

THE EFFECT OF LIGHT ON MICRO-ENVIRONMENT AND SPECIFIC LEAF AREA WITHIN THE GAP, SUBTROPICAL FOREST, CHINA

SUPAPORN BUAJAN¹, LIU JINFU^{1*}, HE ZHONGSHENG¹, FENG XUEPING¹ AND ABRAR MUHAMMAD²

¹College of Forestry, Fujian Agriculture and Forestry University, Fuzhou 350002, China.

²Fujian Provincial Key Laboratory of Insect Ecology, Department of Plant Protection, Fujian Agriculture and Forestry University, Fuzhou 350002, China.

*Corresponding author email: fjlfj@hotmail.com

Abstract

Each gap has its own environment, which effect on species growth. Light is the most changes when gap creates. Hence, this study explored whether light has effect on micro-environment and determined the effect of light on specific leaf area (SLA) of species regeneration layer within nine sampling gaps and non-gap. In growing season, environment factors such as light intensity (LI), air temperature (AT), air relative humidity (RH), soil temperature (ST), and soil water content (SWC) were collected. Leaf samples were collected to measure the SLA, nitrogen (N) and phosphorous (P) content. We found that LI had a positive significant correlation with the ST and AT but negative significant correlation with the RH, which these correlation were inversed in non-gap area. The significant different of LI between gap size were found, which the highest average LI occurred in the large gap size meanwhile, the lowest average LI occurred in the small gap size. The spatial heterogeneity of LI differ among the gap depends on the topography, slope direction, and location of trees at each direction. In medium and large gap size, LI had a negative significant correlation with the SLA ($r = -0.248$, $p = 0.04$ and $r = -0.264$, $p = 0.008$). At all directions, the SLA increases with a decreasing LI. Our results concluded that LI had effect on micro-environment in different gap size and SLA in each direction within the gap when compared with non-gap. In addition, SLA had a positive significance with N and P content.

Key words: Micro-environment, Specific leaf area, Subtropical forest, Light intensity.

Introduction

Gaps are the eventuate of forest disturbance created by trees or tree branches falling. Many forest ecologists have studied forest gaps as a basic principle of ecological theory (Yamamoto, 2000). Many researchers have studied how forest gaps maintain species diversity (Denslow, 1987; Bianba *et al.*, 2004; Long *et al.*, 2005; Sapkota *et al.*, 2009; Egbe *et al.*, 2012; Duguid *et al.*, 2013; Dee & Menges, 2014) and promote species establishment (McGuire *et al.*, 2001; Collins & Battaglia, 2008; Nascimento *et al.*, 2012). When a gap is created, light is the most notable factor that changes, and the change depends on the gap size and the way the gap was created (Yamamoto, 2000). Light intensity is the most important factor affecting species regeneration and establishment (Théry, 2001). Light affects the establishment of seedlings, especially for shade-intolerant species. When light increases, it directly affects the temperature in the gap area, so species that need increased temperature for germination have an opportunity to regenerate in a gap area, and without a gap, some of these species cannot be regenerated (Price *et al.*, 2001; Zhu *et al.*, 2014). Moreover, light affects the micro-environment within the forest gap (Gray *et al.*, 2002; Zhang & Wang, 2006; Duan *et al.*, 2013).

Light intensity also affects plant traits (Rice & Bazzaz, 1989; Navas & Garnier, 2002), such as leaf plasticity (Scoffoni *et al.*, 2015), that can reveal how a plant responds to the environment. Specific leaf area (SLA) is one of the leaf traits that is easy to measure and related to other leaf traits such as relative growth rate (Cornelissen *et al.*, 1996), and nitrogen and phosphorus content (Garnier *et al.*, 1997; Wright & Westoby, 2001; Gulias *et al.*, 2003; Liu *et al.*, 2009; An & Shangguan, 2012). Most studies of the effects of light intensity on

SLA have focused on seedlings. Research on effects of light intensity on SLA in natural forest conditions is limited, so studies of the response of SLA to light intensity in natural conditions, especially in the species regeneration layer, are of great importance.

In this study, we investigated the characteristics of micro-environments within forest gaps of various sizes, as well as non-gap areas, with a high-resolution regular grid system (3 × 3m). The environmental factors studied were light intensity, air temperature, air humidity, soil temperature, and soil water content. Leaf samples of every species in the regeneration layer (< 2 cm dbh, height 2-5 m.) were collected from five different directions within each gap to determine SLA, N, and P. The aims of this study were: (1) to determine the effect of light intensity on micro-environments in different-sized gaps and non-gaps; and (2) to evaluate the effect of light intensity in different-sized gaps on the SLA in the species regeneration layer. We expected that the effect of light on the micro-environments and SLA in different-sized gaps would be different. The results of this study will provide a better understanding of the effect of light on micro-environments and SLA of species regeneration layer in forest gaps in the *Castanopsis kawakamii* Nature Reserve.

Materials and Methods

Site descriptions: The study site was located in the *C. kawakamii* Nature Reserve in Sanming City (26°10'–26°12'N, 117°26'–117°28'E), Fujian Province, China. The Sanming *C. kawakamii* Nature Reserve, the authority responsible for national parks, and the relevant regulatory body concerned with protection of wildlife gave permission to conduct the study on this site. We confirm that the field studies did not involve endangered or protected species. This area is an evergreen broad-leaf

forest with a highly pure stand of *C. kawakamii*. It borders Wuyi Mountain on the northwest and Daiyun Mountain on the southeast. The climate in this region is a mid-subtropical monsoon climate with mean annual temperature of 19.5°C, minimum temperature of -5.5°C, the maximum temperature of 40°C, mean annual relative humidity of 81%, and mean annual precipitation of 1,749 mm. Most of the precipitation (79%) occurs from March to August (He *et al.*, 2012).

Experimental area: Gap sampling was performed based on the standard requirement of a minimum area of 30 m² and tree heights in the gap less than two-thirds the height of the surrounding canopy (Runkle, 1992). We measured the gap area using the two hemispherical photographs (THP) method. The photos of each gap were taken by using a fish-eye lens, and then we calculated the area of the gap in the photos using Adobe Illustrator CC 2014 (Adobe Systems Computer Software Company, California, USA). The range of tree heights around the forest gaps was approximately 15–30 m (He *et al.*, 2011). The THP method is based on an equidistant projection of the sky hemisphere ($\theta/90 = r/R$), as described by Hu and Zhu (2009). Every gap has a polygonal shape. After calculating the area of each gap, the gaps were classified

into three categories: small (approximately 30–50 m²), medium (approximately 70–100 m²), and large (more than 150 m²). The geographical factors and features of each gap and non-gap area are shown in Table 1. In non-gap areas, three plots (15 × 15 m) were sampled. In each gap, the size, width, and length of the gap were measured. A grid was made to cover the entire area of the gap (resolution 3 × 3 m) (Fig. 1).

Environmental variables measured: At every measuring point, the environmental variables (air temperature, air relative humidity, and light intensity) were recorded. The air temperature and air relative humidity were measured using TES-1360A handheld digital thermo-hygrometers (Taiwan TAISHI TES Wuxi YAMEI Technology Co. Ltd., Taipei, Taiwan). The light intensity was measured using a light intensity meter. The soil temperature at the surface (ST0), at 5 cm. (ST5) and at 10 cm. (ST10) depth were measured using a 6300 needle soil thermometer (Spectrum Technologies, Inc., Aurora, USA) and soil water content were measured using a TZS-IIW soil moisture and temperature measuring instrument (Zhejiang Top Instrument Co., Ltd, Hangzhou, China). The collecting data done in growing season (August 2014).

Table 1. Topographical factors and features of each forest gap and non gap at the study site.

Gap no. Factor	Small gap size			Medium gap size			Large gap size			Non gap
	1	5	6	3	7	8	2	4	9	
Topographical										
Slope	30°	10°	28°	32°	32°	30°	33°	34°	21°	27°
Altitude (msl.)	236.4	226.7	246.9	275.4	300.0	262.3	249.5	283.7	226.8	245.5
Slope direction	E→W	N→S	S→N	S→N	S→N	N→S	E→W	E→W	E→W	N→S
Gap feature										
Gap area (m ²)	34.78	30.28	48.52	81.25	72.84	81.50	216.72	182.56	198.59	-
Gap maker	Branch fall	Branch fall	Branch fall	Tree fall	Tree fall	Tree fall	Tree fall	Tree fall	Tree fall	-

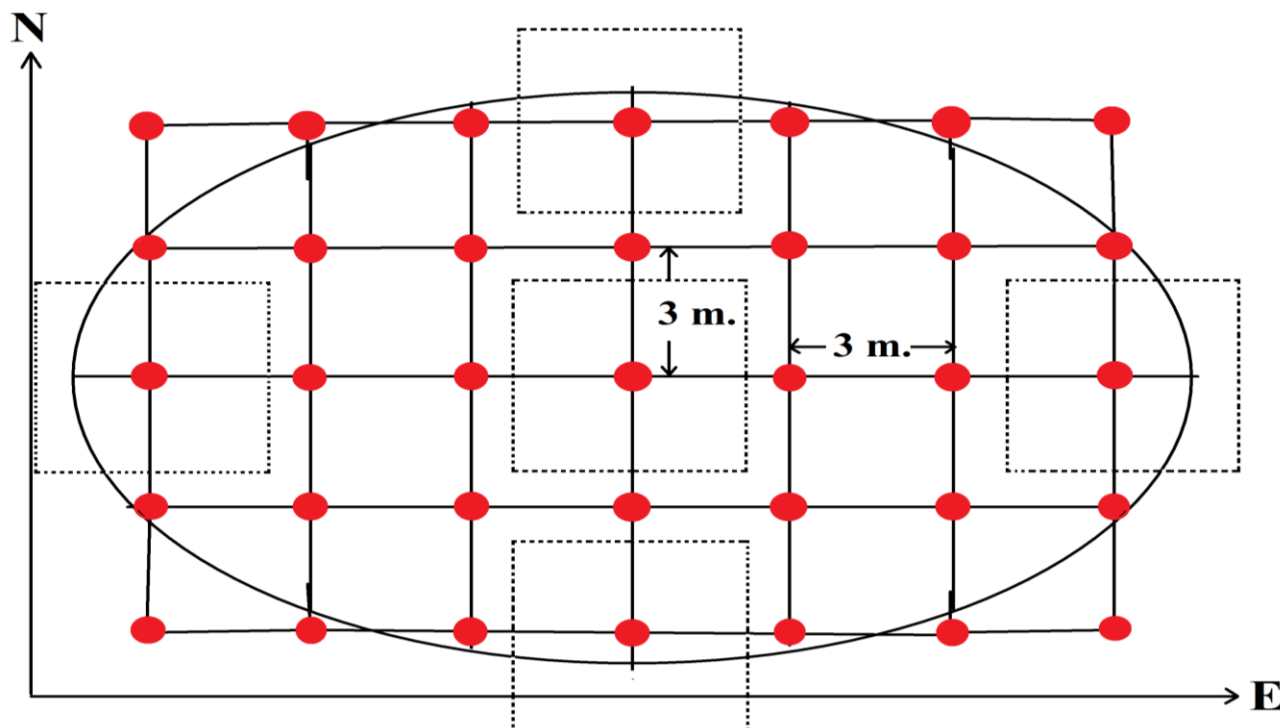


Fig. 1. Grid points (3 × 3 m) in each forest gap and non-gap area for the measured environmental factors. The oval denotes the gap area, red dots denote the points, and dashed square denotes the plant collecting plots in five directions. (In non-gaps, three 15 × 15 m plots were made, and then the grid points were the same as in the gaps).

Plant leaf collection and analysis: In each direction around the sampling plot (south, east, north, west, and center) (Fig. 1), leaves that were young but not fully expanded and hardened, and without obvious symptoms of pathogen or herbivore attack were collected from every species (see the species list in Table 6) in the regeneration layer (<2 cm dbh, height 2–5 m) to measure the specific leaf area (SLA), nitrogen (N), and phosphorus (P) content. Ten leaves from each species were collected for SLA measurement and the SLA values were calculated as an average from these samples (Granier, 2001). We used 0.2 g of dried ground leaves to determine N content (%N) with a vario Max CN Element Analyzer (elementar Analysensysteme GmbH, Hanau, Germany). The phosphorus (P) content was determined by digestion of 2.0 g of dried leaf sample in a HNO₂:HClO₄ mixture (5:1 ratio), heated at 300°C. Ammonium molybdate solution was used to generate color (Murphy & Riley, 1962), and the absorption was measured using a spectrophotometer at $\lambda = 700$ nm.

Data analysis: The average, maximum, and minimum of environmental data values were calculated using Microsoft Excel 2007. The variation in light intensity among and between the three gap size groups and the non-gap areas was evaluated by one-way ANOVA and multiple comparisons using the Tukey's post-hoc test method. The correlations between environmental variables and between leaf parameters (SLA, N, and P) were calculated using the Pearson correlation method. Significant differences among the treatment averages for different variables were tested at $p \leq 0.05$. All data were analyzed using the program SPSS 16.0.

Geostatistical methods: We utilize geostatistical techniques to examine the spatial variability of light intensity within gap area and non-gap. We figure the unsampled points of light intensity using the semivariograms autocorrelation as this equation (Bohling, 2000):

$$r(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [Z(X_i + h) - Z(x_i)]$$

when $r(h)$ = Semivariance for interval distance class h
 $Z(x_i)$ = measured sample value at point i
 $Z(x_i+h)$ = measured sample value at point $i+h$
 $N(h)$ = total number of sample couples for the log interval h

It had a three parameters to identify the spatial variability of light intensity as nugget, sill, and range, the ratio of nugget to sill demonstrate the level of spatial dependence, which last than 0.25 mean strong spatial dependence, between 0.25-0.75 mean medium spatial dependence and more than 0.75 mean weak spatial dependence (Cambardella *et al.*, 1994). The spatial heterogeneity of light intensity in each gap was created by the Kriging spatial interpolation analysis method using the program GS⁺ Geo Statistics for the Environmental Sciences version 7 (Gamma Design Software, Plainwell, MI, USA). Maps of the soil properties were produced with GS+ software, following the ordinary block kriging with a block size of 2m × 2m (Bohling, 2000).

Results

Micro-environments within gaps and non-gaps: A total of nine gaps in this study were classified according to their size: small size (gaps 1, 5 and 6); medium size (gaps 3, 7 and 8); and large size (gaps 2, 4 and 9). The spatial heterogeneity of the average light intensity (lux) in each gap and non-gap (Fig. 2). From the ration of nugget to sill shown that gap 1, 3, 4, 8, and 9 had a weak spatial dependence. Gap 2, 6, and non-gap had a medium spatial dependence, while in the gap 5 and 7 had a strong spatial dependence. Parameter of semivariograms model of LI of each gap and non-gap are shown in Table 2.

We found that average light intensity had statistically significant differences between the three gap sizes and the non-gap areas ($F_{(3,8)} = 18.06$, $p = 0.001$). The multiple comparison analysis by the Tukey's post-hoc test showed that the average light intensity was statistically significantly lower in small gaps (869.10 ± 104.04 lux) and non-gap areas (571.00 ± 143.12 lux) compared with the medium gap (1529.6 ± 214.34 lux; $p = 0.040$, 0.050) and large gaps (1854.6 ± 391.80 lux; $p = 0.004$, 0.001). There were no statistically significant differences between the small gaps and non-gap areas ($p = 0.470$) nor between the medium gaps and large gaps ($p = 0.403$). No significant differences were found in light intensity among the five directions within the gaps. The relationships between the climate factors and the soil variables were examined using the Pearson correlation method, and the correlation coefficients (r) are shown in Table 3. We found a positive significant correlation between light intensity and soil temperature in every gap size, but not in the non-gap. Moreover, light intensity had a positive significant correlation with air temperature in the small and large gap size, but the negative significant correlation appeared in the non-gap area. The relationship between air temperature and air relative humidity in all gap size and non-gap area were a negative significant correlation.

Specific leaf area (SLA) and light intensity in gap sizes and non-gap: From the plant function traits investigation, we received the total number of plant species in each forest gap and also in the non-gap area (Table 4). In every forest gap, we found that most of the same species that located in a different direction had different SLA value. For example in gap no. 2 (large gap size), *Machius grijsii* Hance that grow at the center have SLA lower than *Machius grijsii* Hance that located at the North direction of gap. *Symplocos lancifolia* Sieb. et Zucc that located at the East direction have SLA value higher than which one located at the South and North directions (SLA = 23.44, 20.14 and 15.25 m²/kg, respectively) when compared with light intensity in each direction (Fig. 3). We found the negative relationship between them. This relationship between SLA value and light intensity were found in the medium and large gap size and non-gap, while in the small gap had a little positive relationship. Pearson correlation was conducted for the relationship between SLA value and light intensity. We found a significant negative correlation between the average light intensity and the SLA values in large gaps ($r = -0.264$, $p = 0.008$) and medium gaps ($r = -0.248$, $p = 0.014$) (Fig. 4), whereas in the small gaps and the non-gaps, SLA and light intensity were not significantly correlated.

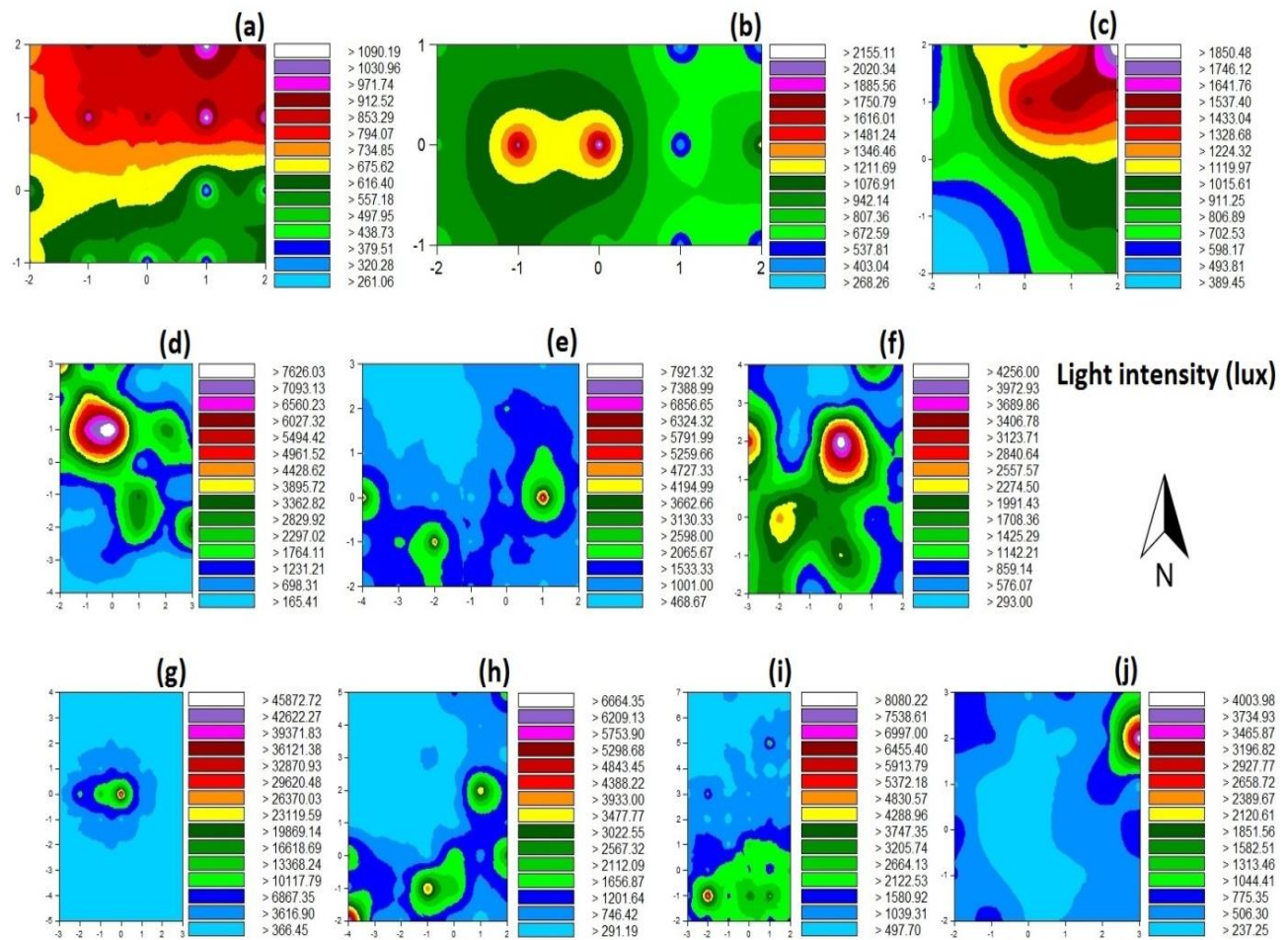


Fig. 2. Map of spatial heterogeneity of average light intensity (lux) in the gaps and non-gap areas: (a) gap 1; (b) gap 5; (c) gap 6; (d) gap 3; (e) gap 7; (f) gap 8; (g) gap 2; (h) gap 4; (i) gap 9; and (j) non-gap.

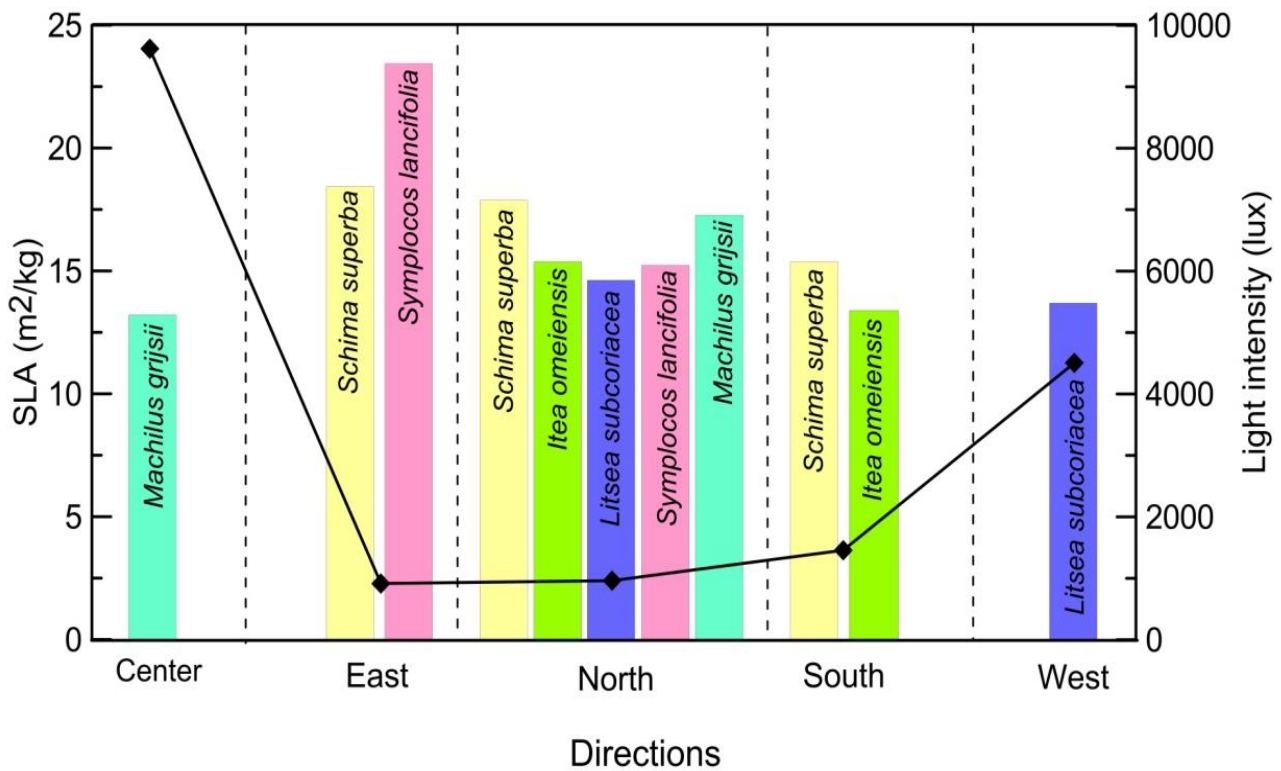


Fig. 3. SLA value (m²/kg) of each species compared with light intensity (lux) in each direction of gap no.2.

In this study, we found two species (*Litsea subcoriacea* Yang et P. H. Huang and *Schima superba* Gardn. et Champ) that grew in every gap. The SLA values of each of these species in the different-sized gaps were compared. The SLA in both species had a significant negative correlation with light intensity in the large gaps (*Litsea subcoriacea*, $r = -0.613$, $p = 0.017$; *Schima superba*, $r = -0.848$, $p = 0.004$) whereas, in the small gaps, medium gaps, and non-gaps, no significant correlation was found.

Relationship between SLA and N and P content in leaves: The correlation coefficients of SLA versus nitrogen and phosphorus in the leaf samples were calculated by the Pearson correlation method. The significant correlations are shown in Table 5. In every gap except gap 2, 4, and 8, the SLA values had a significant positive correlation with %N. In gap 5, the strong positive correlation with N was $r = 0.775$ ($p \leq 0.01$). Moreover, we found a significant positive correlation with P in every gap except gaps 1, 4, and 8, and the non-gap areas.

Table 2. Fitted model types and parameters for the semivariograms of LI (lux) of each gap and non gap in summer season.

Gap no.	Model	Nugget (C ₀)	Sill (C ₀ + C)	Range	C ₀ /C ₀ + C	R ²
1	Gaussian	100.000	118600.000	2.1755	0.999	0.537
5	Linear	384687.23	384687.23	3.2067	0.000	1.000
6	Exponential	172000.00	655000.00	12.0720	0.737	0.875
3	Spherical	250000.00	3584000.00	2.1650	0.930	0.966
7	Linear	3606651.74	3606651.74	3.2726	0.000	0.731
8	Spherical	166000.00	1098000.00	1.7820	0.849	0.203
2	Gaussian	48100000	121750000	6.0214	0.605	1.000
4	Exponential	1000.00	1151000.00	1.5180	0.999	0.833
9	Gaussian	1700000	7510000	18.2385	0.774	0.698
Non gap	Gaussian	308000	1027000	11.1024	0.700	0.909

Table 3. Correlation coefficients (r) for the relationships between environmental factors and soil variables in each size gap and non-gap.

		ST0	ST5	ST10	SWC	LI	AT	RH		
Small (n=295)	ST0		0.961**	0.700**	-0.268**	0.149**	0.126**	-0.599**	Medium (n=660)	
	ST5	0.885**		0.840**	-0.280**	0.122**	0.123**	-0.589**		
	ST10	0.583**	0.762**		-0.140**	ns	0.142**	-0.498**		
	SWC	0.125*	0.179**	0.158**		ns	ns	0.074*		
	LI	0.222**	0.171**	0.108*	ns		ns	-0.069*		
	AT	0.693**	0.614**	0.353**	.096*	0.211**		-0.122**		
	RH	-0.634**	-0.618**	-0.364**	-0.199**	ns	-0.870**			
Large (n=930)	ST0		0.894**	0.244**	ns	ns	0.349**	-0.325**	Non-gap (n=180)	
	ST5	0.846**		0.650**	ns	ns	0.433**	-0.437**		
	ST10	0.433**	0.784**		ns	ns	0.342**	-0.394**		
	SWC	ns	ns	ns		0.312**	ns	ns		
	LI	0.230**	0.114**	ns	ns		-0.143*	0.166*		
	AT	0.733**	0.646**	0.322**	0.086**	0.144**		-0.867**		
	RH	-0.477**	-0.460**	-0.249**	-0.164**	-0.078**	-0.735**			

**= Correlation is significant at the 0.01 level; *= Correlation is significant at the 0.05 level; ns, not significant

Table 4. Number of species in regeneration layer (< 2 cm dbh, height 2-5 m.) in each forest gap and non gap.

Class size	Small gap			Medium gap			Large gap			non gap
	1	5	6	3	7	8	2	4	9	
Center	5	3	7	3	2	2	3	4	5	3
East	5	2	5	10	5	4	5	5	7	4
North	3	3	3	6	4	7	5	9	8	4
South	7	5	5	8	4	5	5	8	9	5
West	6	4	10	5	6	5	4	5	3	6
Total	15	11	19	16	15	19	14	18	19	13
Average	15			16			17			13

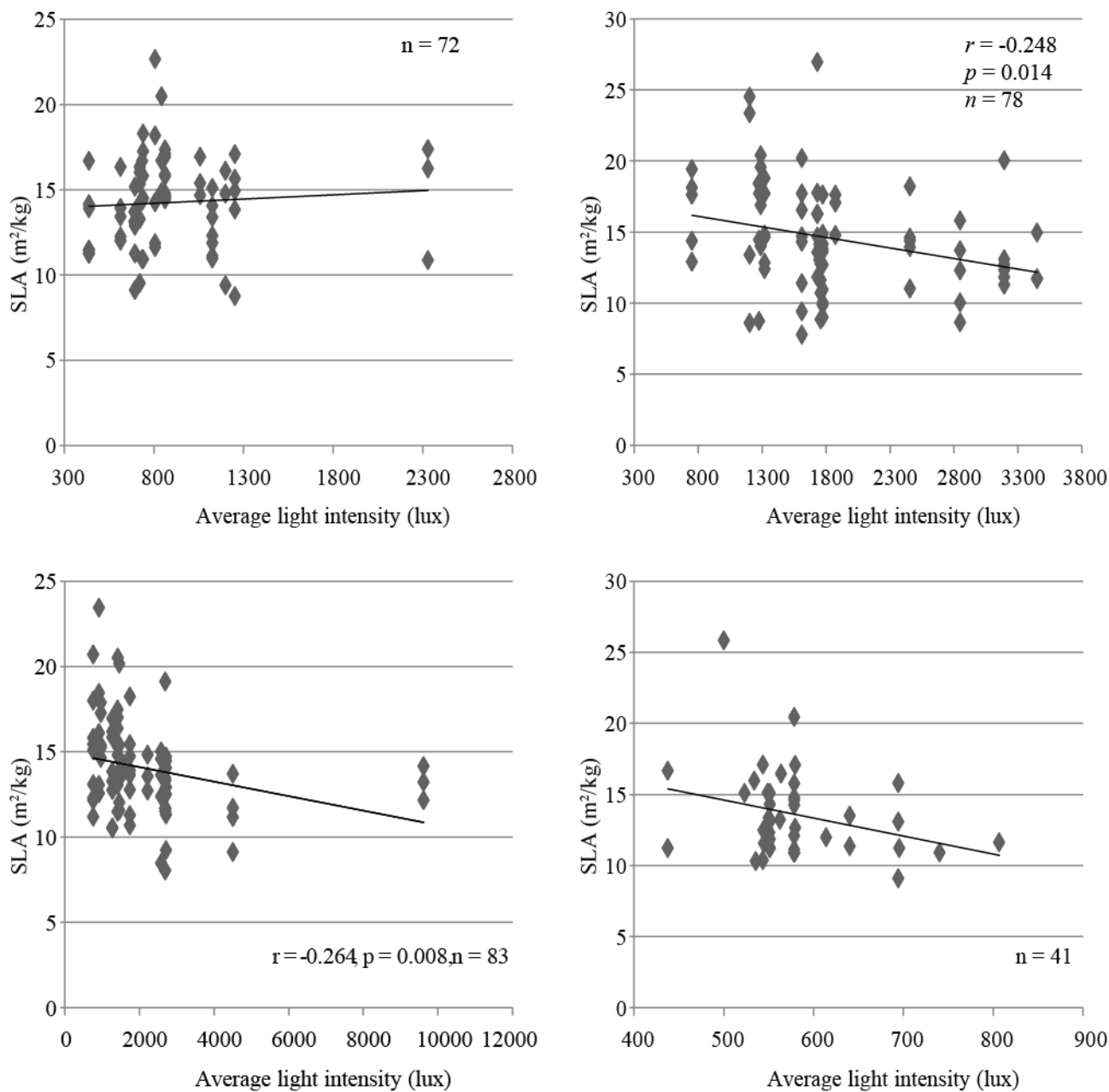


Fig. 4. Relationship between average light intensity (lux) and SLA (m²/kg) in (a) small gaps; (b) medium gaps; (c) large gaps; and (d) non-gap areas.

Table 5. Correlation coefficients between SLA values (m²/kg) and nitrogen (%) and phosphorus (g/kg) content in leaf samples.

SLA (m ² /kg) gap no.	Nitrogen (%)	Phosphorus (g/kg)
Gap 1	0.341*	ns
Gap 2	ns	0.412*
Gap 3	0.337*	0.314*
Gap 4	ns	ns
Gap 5	0.775**	0.595**
Gap 6	0.306*	0.328*
Gap 7	0.451*	0.555**
Gap 8	ns	ns
Gap 9	0.351*	0.496**
Non-gap	0.404*	ns

* p < 0.05; ** p < 0.01; ns = Not significant

Discussion

Effects of light in gaps and non-gap: Light intensity differed among the different-sized gaps as compared to the non-gap, and the highest light intensity occurred in the center of the largest gap size. Light is the main factor that affects other environmental variables, and the light effect on the micro-environment of the gaps and non-gap were notably different. As the previous study, the varieties of micro environment were amazingly noteworthy among the gap sizes in *C. kawakamii* forest (He *et al.*, 2012). This finding related with Zhang & Wang (2006) reported that the micro-environment of forest gaps in a subalpine coniferous forest differences between gap and canopy, especially with respect to light and soil temperature.

Table 6. Species list in this study.

Family	Scientific name
Aquifoliaceae	<i>Ilex chinensis</i> Sims (<i>Ilex purpurea</i> Hassk.) <i>Ilex dasyphylla</i> Merr <i>Ilex elmerrilliana</i> S. Y. Hu <i>Ilex fioidea</i> Hemsl <i>Ilex formosana</i> Maxim <i>Ilex pubescens</i> Hook. et Arn
Araliaceae	<i>Dendropanax dentiger</i> (Harms) Merr
Daphniphyllaceae	<i>Daphniphyllum oldhamii</i> (Hemsl.) Rosenthal.
Elaeocarpaceae	<i>Elaeocarpus chinensis</i> (Gardn. et Champ.) Hook. f. ex Benth <i>Elaeocarpus sylvestris</i> (Lour.) Poir
Ericaceae	<i>Vaccinium carlesii</i> Dunn
Euphorbiaceae	<i>Antidesma japonicum</i> Sieb. et Zucc
Fabaceae	<i>Archidendron lucida</i> (Benth.) Nielsen (<i>Pithecellobium lucidum</i> Benth.)
Fagaceae	<i>Castanopsis carlesii</i> (Hemsl.) Hayata <i>Castanopsis fargesii</i> Franch. <i>Castanopsis kawakamii</i> Hayata <i>Lithocarpus glaber</i> (Thunb.) Nakai
Juglandaceae	<i>Engelhardtia fenzelii</i> Merr.
Lauraceae	<i>Cinnamomum austro-sinense</i> H. T. Chang <i>Cinnamomum chekiangense</i> se Nakai <i>Lindera communis</i> Hemsl <i>Lindera nacusua</i> (D. Don.) Merr <i>Litsea subcoriacea</i> Yang et P. H. Huang <i>Machilus grijsii</i> Hance <i>Machilus leptophylla</i> Hand. -Mazz. <i>Machilus versicolora</i> S. K. Lee & F. N. Wei <i>Neolitsea aurata</i> (Hay.) Koidz <i>Neolitsea cambodiana</i> Lec. var. <i>glabra</i> Allen
Leguminosae	<i>Ormosia xylocarpa</i> Chun ex Merr. et L. Chen
Magnoliaceae	<i>Fissistigma oldhamii</i> (Hemsl.) Merr <i>Michelia skinneriana</i> Dunn <i>Tsoongiodendron odorum</i> Chun
Myrtaceae	<i>Syzygium buxifolium</i> Hook. et Arn
Proteaceae	<i>Helicia cochinchinensis</i> Lour
Rubiaceae	<i>Diplospora dubia</i> (Lindl.) Masam. (<i>Tricalysia dubia</i> (Lindl.) Ohwi) <i>Randia cochinchinensis</i> (Lour.) Merr.
Sabiaceae	<i>Meliosma rigida</i> Sieb. et Zucc
Saxifragaceae	<i>Itea omeiensis</i> C. K. Schneid.
Symplocaceae	<i>Symplocos cochinchinensis</i> (Lour.) S. Moore <i>Symplocos lancifolia</i> Sieb. et Zucc <i>Symplocos stellaris</i> Brand <i>Symplocos sumuntia</i> Buch. -Ham. ex D. Don
Theaceae	<i>Adinandra millettii</i> (Hook. et Arn.) Benth. et Hook. f. ex Hance <i>Camellia fraterna</i> Hance in Ann. <i>Camellia octopetala</i> Hu <i>Eurya loquaiana</i> Dunn <i>Eurya nitida</i> Korthals <i>Schima superba</i> Gardn. et Champ

In our study, light intensity had a significant positive correlation with ST0 and ST5 in all three gap sizes, but this correlation was not significant in non-gap areas, indicating that light in the gaps had a strong effect on the soil temperature, especially near the soil surface where solar radiation increases the soil temperature. This result was similar to a study of forest gaps in tropical forests that found the soil temperatures were directly affected by solar radiation (Tokiman & Nuruddin, 2005). The outcomes of the previous study were comparative with the present study, that air and soil temperature were various with gap size with highest at the center of a gap then gradually to the gap edge and under canopy (He *et al.*, 2012). Air temperature in the small and large gaps was influenced by light intensity, whereas in the medium gaps, it was not influenced. This might be the effect of the wind on air temperature in the medium gaps was stronger than light intensity. In an open area like a gap, wind speed can diminish the air temperature by overwhelming the hot air and supplanting it with cooler air (Orzel, 2010). Moreover, the relationship between light intensity and air temperature in gap areas was the opposite of that observed in non-gap, demonstrating that light intensity had a strong effect on micro-environments in the gaps. The effects of light intensity in the present study are similar to findings on the effect of forest gap size and within-gap position on the microclimate in *Pinus koraiensis*-dominated broad-leaved mixed forest (Feng *et al.*, 2012). The level of light intensity depends on the size of the gap. The results of our study are similar to those of a study conducted in forests of southern New England that showed that light intensity in larger gaps was higher than in smaller gaps (Duan *et al.*, 2013). On the top of that, light intensity had a significant negative correlation with air relative humidity in the medium and large gap size, but in the non-gap was a contrary relationship.

The spatial heterogeneity of average light intensity in each gap examined in our study (Fig. 2) and the results demonstrated that there were no significant differences in light intensity among the five within-gap directions in all three gap sizes. The spatial dependence of light intensity in each gap size and non-gap were difference. This means that the patterns of light intensity in each gap were different, indicating that each forest gap has its own character based on topography, slope direction, aspect, (Canham *et al.*, 1990) and the location of trees in each direction, etc. We observed that in some gaps the highest average light intensity was not located at the center because we measured the light intensity at a height of 1.50 m above the ground, and some gaps had trees higher than 1.50 m at the center, thereby reducing light intensity at the center. For example, at gap 2, the highest average light intensity occurred at the center of the gap because this gap was the largest in size and the center of this gap did not have trees higher than 1.50 m. That situation contrasted with gap 6, which had trees at the center of the gap higher than 1.50 m. This is the reason the light intensity was not highest at the center of gap 6. This finding is supported by Gray *et al.* (2002), who observed that light intensity increased with gap size, but the increase differed according to direction within the gap.

Specific leaf area (SLA) and light intensity in the gaps and non-gap: Light intensity and SLA were significantly correlated in the medium and large gaps, whereas in the small gaps and non-gap, the correlation was not significant. This indicates that light intensity in medium and large gaps is strong enough to affect SLA in the studied plant species. Leaves growing under the light are usually larger and thinner than leaves grown in shadow (Abrams & Kubiske, 1990). This is a mechanism the leaves use to adapt to the environment. At low light, plants produce a large leaf to absorb as much light as possible for photosynthesis; conversely, in high light conditions, plants do not need to produce a large leaf, owing to the suitable light conditions. An *In vitro* experiment with regenerated grapevines showed the same results: in low light, the SLA values of new leaves increased (de Oliveira *et al.*, 2002). In this study, we found that within a gap, the SLA values decreased in the direction that had a high light intensity. On the contrary, they increased in the direction that had low light intensity. Similar findings were reported in a study of *Syringa oblata* leaves under different light conditions (Xiao *et al.*, 2015). The SLA response to light intensity we observed in each forest gap is similar to that observed in many studies on the relationship of SLA and light intensity. Liao and his team studied the growth of four *Mosla* species affected by light intensity, and they found that when light intensity increased, the SLA values decreased (Liao *et al.*, 2006). Devkota and Kumer (2010) conducted experiments on *Centella asiatica* under different light levels and found that the highest SLA was under 70% shadow, whereas the lowest SLA was under the complete light. One study found that when the light intensity decreased, the specific leaf area of *Ambrosia trifida* increased (Wang *et al.*, 2012). SLA is the ratio between leaf area and leaf dry mass, and light affects leaf morphology by diminishing the leaf area and increasing leaf thickness. Aforementioned, leaves in the sun are usually denser than leaves in the shadows. This is the reason the SLA values were lower with increasing light. Light intensity in the large gaps had an effect on the SLA of both species (*Litsea subcoriacea* Yang et P. H. Huang and *Schima superba* Gardn. et Champ) whereas, in the small and medium gaps, it did not, indicating that those species responded to the high light intensity in the large gaps. The light intensity in the small and medium gaps may not be strong enough to affect the SLA of those species.

We know that SLA is related to the relative growth rate (RGR) and thus can be used as an indicator to determine the growth of plant species (Cornelissen *et al.*, 1996). Wright and Westoby (2000) done an experiment with 28 species, seedlings were grown in favorable conditions to find the relationship between RGR and four variables: leaf nitrogen productivity (LNP), leaf nitrogen concentration per unit area (LNCA), specific leaf area (leaf area per unit leaf mass, SLA), and leaf mass ratio (ratio of leaf to the total mass, LMR). The results showed that SLA has the strongest correlation with RGR (Wright & Westoby, 2000). Shipley (2006) also studied the relationship of RGR and SAL. He found the importance of RGR increased with increasing SLA. This relationship was also found in seedlings of invasive species in the Mediterranean region: species that have a high RGR also have a high SLA (Grotkopp & Rejmánek, 2007). Some species in our study i.e. *Dendropanax dentiger* (Harms) Merr and *Symplocos sumuntia* Buch. -Ham. ex D. Don

did not follow this relationship because the SLA values varied in each species (different species had different SLA values) and might be influenced by other environmental factors such as soil nutrient, which wasn't dominated by light intensity. No effect of light intensity on the SLA values of plant species in non-gap areas was detected when compared with gap areas, because in the non-gap areas light intensity was not the main factor stimulating plant growth. This is the reason the SLA values of plants in non-gap areas did not vary according to within-gap direction. By contrast, in the forest gaps, light is the main factor that directly influences plant growth.

Relationship between SLA and N and P content in leaves:

Specific leaf area (SLA) is also related to nitrogen (N) and phosphorus (P) content in leaves both in gap and non-gap areas. Our findings are in agreement with Bongers and Popma (1990) and Jayasekera (1992), who observed that the N concentration in leaves is closely related to the P concentration, which is further related to SLA. Nitrogen is the main nutrient for plant growth and a basic component of chlorophyll and protein in the leaf (Stocking & Ongun, 1962). The results of the present study are consistent with those of Garnier *et al.* (1997), who investigated the SLA and nitrogen content in leaves of annual and perennial species under natural conditions. They observed a positive significant correlation between SLA and leaf N content based on mass in perennial species. Liu *et al.* (2009) also observed a strong relationship between SLA and leaf N in all tree species in their research. Other studies carried out to determine the relationship between SLA and nitrogen content in leaves have also shown a positive relationship (Gulias *et al.*, 2003; An & Shangguan, 2012; Grubb *et al.*, 2015). Moreover, the conclusion from Wright & Westoby (2001) regarding the relationship between SLA and leaf nitrogen content demonstrated that N concentration in leaves could be used as a major trait when considered along with SLA in relation to relative growth rate. The relationship of SLA and N content observed in this study indicates that light had an effect on plant growth in the forest gaps when compared with non-gap. Forest management in this area should consider the gap effects of light on plant growth. The results from this study indicate that light in the medium and large gaps has an effect on SLA, which is related to plant growth. The forest ecologist must pay attention to these medium and large gaps.

Conclusion

Light is the main factor in forest gaps as compared to non-gap; it has a positive correlation with soil temperature and air temperature, and a negative correlation with air humidity. The spatial heterogeneity of average light intensity differed in each forest gap in our study area depending on topography, slope direction, and the features of the trees in each surrounding direction within the gap. Light intensity increased with increasing gap size. Leaf traits such as SLA responded to the micro-environment within forest gaps as compared to non-gap. SLA was directly affected by the light intensity in medium and large gaps, indicating that light in the medium and large gaps had a stronger effect on SLA when compared to small gaps and non-gap. The SLA had a significant positive effect on N and P content in the leaves, and those variables were related

to the relative growth rate, indicating that light affects plant growth in the gaps when compared to the non-gap. The results of this study will help to better understand the response of plants to different natural micro-environmental factors within forest gaps.

Acknowledgements

We are grateful to Qi Lixa, Tang Rong, Kuang Kaijin, Huang Jiahang, Ao Xinghai, Su Songjin, Zhan Yinhu, and Zhou Shanshan for assistance with field and laboratory work. We also thank the Sanming *Castanopsis kawakamii* Nature Reserve for permission to conduct the study on that site. We are grateful as well to two anonymous reviewers for valuable suggestions during the revision of the manuscript.

References

- Abrams, M.D. and M.E. Kubiske. 1990. Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: Influence of light regime and shade-tolerance rank. *Forest Ecol. Manag.*, 31(4): 245-253.
- An, H. and Z. Shangguan. 2012. Generality of leaf traits relationships of dominant species along the secondary succession in the Loess Plateau of China. *Afr. J. Biotechnol.*, 11(7): 1624-1631.
- Bianba, D., Q. Guo, B. Ci and D. Luo. 2004. Effects of gap in primitive subalpine fir forest on diversity of herb and shrub in Tibet. *J. Appl. Ecol.*, 15(2):191-194.
- Bohling, G. 2000. GS+ for Windows, Version 3.11. 12, Gamma Design Software, Plainwell, USA. *Computers & Geosciences*, 26(7): 855-863.
- Bongers, F. and Popma, J.1990. Leaf characteristics of the tropical rain forest flora of Los Tuxtlas, Mexico. *Bot. Gaz.*, 151: 354-365.
- Cambardella, C.A., T.B. Moorman, T.B. Parkin, D.L. Karlen, J.M. Novak, R.F. Turco. and A.E. Konopka. 1994. Field-scale variability of soil properties in central Iowa soils. *Soil Sci. Soc. Amer. J.*, 58(5): 1501-1511.
- Canham, C.D., J.S. Denslow, W.J. Platt, J.R. Runkle, T.A. Spies and P.S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. Forest Res.*, 20(5): 620-631.
- Collins, B. and L.L. Battaglia. 2008. Oak regeneration in southeastern bottomland hardwood forest. *Forest Ecol. Manag.*, 255(7): 3026-3034.
- Cornelissen, J.H.C., P.C. Diez and R. Hunt. 1996. Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *J. Ecol.*, 84:755-765.
- de Oliveira, M.C., M.G.D. Carvalho, C.J.D. Silva and A.A. Werle. 2002. New biflavonoid and other constituents isolated from *Luxemburgia nobilis*. *J. Braz. Chem. Soc.*, 13(1): 119-123.
- Dee, J.R. and E.S. Menges. 2014. Gap ecology in the Florida scrubby flatwoods: effects of time-since-fire, gap area, gap aggregation and microhabitat on gap species diversity. *J. Veg. Sci.*, 25(5): 1235-1246.
- Denslow, J.S. 1987. Tropical rainforest gaps and tree species diversity. *Annu. Rev. Ecol. Evol. Syst.*, 18: 431-451.
- Devkota, A. and J.P. Kumar. 2010. Effect of different light levels on the growth traits and yield of *Centella asiatica*. *Middle East J. Sci. Res.*, 5(4): 226-230.
- Duan, W.B., L.X. Wang, L.X. Chen, S. Du, Q.S. Wei and J.H. Zhao. 2013. Effects of forest gap size and light intensity on herbaceous plants in *Pinus koraiensis*-dominated broadleaved mixed forest. *J. Appl. Ecol.*, 24(3): 614-620.

- Duguid, M.C., B.R. Frey, D.S. Ellum, M. Kelty and M.S. Ashton. 2013. The influence of ground disturbance and gap position on non-gap plant diversity in upland forests of southern New England. *Forest Ecol. Manag.*, 303: 148-159.
- Egbe, E.A., G.B. Chuyong, B.A. Fonge and K.S. Namuene. 2012. Forest disturbance and natural regeneration in an African rainforest at Korup National Park, Cameroon. *Int. J. Biodivers. Conserv.*, 4(11): 377-384.
- Feng, J., W.B. Duan and L.X. Chen. 2012. Effects of forest gap size and within-gap position on the microclimate in *Pinus koraiensis*-dominated broadleaved mixed forest. *J. Appl. Ecol.*, 23(7): 1758-66.
- Garnier, E., P. Cordonnier, J.L. Guillermin and L. Sonié. 1997. Specific leaf area and leaf nitrogen concentration in annual and perennial grass species growing in Mediterranean old-fields. *Oecologia*, 111(4): 490-498.
- Garnier, E., B. Shipley, C. Roumet and G. Laurent. 2001. A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Funct. Ecol.*, 15(5): 688-695.
- Gray, A.N., T.A. Spies and M.J. Easter. 2002. Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests. *Can. J. For. Res.*, 32(2): 332-343.
- Grotkopp, E. and M. Rejmanek. 2007. High seedling relative growth rate and specific leaf areas are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. *Am. J. Bot.*, 94(4): 526-532.
- Grubb, P.J., T. Marañón, F.I. Pugnaire and L. Sack. 2015. Relationships between specific leaf area and leaf composition in succulent and non-succulent species of contrasting semi-desert communities in south-eastern Spain. *J. Arid Environ.*, 188: 69-83.
- Gulias, J., J. Flexas, M. Mus, J. Cifre, E. Lefi and H. Medrano. 2003. Relationship between maximum leaf photosynthesis, nitrogen content and specific leaf area in Balearic endemic and non-endemic Mediterranean species. *Ann. Bot.*, 92(2): 215-222.
- He, Z.S., J.F. Liu, S.Q. Zheng, W. Hong, C.Z. Wu and D.W. Xu. 2011. Study on the characteristics of gap border trees in *Castanopsis kawakamii* Natural Forest. *J. Fujian College of Forest.*, 31(3): 207-211.
- He, Z.S., J.F. Liu, C.T. Wu, S.Q. Zheng, W. Hong, S.J. Su and C.Z. Wu. 2012. Effects of forest gaps on some microclimate variables in *Castanopsis kawakamii* natural forest. *J. Mt. Sci.*, 9(5): 706-714.
- Hu, L. and J. Zhu. 2009. Determination of the tridimensional shape of canopy gaps using two hemispherical photographs. *Agric. For. Meteorol.*, 149(5): 862-872.
- Jayasekera, R. 1992. Elemental concentrations in a tropical mountain rain forest in Sri Lanka. *Vegetatio*, 98(1): 73-81.
- Liao, J.X., X.Y. Zou, Y. Ge and J. Chang. 2006. Effects of light intensity on growth of four *Mosla* species. *Bot. Stud.*, 47(4): 403-408.
- Liu, F., M. Zhang, W. Wang, S. Chen, J. Zheng, W. Yang, F. Hu and S. An. 2009. Photosynthesis in relation to leaf nitrogen, phosphorus and specific leaf area of seedling and sapling in tropical mountain rain forests of Hainan Island, south China. *Frontiers of Forestry in China*, 4(1): 75-84.
- Long, C., S. Yu, Z. Xiong and L. Wei. 2005. Species diversity and regeneration in forest gaps of the Karst forest in Maolan National Nature Reserve, Guizhou Province. *Chinese Biodiv.*, 13(1): 43-50.
- McGuire, J.P., R.J. Mitchell, E.B. Moser, S.D. Pecot, D.H. Gjerstad and C.W. Hedman. 2001. Gaps in a gappy forest: plant resources, longleaf pine regeneration, and non-gap response to tree removal in longleaf pine savannas. *Can. J. For. Res.*, 31(5): 765-778.
- Murphy, J. and J.P. Riley. 1962. A modified single solutions method for the determination of phosphate in natural waters. *Anal. Chim. Acta.*, 27: 31-36.
- Navas, M.L. and E. Garnier. 2002. Plasticity of whole plant and leaf traits in *Rubia peregrina* in response to light, nutrient and water availability. *Acta Oecol.*, 23(6): 375-383.
- Nascimento, A.R.T., A.B. Giroldo, G.M. Araújo and P.P.F. Silva. 2012. Gap area and tree community regeneration in a tropical semideciduous forest. In: *Tropical Forests* (Ed.): P. Sudarshana. Available from: <http://www.intechopen.com/books/tropicalforests/gap-area-and-tree-community-regeneration-in-a-tropical-semideciduous-forest>.
- Orzel, C. 2010. Wind and Temperature: Why Doesn't Windy Equal Hot?. Available at: <http://scienceblogs.com/principles/2010/08/17/wind-and-temperature-why-doesn/> [accessed on 6 February 2016].
- Price, D.T., N.E. Zimmermann, P.J. Van Der Meer, M.J. Lexer, P. Leadley, I.T. Jorritsma, J. Schaber, D.E. Clark, P. Lasch, S. McNulty and J. Wu. 2001. Regeneration in gap models: Priority issues for studying forest responses to climate change. *Clim. Chang.*, 51(3-4): 475-508.
- Pulliam, H. 2000. On the relationship between niche and distribution. *Ecol. Lett.*, 3(4): 349-361.
- Rice, S.A. and F.A. Bazzaz. 1989. Growth consequences of plasticity of plant traits in response to light conditions. *Oecologia*, 78(4): 508-512.
- Runkle, J.R. 1992. Guidelines and sample protocol for sampling forest gaps. *U.S. For. Serv. Gen. Tech. Rep. PNW-GTR-283*.
- Sapkota, I.P., M. Tigabu and P.C. Odén. 2009. Species diversity and regeneration of old-growth seasonally dry *Shorea robusta* forests following gap formation. *J. For. Res.*, 20(1): 7-14.
- Scoffoni, C., J. Kunkle, J. Pasquet-Kok, C. Vuong, A.J. Patel, R.A. Montgomery, T.J. Givnish and L. Sack. 2015. Light-induced plasticity in leaf hydraulics, venation, anatomy, and gas exchange in ecologically diverse Hawaiian lobeliads. *New Phytol.*, 207(1): 43-58.
- Shipley, B. 2006. Net assimilation rate, specific leaf area and leaf mass ratio: which is most closely correlated with relative growth rate? A meta-analysis. *Fungal Biol.*, 20(4): 565-574.
- Stocking, C.R. and A. Ongun. 1962. The intracellular distribution of some metallic element in leaves. *Am. J. Bot.*, 49(3): 284-289.
- Théry, M. 2001. Forest light and its influence on habitat selection. *Plant Ecol.*, 153(1-2): 251-261.
- Tokiman, L.L. and A.A. Nuruddin. 2005. Air and soil temperature characteristics of two sizes of forest gap in tropical forest. *Asia J. of Plant Sci.*, 4(2): 144-148.
- Wang, R., B. Sun, J.D. Li, G.J. Wang, J.N. Sun, X.R. Wang and R.T. Zhong. 2012. Effects of light intensity on the phenotypic plasticity of invasive species *Ambrosia trifida*. *J. Appl. Ecol.*, 23(7): 1797-1802.
- Wright, I.J. and M. Westoby. 2000. Cross-species relationships between seedling relative growth rate, nitrogen productivity and root versus leaf function in 28 Australian woody species. *Funct. Ecol.*, 14(1): 97-107.
- Wright, I.J. and M. Westoby. 2001. Understanding seedling growth relationships through specific leaf area and leaf nitrogen concentration: generalizations across growth forms and growth irradiance. *Oecologia*, 127(1): 21-29.
- Xiao, H., C. Wang, J. Liu, L. Wang and D. Du. 2015. Insights into the differences in leaf functional traits of heterophyllous *Syringa oblata* under different light intensities. *J. For. Res.*, 26(3): 613-621.
- Yamamoto, S.I. 2000. Forest gap dynamics and tree regeneration. *J. For. Res.*, 5(4): 223-229.
- Zhang, Y.B. and K.Y. Wang. 2006. Microenvironment of forest gaps and its effects on the growth of naturally regenerated seedling of different ages in subalpine *Abies faxoniana* forest. *Chinese J. Plant Ecol.*, 30(6): 941-946.
- Zhu, J.J., D.L. Lu and W.D. Zhang. 2014. Effects of gaps on regeneration of woody plants: a meta-analysis. *J. For. Res.*, 25(3): 501-510.