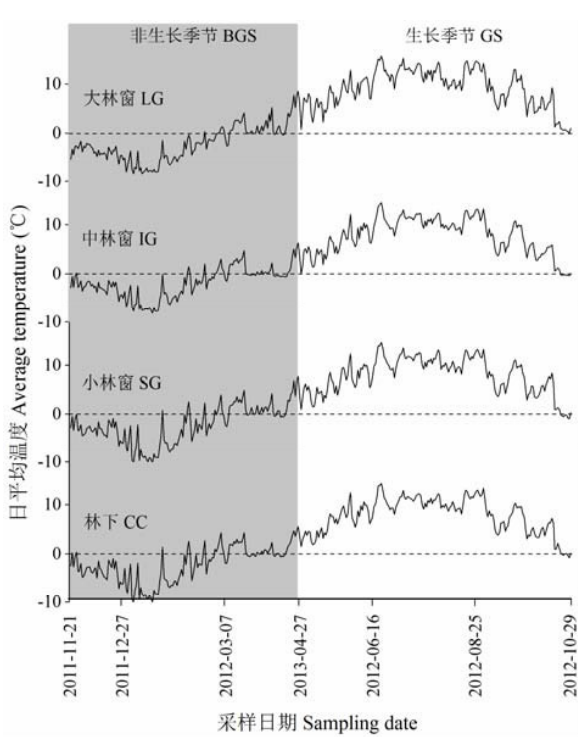


图 1 不同林窗下的日平均温度

Fig. 1 Daily means temperature in sampled gaps and the closed canopy

LG, 大林窗, large gap; IG, intermediate gap, 中林窗; SG, small gap, 小林窗; CC, the closed canopy, 郁闭林下; BGS, beyond growing season, 非生长季节; GS, growing season, 生长期季节; 下同, the same below

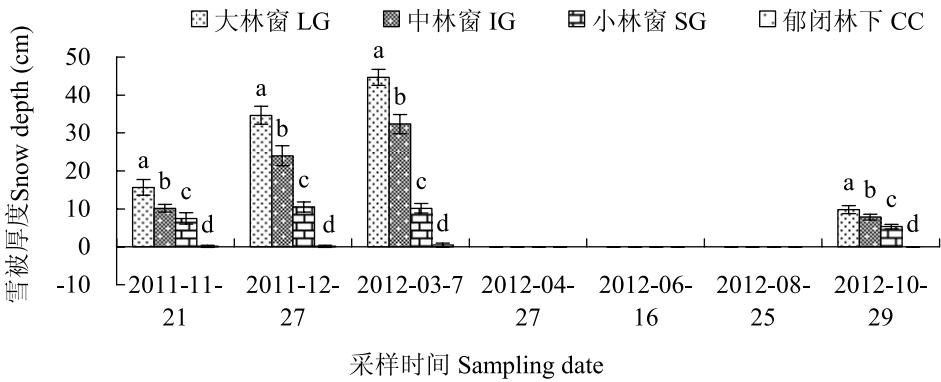


图2 不同大小林窗和郁闭林下的雪被厚度
Fig. 2 Snow depths in forest gaps and the closed canopy

表2 各关键时期不同大小林窗和郁闭林下调落叶日平均温度

林窗类型 Types of gap	初冻期	深冻期	融化期	生长初期	生长中期	生长后期
	Onset of soil freezing period	Soil deep freezing period	Soil thawing period	Early growth period	Mid-growing period	Later growth period
大林窗 Large gap	-0.56±0.16 ^a	-1.39±0.19 ^a	2.98±0.41 ^a	9.78±1.04 ^a	12.51±0.41 ^a	7.94±0.74 ^a
中林窗 Intermediate gap	-1.6±0.13 ^b	-2.12±0.29 ^b	2.16±0.36 ^b	9.4±1.08 ^a	12.34±0.54 ^{ab}	5.68±0.51 ^b
小林窗 Small gap	-1.98±0.15 ^c	-2.13±0.33 ^b	1.95±0.34 ^b	6.16±0.96 ^b	11.63±0.44 ^b	5.66±0.63 ^b
郁闭林下 Closed canopy	-2.4±0.12 ^d	-3.14±0.45 ^c	0.59±0.14 ^c	6.04±0.53 ^b	10.13±0.55 ^c	4.37±0.55 ^c

不同小写字母表示差异显著(独立样本 *t* 检验, *P* < 0.05)。

根据前期监测,按高山植物的非生长季节(冬季)和生长季节进行样品采集,具体为:非生长季节的初冻期(12月27日, onset of soil freezing period, OF)、深冻期(3月7日, soil deep freezing period, DF)、融化期(4月27日, soil thawing period, TP);生长季节的初期(6月16日, early growth period, EP)、中期(8月25日 mid-growing period, MP)和后期(10月29日, later growth period, LP)。每次采样时随机从每个样方捡回10袋凋落叶,去除杂物后,于65℃烘干至恒重并称量,计算凋落叶失重率。2种凋落叶的初始化学特征见表3。

表3 红桦和岷江冷杉凋落叶初始质量特征(平均值±标准偏差, n=5)

物种 Species	碳/(g/kg)	氮/(g/kg)	磷/(g/kg)	碳比氮 C/N	木质素比氮
	Organic carbon	Nitrogen	Phosphorus		Lignin/N
红桦 <i>Betula albo-sinensis</i>	484.27 ^b ±17.00	10.41 ^b ±0.79	0.82 ^b ±0.08	46.52 ^a ±1.76	25.86 ^a ±0.45
岷江冷杉 <i>Abies faxoniana</i>	505.85 ^a ±30.64	11.43 ^a ±1.11	1.71 ^a ±0.11	44.26 ^a ±2.01	19.81 ^b ±0.39

1.3 数据处理与统计分析

半分解时间($T_{50\%}$)、95%分解时间($T_{95\%}$)、质量损失率和质量损失速率^[16-17]按如下公式计算:

50% 分解时间 = $-\ln(1 - 0.50)/(k)$

95% 分解时间 = $-\ln(1 - 0.95)/(k)$

质量损失率 $L_t(\%) = 100 \times (M_t - M_0) / M_0$

各关键时期每 30 *d* 质量损失速率 $V_t(\% d^{-1}) = 30 \times (M_{t-1} - M_t) / M_0 \times 100 / D_{\Delta t}$

各关键时期质量损失占全年比率 $R_t(\%) = 100 \times (M_{t-1} - M_t) / (M_0 - M_6)$

式中, M_t 为 *t* 时刻凋落叶干质量(g), M_0 为初始干重(g), $(M_{t-1} - M_t)$ 为相邻采样时间凋落叶残留量差($t = 1, 2, 3 \cdots 6$), $D_{\Delta t}$ 为相邻采样时间间隔天数。

用单因素方差分析(one-way ANOVA)检验凋落叶日均温、质量损失率、损失速率在不同林窗间的差异显著性;用 Pearson 相关分析检验日均温、冻融循环次数与质量损失速率之间的相关关系。显著性水平设为 $P = 0.05$, 数值以平均值 $\pm$ 标准误(mean $\pm$ SE)表示。数据分析采用 SPSS 20.0 (IBM SPSS Statistics Inc., Chicago, IL, USA)软件包进行。

2 结果与分析

2.1 质量损失率

分解 1a 后,红桦和的岷江冷杉凋落叶质量损失率分别为 27.25—30.12%和 27.04—27.96% (图 3)。2 种凋落叶半分解和 95%分解时间分别为 2.015—2.413 a、2.110—2.557 a 和 8.708—10.428 a、9.121—11.053 a,红桦凋落叶分解周期随林窗面积增加而增加,岷江冷杉凋落叶则相反(表 4)。与郁闭林下相比,林窗形成显著($P < 0.05$)影响非生长季节(初冻期、深冻期和融化期)岷江冷杉凋落叶的质量损失率,且林窗面积越大其质量损失率越高;而对红桦凋落叶质量损失率无显著影响($P > 0.05$)。

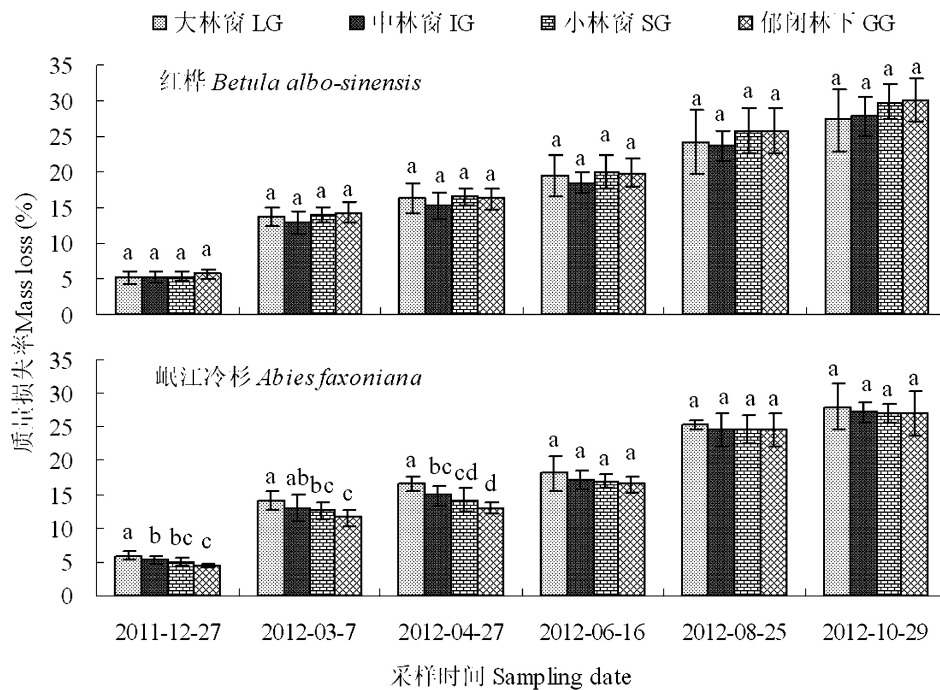


图 3 不同大小林窗和郁闭林下的凋落叶质量损失

Fig. 3 Mass losses of foliar litter in forest gaps and the closed canopy

表 4 不同大小林窗和郁闭林下凋落叶分解特征

Table 4 Some properties during the decomposition of foliar litter in forest gaps and the closed canopy

物种 Species	林窗类型 Types of gap	回归方程 Regression models	分解系数/k Decomposition constant /k	相关系数 R ² Correlation coefficient R ²	半分解时间/a Time of half decomposition	95%分解时间/a Time of 95% decomposition
红桦 <i>Betula albo-sinensis</i>	大林窗	$y = 96.476e^{-0.287t}$	0.287	0.987	2.413	10.428
	中林窗	$y = 97.412e^{-0.306t}$	0.306	0.994	2.266	9.794
	小林窗	$y = 96.927e^{-0.321t}$	0.321	0.991	2.157	9.324
	郁闭林下	$y = 97.503e^{-0.344t}$	0.344	0.995	2.015	8.708
岷江冷杉 <i>Abies faxoniana</i>	大林窗	$y = 97.494e^{-0.328t}$	0.328	0.992	2.110	9.121
	中林窗	$y = 97.684e^{-0.307t}$	0.307	0.993	2.256	9.751
	小林窗	$y = 97.182e^{-0.283t}$	0.283	0.986	2.449	10.585
	郁闭林下	$y = 97.286e^{-0.271t}$	0.271	0.980	2.557	11.053

2.2 质量损失速率

2 种凋落叶分解速率总体上呈现逐渐减慢再增加的趋势(图 4)。林窗形成显著($P<0.05$)影响了深冻期、融化期和生长后期红桦凋落叶的质量损失速率,显著增加了融化期质量损失速率,且随林窗面积增大而增加。对岷江冷杉而言,林窗形成显著($P<0.05$)影响了初冻期、融化期和生长初期凋落叶的质量损失速率。林窗形成后显著($P<0.05$)增加了初冻期、深冻期和融化期岷江冷杉凋落叶的质量损失速率,且质量损失速率随林窗面积增大而增加;显著降低了减小降低了生长季节后期岷江冷杉凋落叶的质量损失速率,且质量损失速率随林窗面积增大而降低。

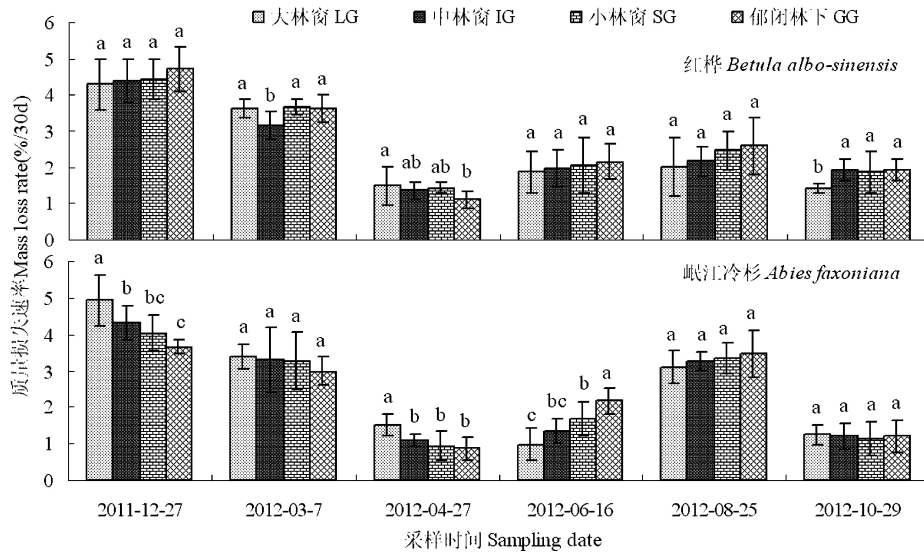


图 4 不同大小林窗和郁闭林下的凋落叶分解速率

Fig. 4 Mass loss rates of foliar litter in forest gaps and the closed canopy

由图 5 可得,林窗显著($P<0.05$)影响了 2 种凋落叶第一年的质量损失速率。林窗形成后显著降低了 2 种凋落叶第一年生长季节质量损失速率,且林窗面积越大质量损失速率越低;显著增加了红桦凋落叶非生长季节和岷江冷杉凋落叶非生长季节以及第一年的质量损失速率,且林窗面积越大质量损失速率越高。总体上,2 种凋落叶质量损失速率在第一年非生长季节显著($P<0.05$)高于生长季节。

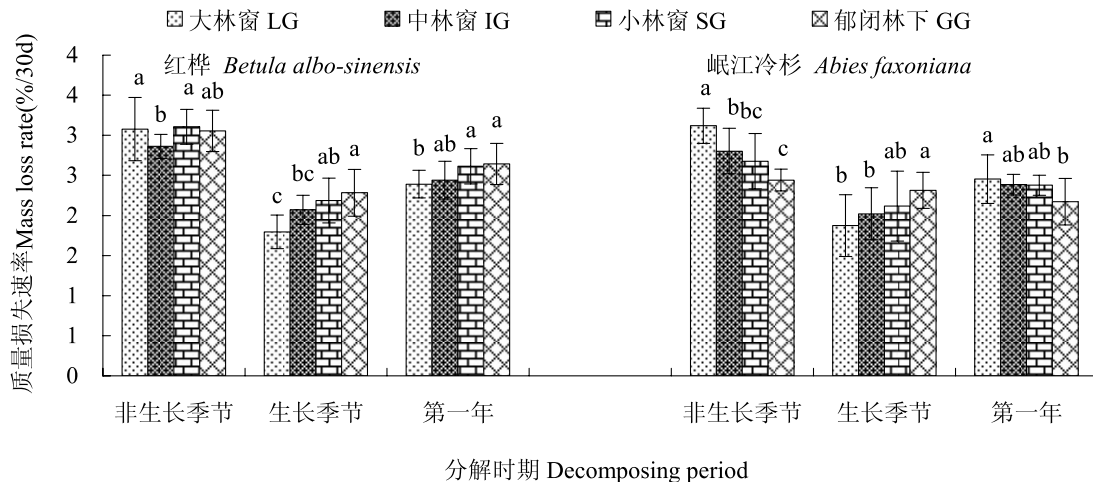


图 5 冬季和生长季节凋落叶分解速率

Fig. 5 Mass loss rates of foliar litters in forest gaps and the closed canopy in winter and the growing season

2.3 各关键时期的质量损失比率

由图 6 可得,2 种凋落叶各关键时期质量损失所占比例为第一年深冻期>生长中期>初冻期>生长初期>生长后期>融化期。4 种不同面积林窗内(从大林窗、中林窗、小林窗到林下)红桦和岷江冷杉凋落叶第一年非生长季节质量损失分别占第一年的 60.18%、54.46%、55.34%、53.83%和 59.09%、54.37%、52.22%、50.23%,非生长季节显著($P<0.05$)高于生长季节。

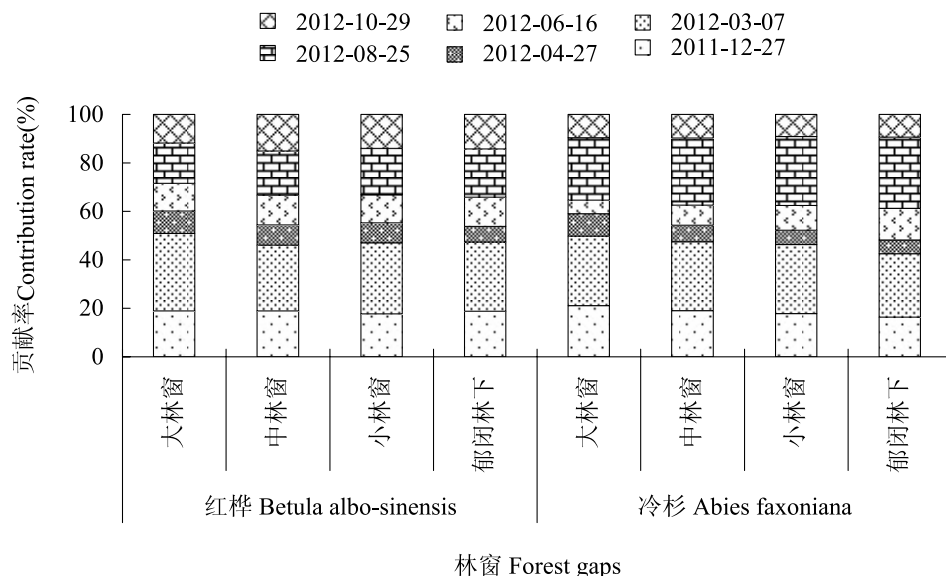


图 6 各关键时期质量损失在全年分解过程中所占的比率

Fig. 6 Ratios of mass losses at each critical stage compared to the entire decomposition year

3 讨论

与假设基本一致,川西高山森林林窗对凋落叶分解有显著影响:促进了冬季凋落叶分解,抑制生长季节的凋落叶分解,尤其是对岷江冷杉凋落叶分解过程作用更为明显。一方面,林窗面积越大,冬季形成雪被的厚度也越厚,林窗内雪被覆盖的时间也越长(图 2),雪被的保温作用能持续促进凋落叶分解。并且,大林窗内的凋落叶在雪被融化期可接收更多雪融水和降水的淋洗作用,促进凋落叶内可溶解性组分的流失。另一方面,在生长季节,由于缺乏林冠对光照的过滤和拦截作用,林窗内的太阳辐射显著高于郁闭林下,且这种作用随林窗面积增加和增强^[18]。这促进了林窗内凋落叶水分的蒸发,不利于土壤无脊椎动物和微生物对凋落物分解的贡献,进而抑制凋落叶分解。这表明林窗形成对微环境的改变能深刻影响高寒森林地下生态系统的物质循环。

在高寒森林生态系统中,尽管冬季低温不利于土壤动物^[19]和微生物^[17]对凋落叶的降解,季节性雪被^[3]和冻融循环^[14,16]能显著作用于冬季凋落叶分解。已有的研究表明,雪被融化的淋洗作用和冻融循环的物理破碎^[3,14,16]都能显著促进凋落叶分解。同时,雪被覆盖环境中存活的土壤动物^[20-21]和微生物活性^[5]也能促进冬季凋落叶分解。本研究中,红桦和岷江冷杉冬季凋落叶分解占全年分解的比例分别为 53.83—60.18%和 50.23—59.09%,高于生长季节(图 6)。这说明冬季凋落叶分解对高山森林物质循环具有十分重要的作用^[17]。另一方面,林窗形成能改变雪被环境、土壤冻融格局^[22]和耐寒微生物的活性^[23],直接或间接影响冬季凋落叶分解^[12]。本研究中,林窗形成显著提高了非生长季节 2 种凋落叶质量损失速率。地表凋落叶日均温度和土壤冻融循环与深冻期等关键时期质量损失速率显著相关(表 5)。这表明林窗形成改变了林窗内冬季环境条件,对川西高山森林冬季凋落叶分解产生了重要影响^[2,24]。

表 5 日均温度 (T) 和冻融循环次数 (F) 与凋落叶各关键时期质量损失速率的相关性分析

Table 5 Correlation analyses between daily mean temperature and frequencies of freeze-thaw cycle and mass loss rates of foliar litters at critical decomposition period

类别 Types	物种 Species	初冻期 Onset of soil freezing period	深冻期 Soil deep freezing period	融化期 Soil thawing period	生长初期 Early growth period	生长中期 Mid-growing period	生长后期 Later growth period
日均温 (T)	红桦 <i>Betula albo-sinensis</i>	-0.201	0.607 **	0.687 **	-0.139	-0.236	0.077
Average temperature	岷江冷杉 <i>Abies faxoniana</i>	0.691 **	0.422 *	-0.230	0.564 **	-0.182	-0.007
冻融循环 (F)	红桦 <i>Betula albo-sinensis</i>	-0.173	0.151	0.355 *	0.079	-	0.085
Frequency of soil freeze-thaw cycle	岷江冷杉 <i>Abies faxoniana</i>	0.581 **	0.587 **	0.650 **	0.280	-	0.023

*, $P < 0.05$; **, $P < 0.01$.

林窗对凋落物分解的影响常常随林窗面积大小而发生变化,但已有的研究结果具有不确定性^[24-28]。有研究者发现,大林窗中凋落物的质量损失速率比小林窗和林下低^[25-26],也有研究者认为林窗面积大小对凋落物分解影响不显著^[27-28],甚至在大林窗中凋落物分解更快^[29]。本研究发现,在 1 年分解过程中,2 种凋落叶在生长季节的质量损失速率随林窗面积增加而减小,在非生长季节的岷江冷杉凋落叶以及融化期的红桦凋落叶的质量损失速率随林窗面积增加而增加,而初冻期和深冻期红桦凋落叶质量损失速率在不同面积林窗内差异不显著(中林窗除外)。如前所述,不同面积林窗由于冬季雪被覆盖以及生长季节水分蒸发量差异等限制着分解者群落的定着,直接影响林内凋落叶的分解过程。研究表明,凋落物质量(quality)是植物残体自身分解的关键因子^[30],控制着中小尺度上凋落物的分解过程^[31]。本研究中红桦和岷江冷杉分别是阔叶和针叶凋落叶,其基质质量存在显著差异(表 3),因此对环境变化的响应过程和时间也存在不同(图 3)。综上所述,川西高山森林林窗面积大小对凋落叶分解产生显著影响,且阔叶和针叶凋落叶在非生长季节与生长季节对林窗的响应存在明显差异。

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