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# 生态学报

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# 生态学报 (SHENTAI XUEBAO)

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封面图说:冬天低空飞翔的丹顶鹤——丹顶鹤是鹤类中的一种,因头顶有“红肉冠”而得名。是东亚地区特有的鸟种,因体态优雅、颜色分明,在这一地区的文化中具有吉祥、忠贞、长寿的象征,是传说中的仙鹤,国家一级保护动物。丹顶鹤具备鹤类的特征,即三长——嘴长、颈长、腿长。成鸟除颈部和飞羽后端为黑色外,全身洁白,头顶皮肤裸露,呈鲜红色。丹顶鹤每年要在繁殖地和越冬地之间进行迁徙,只有在日本北海道等地是留鸟,不进行迁徙,这可能与冬季当地人有组织地投喂食物,食物来源充足有关。

彩图提供:陈建伟教授 北京林业大学 E-mail: cites.chenjw@163.com

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## 粤北山地常绿阔叶林自然干扰后冠层结构 与林下光照动态

区余端<sup>1,\*</sup>, 苏志尧<sup>2</sup>

(1. 广东海洋大学农学院, 湛江 524088; 2. 华南农业大学林学院, 广州 510642)

**摘要:**以粤北车八岭2008年受冰灾破坏的山地常绿阔叶林为研究对象,设置2 hm<sup>2</sup>固定样地开展连续3a(2008—2010年)的群落调查,并采用半球面影像技术(Hemispherical photography)获取冠层结构和林下光照指标,分析灾后森林演替过程中冠层结构和林下光照的动态。研究发现:1)灾后森林恢复过程中,样地林下光照(直射光、散射光和总光照)均随林冠开度的减少、叶面积指数的增加而减少;2)从2008到2010年,各年度冠层结构和林下光照的差异均极显著( $P<0.0001$ ),但年间差异程度有逐年减少的趋势;3)灾后森林恢复前3a,林下直射光对林下总光照的贡献大于散射光,其时空波动性也大于散射光;4)林冠开度对冠层结构的反映程度比叶面积指数高,冠层结构对林下散射光的影响比对直射光大。灾后林木先是迅速生长然后生长速度缓慢下来并逐渐稳定,随森林逐渐郁闭林下光照也随之减少,其中林冠开度用于评价冠层结构动态的效果更佳,林下直射光比散射光的时空变化更复杂。

**关键词:**常绿阔叶林; 冠层结构; 林下光照; 冰灾; 典型相关分析

### Dynamics of canopy structure and understory light in montane evergreen broadleaved forest following a natural disturbance in North Guangdong

OU Yuduan<sup>1,\*</sup>, SU Zhiyao<sup>2</sup>

1 College of Agriculture, Guangdong Ocean University, Zhanjiang 524088, China

2 College of Forestry, South China Agricultural University, Guangzhou 510642, China

**Abstract:** Natural disturbance is an important factor causing dynamic changes in forest canopies. An ice storm in southern China in 2008 was responsible for extensive damage to the forest ecosystem. The considerable distribution of canopy gaps created by the ice storm caused dynamic changes in the forest canopy. Therefore, studies to reveal the effects of the ice storm on forest regeneration and to monitor the restoration of damaged forest ecosystems will have significant implications for forestry research. Following the ice storm of 2008, a montane evergreen broad-leaved forest in Chebalong National Nature Reserve in northern Guangdong was investigated and a successive 3-year (2008—2010) community study of the 2 hm<sup>2</sup> permanent plot was launched. We analyzed the changes in canopy structure (Canopy Openness and Leaf Area Index) and understory light (Transmitted Direct Solar Radiation, Transmitted Diffuse Solar Radiation and Transmitted Total Solar Radiation) in the forest following the ice storm using hemispherical photography to acquire canopy structure and understory light indexes. A quantitative study on the temporal and spatial variations in canopy structure and understory light as well as on environmental heterogeneity in the forest canopy is of considerable importance. Hemispherical photography is an example of optical remote sensing technology used to measure the parameters of canopy structure and understory light, and has now

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\* 通讯作者 Corresponding author. E-mail: ouyuduan@126.com

been widely recommended in the field of ecological research. The Kruskal-Wallis test (a non-parametric alternative to one-way ANOVA) and canonical correlation analysis were employed to analyze the changes in canopy structure and understory light. The main conclusions of this study are described in the following: 1) As the canopy openness shrank and the leaf area index increased, the understory light decreased in the forest during the recovery process following the ice storm; 2) A highly significant difference ( $P < 0.0001$ ) was detected in canopy structure and understory light during the 3 years, but between-year differences showed a tendency to decrease as the forest recovered from 2008 to 2010; 3) In the first three years of forest recovery, transmitted direct solar radiation demonstrated a greater spatial-temporal fluctuation and provided a greater contribution to total solar radiation than did transmitted diffuse solar radiation; 4) Canopy openness was more sensitive than leaf area index as an indicator of canopy structure change, while canopy structure had a greater influence on transmitted diffuse solar radiation than transmitted direct solar radiation. Initially, the trees in the ice storm damaged forest grew rapidly during the recovery period following the storm, but the growth slowed down gradually and stabilized. There was a gradual reduction in the understory light as the forest closed due to tree growth. Canopy openness is better for the evaluation of the dynamic effects of canopy structure. The spatial and temporal variations of transmitted direct solar radiation were more complex than transmitted diffuse solar radiation. Therefore, research to study the effects of an ice storm on canopy structure of a subtropical forest to reveal dynamics of canopy structure and understory light, and to monitor the restoration of a damaged forest ecosystem, will have significant implications for both theoretical and applied forest restoration efforts.

**Key Words:** evergreen broadleaved forest; canopy structure; understory light; ice storm; Canonical Correlation Analysis

自然干扰是引起森林冠层动态变化的重要因素,2008年的中国南方冰灾给该地区森林生态系统以重创<sup>[1]</sup>,在森林冠层形成大量大小不一、分布不均的林冠空隙<sup>[2-4]</sup>,引起森林冠层的动态变化。冰灾后林冠结构的动态主要由林冠空隙的更新来决定,林冠空隙的更新存在着不确定性<sup>[5-7]</sup>。一方面,林冠空隙可以由树木的侧方生长或垂直生长来填充,使林冠空隙缩小或郁闭;另一方面,林冠空隙周围的树木很容易遭受暴风的袭击和昆虫的侵害,使林冠空隙扩大或增加<sup>[8]</sup>。林冠是由冠层乔木的枝叶和层内空隙所构成,因此森林冠层结构可以由叶面积指数(单位面积上所有叶子面积的总和与该单位林地面积的比值)和林冠开度(从林地某个点向上仰视,未被树木枝叶所遮挡的天空球面的百分数)来反映。叶面积指数和林冠开度之间关系密切,都可用于评价林冠结构的动态<sup>[9-10]</sup>。

冠层结构能通过控制太阳能的截获量来调节林下光照,因此冰灾后林冠结构的动态对林下光照的数量和质量影响很大<sup>[9,11-13]</sup>。林冠空隙的形成与扩大、郁闭或缩小都会改变林下光照持续时间、光照强度和光合有效辐射<sup>[14]</sup>。林冠结构对光的透射、反射和吸收有很大的作用,并且影响着光照的成分<sup>[15]</sup>。林下光照可分为直射光(穿过林冠空隙直接照射到林下的光)和散射光(从任意方位反射到林下的光)<sup>[16]</sup>。林冠结构的不同导致了直射光和散射光对林下总光照贡献的变化<sup>[17-18]</sup>。林下光照成分对林下环境异质性及动植物的生理生态过程有着重要作用<sup>[19-21]</sup>。

量化林冠结构和林下光照对研究林冠时空变化和林下环境异质性具有重要意义,而半球面影像技术(hemispherical photography)为此提供了一种科学的手段<sup>[21]</sup>。半球面影像技术是一种测量林冠结构和林下光照参数的光学遥感技术,目前已经被广泛应用于生态学领域的研究<sup>[22-24]</sup>。2008年冰灾对森林生态系统的影响引起国内外广泛的关注和研究,包括森林的受灾状况<sup>[25-26]</sup>、林木的受损评估<sup>[4,27]</sup>、林分受灾与地形的关系<sup>[28-29]</sup>等,但关于冰灾后森林恢复的研究甚少<sup>[30]</sup>。冰灾后亚热带森林能否迅速更新和恢复是维护自然生态平衡的首要问题,因此监测冰灾后受损亚热带常绿阔叶林结构的动态,研究冰灾干扰后亚热带山地常绿阔叶林的演替趋势,揭示其变化的规律,在理论和实践上都有重要的意义,能为森林植被恢复、灾后重建和经营管理提供重要的科学依据。

## 1 材料与方法

### 1.1 研究地概况

车八岭国家级自然保护区( $114^{\circ}09'04''$ — $114^{\circ}16'46''E$ ,  $24^{\circ}40'29''$ — $24^{\circ}46'21''N$ )地处广东省东北部的韶关市始兴县境内,全区面积 $7545\text{ hm}^2$ ,区内森林为南岭南缘保存较完整且原生性较强的亚热带常绿阔叶林<sup>[31]</sup>。保护区内地势西北高东南低,最高峰天平架海拔1256 m,最低处樟栎水海拔330 m<sup>[31]</sup>。保护区内土壤形态和结构较为完整,海拔从低到高垂直分布有低地坡积物、谷地水稻土、山地红壤、山地暗红壤、山地黄红壤、山地黄壤、山地表潜黄壤和山地草甸土<sup>[31]</sup>。本地区属于亚热带季风型气候,夏季高温多雨,冬季低温少雨;年平均温度 $19.5^{\circ}\text{C}$ ,最高温度 $38.4^{\circ}\text{C}$ ,最低温度 $-5.5^{\circ}\text{C}$ ;年平均降水量1468.0 mm,蒸发量1356.1 mm<sup>[31]</sup>。

### 1.2 野外取样方法

为了研究冰灾后粤北山地常绿阔叶林的恢复状况,于2008年8月,在车八岭国家级自然保护区一片受冰灾影响严重的山地常绿阔叶林内,建立 $2\text{ hm}^2$ 长期固定样地。固定样地的海拔343—475 m,坡向东偏北 $30^{\circ}$ —东偏南 $21^{\circ}$ ,坡度 $12^{\circ}$ — $44.3^{\circ}$ 。在固定样地内设置50个 $20\text{ m} \times 20\text{ m}$ 的样方,并在每个样方的四角及中心点用PVC管标记。在每个样方中心和对角线四分位处用Nikon 4500 CoolPix®数码相机外接Nikkor FC-E8鱼眼镜头转换器(广角为 $183^{\circ}$ ,正投影)获取半球面林冠影像。相机与鱼眼镜头组合用三脚架置于离地面1.65 m处,保持水平,并使记录的照片顶部与磁北方向重合(用指南针确定方向),镜头朝上,拍摄半球面林冠影像。用相机内置的Fisheye1模式来拍摄半球面影像。所有的照片都用高分辨率( $2272 \times 1704\text{ pixels}$ )获取,并以JPEG图像格式保存(压缩比率1:4)。为了确保光照条件的一致和使直射阳光造成的眩光最小化,拍照选在阴天或无风的天气、日出或日落的时间<sup>[32]</sup>。2009年和2010年的7—8月间均对该固定样地以同样的方法获取林冠半球面影像。

### 1.3 半球面林冠影像分析

用Gap Light Analyzer(GLA, version 2.0, 图像处理软件)<sup>[33]</sup>对冠层照片进行分析<sup>[34-35]</sup>。用GLA中所设定的阈值强度范围(0—225)的中间值去区分冠层照片中的“天空”和“林冠”<sup>[33]</sup>。亮度低于阈值被认为是树叶(黑色);亮度高于阈值被归为天空(白色)<sup>[36]</sup>。经GLA计算以后,用于本文的冠层结构参数包括林冠开度(Canopy Openness, CO)和冠层叶面积指数(Leaf Area Index, LAI),林下光照参数包括林下直射光(Transmitted Direct Solar Radiation, TDir)、林下散射光(Transmitted Diffuse Solar Radiation, TDif)和林下总光照(Transmitted Total Solar Radiation, TTot)。

### 1.4 数据分析

用Kruskal-Wallis非参数方差分析来检验2008—2010年冠层结构(林冠开度和冠层叶面积指数)和林下光照(直射光、散射光和总光照)各因子是否存在年间差异。用相关性分析来检验林下光照(直射光、散射光和总光照)各因子与冠层结构(林冠开度和冠层叶面积指数)各因子间的关系。用典型相关分析(Canonical Correlation Analysis)来研究冠层结构和林下光照这两组变量之间的多元相关关系。典型相关分析借用主成分分析的降维思想分别提取两组变量的代表性指标,用这对指标的相关性来描述两组变量整体的线性关系,所提取出来的指标称为典型变量,指标之间的相关称为典型相关<sup>[37]</sup>。一般可通过特征值加起来已占全部特征值的80%并通过显著检验来判断所要提取的指标对数。两组变量的线性组合函数为:

$$U = a_1 X_1 + a_2 X_2 + \dots + a_p X_p, V = b_1 Y_1 + b_2 Y_2 + \dots + b_q Y_q$$

式中, $a_1, a_2, \dots, a_p$ 和 $b_1, b_2, \dots, b_q$ 为待定系数,其中最大的相关系数即典型相关系数。第一组变量包括 $X_1, X_2, \dots, X_p$ ,第二组变量包括 $Y_1, Y_2, \dots, Y_q$ 。本研究的两组变量分别为冠层结构和林下光照,冠层结构变量组包括林冠开度和冠层叶面积指数;林下光照变量组包括直射光、散射光和总光照。

Kruskal-Wallis非参数方差分析、相关性分析和典型相关分析都在Statistica 8.0中进行。

## 2 结果与分析

### 2.1 林冠结构和林下光照的年际动态

冠层结构(林冠开度和叶面积指数)和林下光照(直射光、散射光和总光照)3a间的差异均极显著( $P <$

0.0001)(图1)。从2008到2010年林冠开度和林下光照均逐渐减小,叶面积指数则逐渐增加,其中2009到2010年这些因子的变幅比2008到2009年小(图1)。样方间冠层结构和林下光照的波动性逐年降低,其年间差距也减小(图1)。

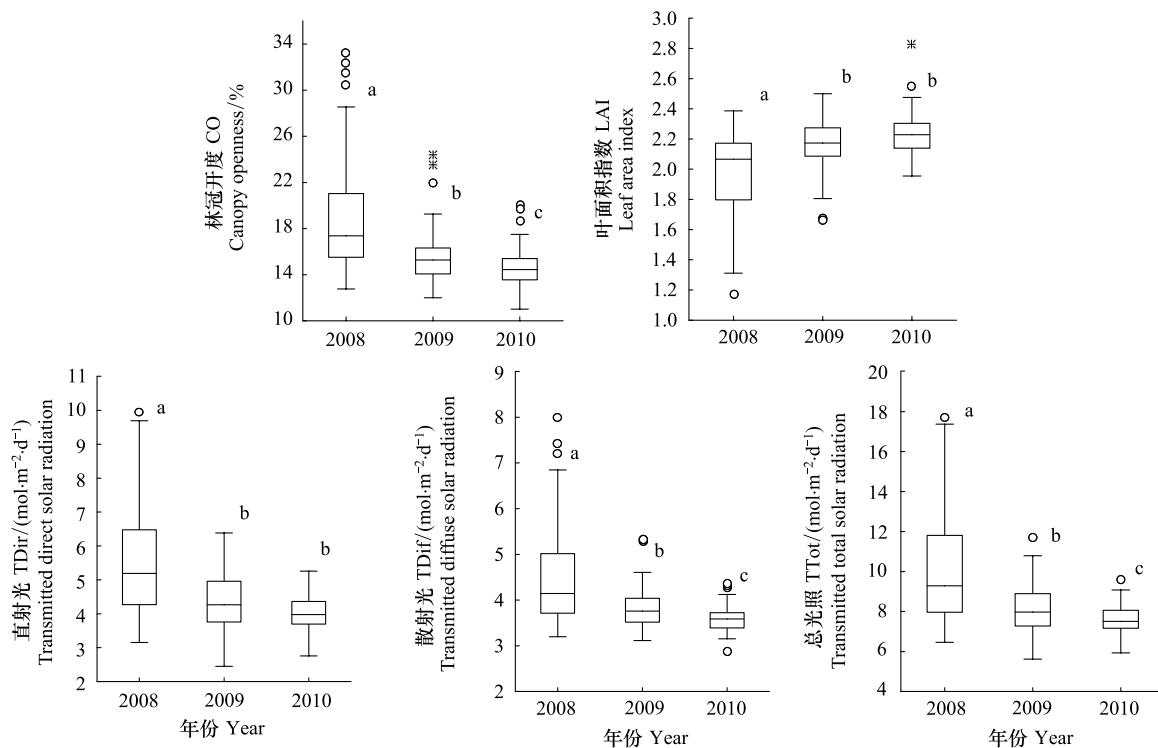


图1 冠层结构和林下光照的年间差异

Fig. 1 Difference of canopy structure and understory light between years

林冠开度的年间差异显著性逐渐降低:2008和2009年差异极显著( $P<0.0001$ );2009和2010年差异显著( $P<0.05$ )(图1)。叶面积指数的年间差异从极显著到不显著:2008和2009年差异极显著( $P<0.0005$ );2009和2010年差异不显著( $P=0.1176$ )(图1)。

直射光的年间差异从极显著到不显著:2008和2009年差异极显著( $P<0.0001$ );2009和2010年差异不显著( $P=0.0747$ )(图1)。散射光的年间差异显著性逐渐降低:2008和2009年差异极显著( $P<0.0005$ );2009和2010年差异显著( $P<0.05$ )(图1)。总光照的年间差异显著性逐渐降低:2008和2009年差异极显著( $P<0.0001$ );2009和2010年差异显著( $P<0.05$ )(图1)。

## 2.2 冠层结构和林下光照的动态关系

从2008到2010年,林下光照(直射光、散射光和总光照)随林冠开度的减少、叶面积指数的增加而减少,林冠结构和林下光照的分布范围也逐渐缩小(图2)。3a林下直射光的量均比散射光多,因此林下直射光对林下总光照的贡献也较大(图2)。

各年度林冠开度与林下光照均呈正相关且极显著,叶面积指数与林下光照均呈负相关,但它们的相关性都在逐年减弱(表1)。林冠结构(林冠开度和叶面积指数)与散射光的相关关系最强,相关性年变化最小;总光照次之;林冠结构与直射光的相关关系最弱,相关性年变化最大(表1)。

从决定系数看,林冠结构(林冠开度和叶面积指数)对林下光照的解释百分比逐年减小(表1)。林冠结构对散射光的控制最大,决定系数年变化最小;总光照次之;林冠结构对直射光的控制最小,决定系数年变化最大(表1)。

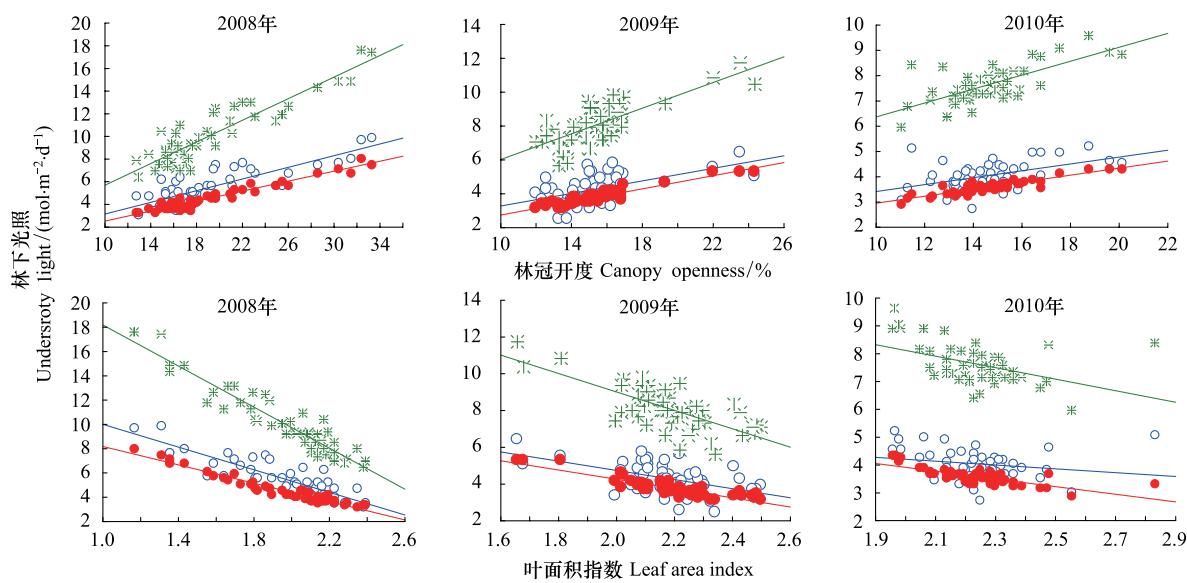


图2 2008—2010年冠层结构和林下光照的关系

Fig. 2 Correlations of canopy structure and understory light from 2008 to 2010

表1 冠层结构和林下光照的相关分析参数

Table 1 Parameters of correlation analysis between canopy structure and understory light

冠层结构和林下光照 Canopy structure & Understory light	年份 Year	回归系数 Regression coefficient		相关系数 Correlation coefficient (r)	P	决定系数 Coefficient of determination( $r^2$ )
		(b)				
林冠开度 CO%						
直射光 TDir	2008	0.257		0.829	<0.0001	0.687
	2009	0.185		0.543	<0.0001	0.295
	2010	0.136		0.480	<0.0005	0.231
散射光 TDif	2008	0.220		0.970	<0.0001	0.941
	2009	0.193		0.944	<0.0001	0.891
	2010	0.140		0.902	<0.0001	0.813
总光照 TTot	2008	0.477		0.912	<0.0001	0.832
	2009	0.379		0.762	<0.0001	0.581
	2010	0.276		0.710	<0.0001	0.503
叶面积指数 LAI						
直射光 TDir	2008	-4.666		-0.877	<0.0001	0.769
	2009	-2.488		-0.524	<0.0001	0.275
	2010	-0.684		-0.202	0.1585	0.041
散射光 TDif	2008	-3.786		-0.972	<0.0001	0.944
	2009	-2.518		-0.883	<0.0001	0.780
	2010	-1.387		-0.750	<0.0001	0.563
总光照 TTot	2008	-8.451		-0.941	<0.0001	0.886
	2009	-5.005		-0.724	<0.0001	0.524
	2010	-2.075		-0.447	<0.005	0.200

就回归系数而言,从2008到2010年林冠结构(林冠开度和叶面积指数)对林下光照的影响逐年减小(表1)。3a的总光照受林冠结构的影响最大;2008年林冠结构对直射光的影响大于散射光;2009和2010年则相反,林冠结构对散射光的影响大于直射光(表1)。

### 2.3 冠层结构和林下光照的典型相关

3a 冠层结构与林下光照两组数据之间有强烈正相关且极显著( $P<0.0001$ ) (表2)。虽然2008和2010年第2个典型根的也通过了显著性检验,但是首个特征值所占全部特征值的比例已大于80%,因此取首个典型根的数据进行分析即可(表2)。3a 冠层结构组变量均解释了冠层结构100%的变异;2008、2009和2010年的冠层结构组变量分别解释了林下光照87.42%、59.34%和57.03%的变异,林下光照组变量则分别解释了冠层结构94.70%、83.92%和71.77%的变异,表示冠层结构对林下光照的影响和控制逐年减小。

表2 典型相关分析的卡方检验和特征值

Table 2 Chi-Square Tests and Eigenvalues in Canonical correlation analysis

典型根 Canonical root		典型相关系数 Canonical $r$	卡方 Chi-square	$P$	不能解释的变异百分比 Lambda prime	特征值 Eigenvalues
2008年	1	0.983	162.177	0.0000	0.029	0.966
	2	0.366	6.600	0.0369	0.866	0.134
2009年	1	0.948	105.941	0.0000	0.010	0.899
	2	0.121	0.676	0.7132	0.985	0.015
2010年	1	0.902	86.359	0.0000	0.153	0.813
	2	0.425	9.152	0.0103	0.820	0.180

表3 冠层结构和林下光照的相互关系及典型变量

Table 3 Correlations and canonical variables of canopy structure and understorey light

	指标 Index	年度 Year		
		2008	2009	2010
相关系数	林冠开度与叶面积指数 CO versus LAI	-0.954	-0.911	-0.818
Correlation coefficient ( $r$ )	直射光与散射光 TDir versus TDif	0.896	0.632	0.534
	直射光与总光照 TTot versus TDir	0.981	0.948	0.941
	散射光与总光照 TDif versus TTot	0.965	0.847	0.789
典型权重	林冠开度 CO	-0.531	-0.881	-0.955
Canonical weights	叶面积指数 LAI	0.480	0.129	0.055
	直射光 TDir	13.561	-5.099	-0.498
	散射光 TDif	8.780	-4.169	-1.294
	总光照 TTot	-22.728	7.555	0.711

从2008到2010年林冠开度和叶面积指数的负相关关系虽然逐年减弱,但相关性依然很强(表3)。3a 林下光照各变量间都呈正相关,但相关关系逐年减弱:直射光与散射光的相关系数降幅最大,直射光与总光照的相关系数降幅最小;直射光与总光照的正相关关系最强,其次是散射光与总光照(表3)。

3a 冠层结构的第1个典型变量中起主要作用的是林冠开度;2008和2009年林下光照的第一个典型变量中起主要作用的是总光照,2010年是散射光(表3)。2008和2009年林冠开度是影响总光照的主要冠层结构因子;2010年林冠开度是影响散射光的主要冠层结构因子。

### 3 结论与讨论

#### 3.1 冠层结构和林下光照的动态关系

从2008到2010年林冠结构和林下光照的年间差异逐渐降低。2008—2009年随着冠层乔木恢复生长,林冠开度总体水平迅速减小,叶面积指数快速增加,林下光照量也明显减少;2009—2010年间林冠开度的减小幅度、叶面积指数的上升幅度以及林下光照量的下降幅度都较往年同期小。叶面积指数在一定程度上是生理活动旺盛的标志<sup>[38]</sup>,说明了灾后林木先是迅速生长然后生长速度缓慢下来并逐渐稳定。这是由于灾后森林会慢慢恢复,没受灾或受灾较轻的乔木会不断扩展其冠幅或重新生长来填补在冰灾中被打开的或原来没被利用上的林冠空隙<sup>[3]</sup>;冠幅增长到一定程度又会受到植物生理生态过程的作用,森林冠层结构的变化逐渐减

少,慢慢稳定下来,林下光照也产生相应的变化。

林下光照随林冠开度的减少,叶面积指数的增加而减少。灾后森林恢复初期,林下直射光的量均高于散射光;冠层结构对林下散射光变异的解释最大。由于乔木枝叶的大小、方向和分布(或者林冠空隙的形状、大小及其分布)都会影响冠层对光的截获<sup>[10]</sup>,因此林分冠层结构逐渐恢复到灾前水平的过程中,冠层结构变得越来越复杂,林下直射光和散射光的变化方式和大小也有所区别。林下直射光受太阳位置、林冠空隙大小、冠层高度、地形等因素的影响,尤其是太阳位置时刻都发生着变化<sup>[39]</sup>,因此林下直射光比散射光的时空变化更复杂<sup>[17-18]</sup>。冰灾后森林逐渐郁闭的情况下,林下光照也随之减少,其中直射光减少的量比散射光多。

### 3.2 冠层结构对林下光照的解释能力

冠层结构和林下光照有很强烈且极显著的相关性,但是随着灾后森林的恢复,冠层结构对林下光照的解释能力逐年降低。这说明了在林冠开度较大、叶面积指数较小的情况下,冠层结构对林下光照受的影响占据了主导地位;但林冠开度较小、叶面积指数较大的情况下,冠层结构对林下光照主导作用慢慢变小,其他因素(如地形)对林下光照的控制慢慢体现<sup>[40-41]</sup>。林冠开度和叶面积指数的负相关关系很强,因此林冠开度和叶面积指数之间可以相互验证。无论是冠层被严重干扰的时期(林分郁闭度较低),还是逐渐恢复的时期(林分郁闭度较高),林冠开度对冠层结构的贡献和解释能力都比叶面积指数高,说明林冠开度用于评价冠层结构动态的效果更佳。

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E-mail: shengtaixuebao@rcees.ac.cn 网 址: www.ecologica.cn

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电话:(010)62941099  
www.ecologica.cn  
shengtaixuebao@rcees.ac.cn

主 编 冯宗炜  
主 管 中国科学技术协会  
主 办 中国生态学学会  
中国科学院生态环境研究中心  
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Shengtaixuebao@rcees.ac.cn

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