Research paper

Understory Light at the Fushan Experimental Forest in Northeastern Taiwan: Watershed and Landscape Perspectives

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【Summary】

Understory light regimes have a major impact on seedling growth and patterns of forest regeneration. Many researchers have reported understory light regimes for relatively small areas, and then extrapolated their results to the landscape level with little knowledge of landscape-level heterogeneity. We used hemispherical photography to characterize understory light regimes at both the watershed and landscape scales within the Fushan Experimental Forest in northeastern Taiwan. We established 20 transects, 7 of which were located in Experimental Watershed #1 and the other 13 were scattered across an area of 150 ha at the Fushan Experimental Forest. Understory light was not normally distributed across the Fushan Experimental Forest, with some microsites having very high light levels due to typhoon-induced canopy damage. Median understory light levels exceeded 15% of the incident sunlight at both the watershed and landscape scales. These light levels are much higher than those reported for many mature tropical and temperate forests in other parts of the world, where understory light levels of < 5% of incident sunlight are common. Aspect, rather than spatial scale, had the largest impact on undercanopy light. In forests with rough topography, utilizing transects that run from the ridge to the valley is more likely to adequately characterize spatial heterogeneity than plots or a few longer transects.

Key words: understory light regime, Fushan Experimental Forest, watershed level, landscape level, hemispherical photography.

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研究報告

台灣東北部福山試驗林之林下光照環境：集水區階層與地景階層之異同

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摘　要

林下光照對小苗的生長及森林的更新有很大的影響，許多研究者在對地景階層的異質性並無深入了解的情形下，就將小範圍內林下光照的調查結果引伸至較大的空間範圍。本研究以半球面影像技術在台灣東北部的福山試驗林，探討小集水區階層及地景階層的林下光照情況。研究共建立二十條樣線，七條位於一號試驗集水區，十三條散布在150 ha的範圍內。由於少數微棲地因颱風造成的林冠損害而有相當高的光照，故福山試驗林之林下光照並非常態分布。福山試驗林在集水區及地景階層林下光照之中位數皆高於林外全光照的15%，較許多熱帶及溫帶森林林下光照不到林外5%的情形高出甚多。在福山試驗林，坡向較空間尺度對林下光照有更大的影響，因此在地形起伏劇烈如福山試驗林的地區，利用多條由稜線延伸至溪谷的樣線，比少數幾條綿延甚長的樣線或樣區更能充分涵蓋空間的異質性。

關鍵詞：林下光照、福山試驗林、集水區階層、地景階層、半球面影像技術。

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INTRODUCTION

Light is a key resource controlling primary productivity and frequently limiting growth in the understory of closed-canopy forests (Monteith 1972, Pearcy 1983, Horng et al. 1994, Valverde and Silvertown 1997, Kuo 2000). Studies in mature tropical and temperate forests indicate that understory light levels are typically < 5% of the incident sunlight (i.e., levels above the tree canopy or in the open with no obstruction; Chazdon and Fetcher 1984, Smith et al. 1992, Turton 1992, Clark et al. 1996). Seedling establishment and growth under closed forest canopies are largely controlled by understory light availability; as such, light plays a central role in regulating forest regeneration (Clark et al. 1993, Horng et al. 1994, Wang et al. 1997, Williams et al. 1999). This observation led to the supposition that canopy gaps create microhabitats with elevated light that lead to enhanced seedling growth and tree establishment (Whitmore 1991). The overall importance of light gaps in maintaining tree diversity is the subject of an ongoing debate (Hubbell et al. 1999), yet the importance of gaps in initiating forest regeneration after a disturbance (Denslow 1987, Platt and Strong 1989, Spies and Franklin 1989, Bellingham et al. 1996) is well established. At the La Selva moist tropical forest in Costa Rica, 75% of tree species require gaps for regeneration (Hartshorn 1978).

Efforts have been put into measuring the understory light regimes of many forests over the past several decades (Anderson 1964, Madgwick and Brumfield 1969, Becker and Smith 1990, Clark et al. 1996, Lin TC et al. 2003). Comparisons of understory light regimes, both within a forest and among forests of different regions, have been used to infer patterns of gap dynamics and forest regeneration (Canham et al. 1990, Lin TC et al. 2003). Studies at the Fushan Experimental Forest (FEF) indicate that due to high understory light availability (on average 10~35% of incident sunlight) the light available in canopy gaps and forest understory is not very different, and understory light does not limit seedling establishment and growth (Mabry et al. 1998, Lin TC et al. 2003). Single-tree replacement, instead of gap dynamics, is more important to forest regeneration at the FEF (Chang et al. 1998, Lee 1992). The key to differences in patterns of forest regeneration between the FEF and that of many tropical and temperate forests is the much-higher understory light levels at the FEF.

Our previous studies of understory light regimes, like those of many other researchers, were conducted on a limited number of transects/plots (Hooper 1976, Conway et al. 1997, Trichon et al. 1998, Hale 2001). Due to practical considerations, sampling transects/plots are often limited in spatial scale relative to the entire area being characterized. In a study in 4 scrub stands in Florida, one 40×40-m plot was used to characterize each stand, and 25 hemispherical (fish-eye) photographs were taken within each plot (Conway et al. 1997). Another study in Sitka spruce plantations in northern Britain used 7 hemispherical photographs taken from each of 2 to five 30×30-m plots to represent the understory light regime in each plantation (Hale 2001). Critical to the applicability of the above approaches to characterizing understory light is the robustness of estimates of heterogeneity of understory light and thus the suitability of using relatively small plots to characterize much-larger areas.

A number of ecological studies have been conducted in Experimental Watershed #1 (WS1), a 36.2-ha watershed, and the results have often been generalized to the entire FEF (1,000 ha), even though the spatial heterogeneity remained unchecked. It has been proposed that scaling up from small to large areas requires new sampling approaches (Caldwell et al. 1993). Becker and Smith (1990) used two 1-km-long transects to measure understory light regimes in a tropical moist forest. Clark et al. (1996) used 15 widely spaced 100-m transects to assess landscape level light regimes and forest structure in a 500-ha stand of old-growth tropical rain forest. These sampling approaches may provide more reliable estimates of understory light regimes at broader scales, but it is not always feasible to carry out such extensive measurements. In the present study, we investigated understory light regimes on 2 spatial scales, the watershed level and landscape level, at FEF and evaluated problems associated with scaling up results from fine to broad scales.

Ecological studies at FEF were initiated in 1992, but most studies covered very limited spatial extents, and little effort has been put into investigating spatial heterogeneity. Because understory light availability is highly affected by the forest canopy development, its heterogeneity could be used to infer the heterogeneity of the forest structure. Thus, results from this study can be used to evaluate the robustness of patterns of forest dynamics across different spatial scales at FEF.

Hemispherical photography has been used to study understory light regimes and canopy structure for approximately half a century (Evans and Coombe 1959, Anderson 1964, Hooper 1976, Salminen et al. 1983, Clark et al. 1996, Lin TC et al. 2003). Because of rapid advances in photographic acquisition and analysis, hemispherical photography has become a popular technique in forest ecological research over the last 2 decades. Because hemispherical photographs taken from the forest understory provide an accurate record of the canopy structure, the technique has been used to study gap dynamics in addition to understory light regimes (Whitmore et al. 1993, Planchais and Pontailler 1999). Several studies have examined potential problems and sources of error of the technique (Roxburgh and Kelly 1995, Lin TC and Chiang 2002, Rhoads et al. 2004), but Robison and McCarthy (1999) documented that different investigators using a variety of photographic acquisition and analysis protocols provided consistent results.

In this study, we utilized hemispherical photography to estimate understory light availability and examined its variability across spatial scales at FEF. Specifically we tested the following hypotheses:

1. understory light availability estimated at the watershed level does not differ from that estimated at the landscape level;
2. understory light availability at a given spatial scale (watershed or landscape) does not differ among different aspects; and
3. the spatial variability of light availability does not differ between direct and indirect solar radiation.

METHODS

Study site

The study was carried out at the Fushan Experimental Forest (FEF) located in northeastern Taiwan (24°34"N, 121°34'E) at elevations ranging from 500 to 1,200 m (Fig. 1). The forest is in a basin surrounded by ridges of the Hseushan Mountain Range (Ayu Mt. to the north, 1,420 m; Hongchai Mt. to the south, 1,140 m; and Chiliang Mt. to the west, 760 m). Between 1993 and 2003, annual precipitation varied from 2,900 to 6,650 mm yr^{-1} with much of the variation attributable to the occurrence or absence of typhoons. Typhoons largely occur between July and September, with infrequent typhoons as early as May and as late as November (Chang 2001), with an average of 1.6 typhoons striking FEF each year (Mabry et al. 1998). The annual mean temperature is 18.6℃, and the annual mean relative humidity is 96% (Hsia and Hwong 1999). The forest is characterized as a moist subtropical mixed evergreen forest without an observable dormant season.

There are 515 plant species belonging

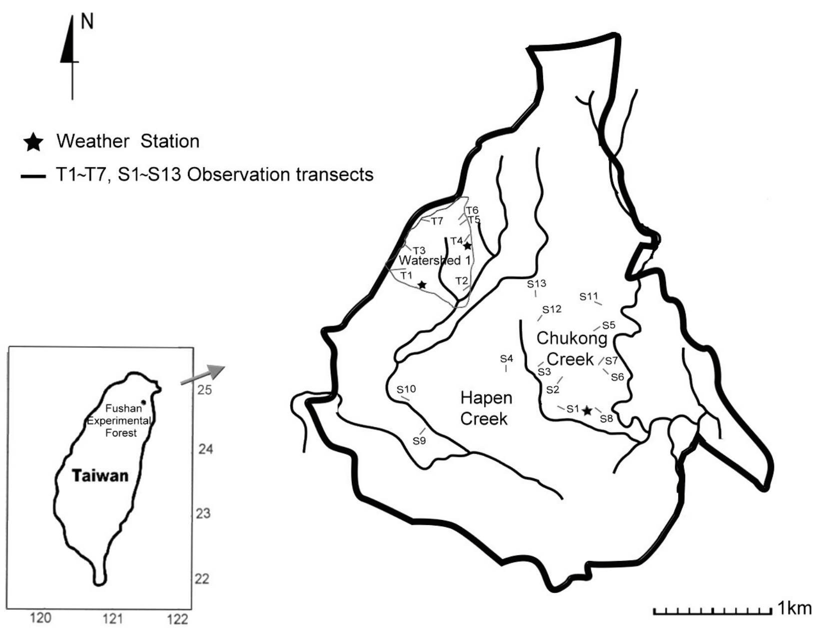

Fig. 1. Location of sample transects in the Fushan Experimental Forest.

to 329 genera and 124 families within the FEF (TFRI 1989). The dominant tree species are *Castanopsis carlesii* var. *sessilis* Nakai, *Machilus thunbergii* (Sieb. et Zucc.) Kostermans, *Engelhardtia roxburghiana* Wall., *Meliosma squamulata* Hance, *Litsea acuminata* (Blume) Kurata, *Diospyros morrisiana* Hance, *Helicia formosana* Hems, and *Pyrenaria shinkoensis* (Hayata) Keng (TFRI 1989). Shrubs were mostly *Ardisia quinquegona* Blume, *Blastus cochinchinensis* Lour, and *Lasianthus fordii* Hance (Lin TT, unpubl. data). The forest is multistoried with scattered tree ferns and shrubs, and with an herbaceous ground cover of 22% on ridges, 71% on slopes and 78% in the valleys (Lin TT, unpubl. data). Based on 2 yr of data, the phenological patterns can be summarized as leafing out in March and April; flower development in April; peak leaf density from April to May; flowering from April to June; fruiting from July to October; and leaf fall for deciduous trees from October to the following February (Lin KC et al. 1997).

Understory light level estimation

Understory light regimes were measured at 2 spatial scales, watershed level and landscape level (Table 1). At the watershed level, 7 transects (T1~T7) running perpendicular to the topographic contours were randomly located in Experimental Watershed 1 (38 ha) with transects ranging from 120~320 m in length (1,400 m total, Table 1). At the landscape level, an additional 13 transects (S1~S13), also running perpendicular to the topographic contours, were located within 110 ha of the FEF ranging from 70 to 310 m in length (2,320 m total, Table 1). All of the 20 transects extended from the ridge to the stream valley. The 13 landscape level transects were not entirely selected at random because considerations were given to avoiding interference with other existing studies as well as areas that are considered sensitive to even mild disturbance.

Between July and September 2001 hemispherical photographs were taken 1.5 m above the ground at 10-m intervals along the transects. Because photographs were taken at both ends of each transect, the number of sampling points for each transect equals the length of the transect divided by 10 plus 1. Therefore, the total sampling points were 147 and 245 at the watershed level and landscape level, respectively. The 10-m interval was chosen to avoid spatial autocorrelation in understory light levels (Becker and Smith

Table 1. Aspect and slope of sample transects within the Fushan Experimental Forest in northeastern Taiwan. Transects T1~T7 were located in Watershed 1 and S1~S13 were located outside watershed 1

Facing	Transect #	Length (m)	Aspect	Slope (°)
East	T1	240	E	30
	T3	320	SE	28
	T4	140	E	30
	T5	200	SE	40
	T7	200	E	30
	S5	170	NE	35
	S11	190	SE	45
West	T2	120	W	30
	S2	190	SW	35
	S10	260	W	30
South	T6	180	SW	40
	S3	150	SW	40
	S4	70	S	25
	S8	190	SE	40
	S12	200	SW	45
North	S1	120	NW	40
	S6	110	NW	15
	S7	160	NE	35
	S9	10	NW	45
	S13	200	N	35

1990). Lin TC et al. (2003) showed that spatial autocorrelations of understory light levels were insignificant at intervals greater than 5 m. Hemispherical photographs were taken using a 35-mm single-lens reflex camera system equipped with an 8-mm F/4 fish-eye lens (Sigma Corporation, Tokyo, Japan) attached to a mechanical camera body (FM2, Nikon Corporation, Tokyo, Japan) with a databack (MF-16, Nikon Data Back, Nikon Corporation). Color photographs (Kodak ASA 400 color positive film) were taken at the stop indicated by the internal automatic exposure of the camera and 1 stop below, as previous work suggested that underexposure may give the best contrast between the sky and the canopy (Chen et al. 1991, Frazer et al. 1997, Hale 2001). Although previously highly sensitive black-and-white negative film was needed to do the analysis, current software handles color film as well (Delta-T 2000). The camera system was pointed directly upward using a self-leveling mount (Rich 1990).

Photographs were digitized with "Photo CD" (Eastman Kodak Company, Rochester, NY, USA) with image files at a 512× 680-pixel resolution (8-bit TIFF images). Photographs were analyzed to estimate direct and indirect site factors (DSF and ISF) using HemiView 2.0 (Delta-T, 2000, Delta-T Devices, Cambridge, UK). DSF and ISF are the proportions of direct and indirect (diffuse) solar radiation reaching a given location, relative to a location with no obstructions (Rich 1990). The DSF is determined by the sun track and is estimated by imposing solar tracks on the digitized image enabling the proportion of open pixels to be calculated (Rich 1989). The ISF is determined by assessing the proportion of pixels classified as sky within the projected image of the hemisphere (Rich 1989). The DSF and ISF respectively can also be viewed as the proportions of direct and diffuse photosynthetic photon flux density (PPFD) incident on a horizontal surface above the canopy that is transmitted to the point where the photograph is taken (Rich 1989).

All photographs were analyzed by 2 people to ensure consistency. In order to maximize the contrast between openings and foliages all hemispherical photographs were acquired early in the morning just before sunrise, just after sunset but prior to dusk, or on overcast days. Rich (1990) and Lin TC and Chiang (2002) provide detailed discussions of hemispherical photography data acquisition, analysis, and interpretation.

Statistical analysis

The normality of the distribution of each data set was examined using the Anderson-Darling test (Theodorsson 1988). For non-normally distributed data, we examined differences in the distribution of understory light indices between the watershed level and landscape level using the non-parametric Kruskal-Wallis test (Sokal and Rohlf 1981). Transects were classified into 4 aspect classes, and differences in the distributions of understory light indices among aspects were also examined using the Kruskal-Wallis test.

RESULTS

The transects covered a wide range of aspects and slopes (Table 1). Slopes of the transects ranged from 15^o to 45^o with a mean of 36^o at the landscape level and from 28^o to 40^o with a mean of 33^o at the watershed level. Transects on the watershed level faced either east (and southeast) or west (and southwest) as the creek gradually runs from north to south (Table 1). At the landscape level, the transect aspects were more variable, with more transects facing the north or south than the east or west. At the watershed level, the distance between transects ranged from 100 to 750 m. At the landscape level, the distance between transects ranged from 80 to 1,700 m with transects that were closely distributed possessing very different aspects.

At both the watershed and landscape levels, the distributions of the ISF and DSF significantly violated the assumption of a normal distribution (Anderson-Darling test, $p < 0.05$), except for the DSF at the watershed level (Anderson-Darling test, $p = 0.124$). For non-normally distributed data, the median provides more information about the central tendency of a distribution (Ott 1977). Therefore, we used medians to compare the distributions of light availability between different spatial scales and among different aspects of the same spatial scale.

There were few microsites (< 15%) that had levels of understory light which were > 35% of the incident sunlight (Fig. 2). The

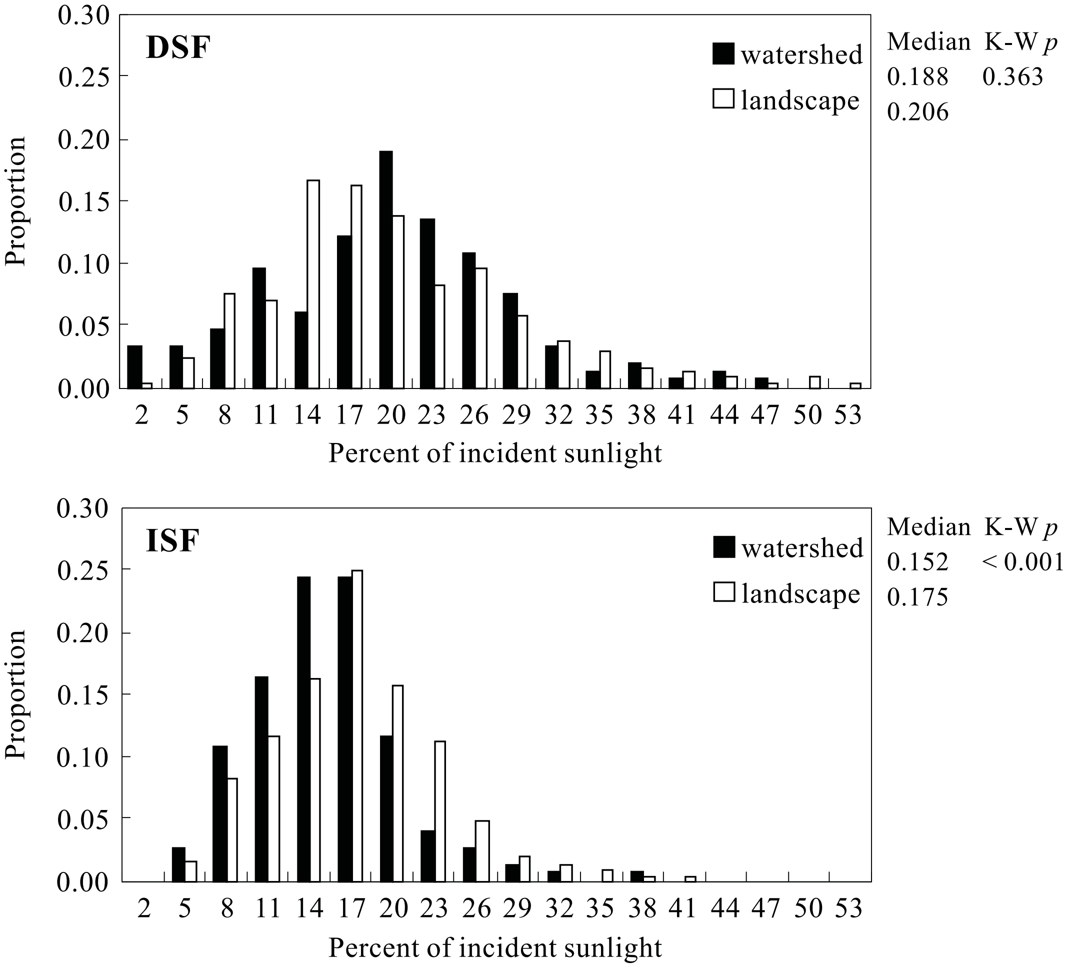

Fig. 2. Distribution of understory light levels at the watershed and landscape levels within the Fushan Experimental Forests. The direct site factor (DSF) and indirect site factor (ISF) are the proportions of direct and indirect (diffuse) solar radiation reaching a given location relative to a location with no obstructions. K-W is the Kruskal-Wallis test.

medians of the 2 understory light indices, ISF and DSF, were higher than 0.15 (Fig. 2). The median of the DSF was 9% lower for transects at the watershed level (0.188) than for transects at the landscape level (0.206), but the distribution of the DSF did not significantly differ between the 2 spatial scales (Kruskal-Wallis test, $p = 0.363$, Figure 2). On the other hand, the distribution of the ISF differed significantly between the 2 spatial levels with the median being 13% higher at the landscape level (0.175) than at the watershed level (0.152, Kruskall-Wallis test, $p < 0.001$; Figure 2).

The distributions of the DSF and ISF significantly differed among aspects at both spatial scales (Kruskal-Wallis test, $p < 0.001$, Table 2). At the watershed level, the median of the DSF at different aspects ranged from 0.123 on a westward-facing slope to 0.253 on a southward-facing slope (i.e., differed by more than 100%), and at the landscape level it ranged from 0.135 on the northward-facing slope to 0.243 on a southward-facing slope (i.e., differed by 80%) (Table 2). Differences in the ISF among different aspects were less prominent than those of the DSF. At the watershed level, the median of the ISF ranged from 0.116 on a westward-facing slope to 0.197 on a southward-facing slope (i.e., differed by 70%) (Table 2). At the landscape level, it ranged from 0.165 on a northward-facing slope to 0.186 on a southward-facing slope (i.e., differed by 13%) (Table 2).

Differences in the medians of light indices for the same aspect across the 2 spatial scales were all < 13%, except for westward-facing slopes in which the DSF and ISF at the landscape level were 64% and 54%, respectively, higher than those at the watershed level (Table 2).

DISCUSSION

Distribution of understory light levels

Studies in tropical and temperate forests as well as the current study at FEF indicate that understory light environments are often not normally distributed (Beck and Smith 1990, Clark et al. 1996). A normal distribution is a prerequisite for parametric statistical procedures such as analysis of variance. The non-normal distribution of light indices at FEF suggests that non-parametric statistical procedures such as the Kruskal-Wallis test that we used in this study were more appropriate for analysis of understory light environments.

The medians of both the DSF and ISF at both spatial scales were higher than 0.15 indicating that more than 50% of the microsites had light availability exceeding 15% of the

Table 2. Understory light levels of transects with different slope aspects at Fushan Experimental Forest in northeastern Taiwan

	Aspect								
	East		West		South		North		Krskal-Wallis
	Median	Mean (SE)	Median	Mean (SE)	Median	Mean (SE)	Median	Mean (SE)	test *p*
Direct site factor									
Watershed 1	0.215	0.218 (0.007)	0.123	0.154 (0.015)	0.253	0.269 (0.022)	--	--	< 0.001
Landscape level	0.191	0.205 (0.012)	0.202	0.225 (0.010)	0.243	0.259 (0.013)	0.135	0.143 (0.007)	< 0.001
Indirect site factor									
Watershed 1	0.157	0.159 (0.004)	0.116	0.129 (0.008)	0.197	0.210 (0.017)	--	--	< 0.001
Landscape level	0.171	0.171 (0.006)	0.179	0.185 (0.006)	0.186	0.194 (0.009)	0.165	0.162 (0.007)	< 0.001

incident sunlight. The understory light levels at FEF are very high compared to values reported for most mature temperate and tropical forests (Chazdon and Fetcher 1984, Canham et al. 1990, Smith et al. 1992, Turton 1992, Clark et al. 1996). There is no evidence of human disturbance at FEF in the last several centuries; as such, the forest qualifies as "old-growth". In old-growth deciduous forests of the eastern US, understory light levels are often only 1% of incident sunlight (Canham 1988). Using hemispherical photography similar to that used in this study, many studies have consistently reported understory light levels of < 5% of incident sunlight (Chazdon and Fetcher 1984, Smith et al. 1992). The short stature of the trees, 10.6 m on average as opposed to 20~32 m in the New World tropics (Clark et al. 1996, Kappelle et al. 1996), and frequent typhoon disturbance at FEF, average of 1.4 each year with a range of 0 to 6 per year over the last 100 yr (Mabry et al. 1998, Chang 2001), are key to the high understory light levels. Because understory light decreases with increasing canopy height (Canham et al. 1990, Botkin 1993, Clark et al. 1996), a short canopy allows more light to penetrate to the understory.

At FEF, defoliation is the main form of canopy damage caused by typhoons; yet the frequent typhoon events seem to have led to a phenotypic/genotypic response of no immediate foliar regrowth, allowing high light transmittance through the canopy for much of the year (Lin TC et al. 1999, 2003). In 1994 when 6 typhoons caused > 6 Mg ha^{-1} of litterfall (Lin KC et al. 2003), the canopy leaf area index (LAI) decreased by as much as 66% on the ridges (Lin TC et al. 2003). Based on a 10-yr record of canopy LAI at FEF, in 2001, the year in which this study was carried out, the forest had high canopy LAIs (Lin TC, unpubl. data). Thus, the measured understory light levels were likely low estimates that could be expected to increase in years following intense typhoons. Phenological surveys indicate that canopy leaf density at FEF reaches peak levels before the end of Mays and it is maintained at a relatively constant level throughout the summer in the absence of typhoon disturbance (Lin KC et al. 1997). The hemispherical photographs used in this study were taken in the summer, but before the first typhoon of 2001, while the canopy was at its highest density. Thus, the observed high understory light levels represent the lowest levels of the year.

Spatial variation in understory light levels

The non-normally distributed light levels are the result of fewer than 15% of the microsites having light levels > 35% of incident sunlight which caused the distribution to be skewed toward the low light end (Fig. 2). The coefficient of skewness (W) for the DSF was statistically significant at $\alpha = 0.1$ at the watershed level (W = 0.236) and at $\alpha = 0.01$ at the landscape level (W = 0.917). For the ISF, the coefficient of skewness was statistically significant at $\alpha = 0.05$ an the watershed level (W = 0.418) and at $\alpha = 0.01$ at the landscape level (W = 0.881). A skewness in the distribution of understory light levels was also reported for a tropical rain forest in Costa Rica (Clark et al. 1996) and is probably common to many forests. The few microsites with high light indices may have been located beneath canopy gaps or severely damaged tree canopies caused by the frequent typhoon disturbance at FEF.

Given that the differences in both the ISF and DSF between the 2 spatial scales were < 15% (Fig. 2), the results for either spatial scale could be used for inter-site comparisons as long as the inter-site differences in understory light levels are greater than 15%. As mentioned above, the light levels estimated for FEF was several times higher than those reported for most temperate and tropical forests. Using measurements taken at either spatial scale at FEF for inter-site comparisons would produce similar results. Thus, the estimate of understory light availability is rather robust, and the pattern observed at spatially more-limited locations such as a watershed can be used to infer landscape-level patterns. However, if inter-site light levels differ by < 15%, then using measurements taken at different spatial scales may give different results. Researchers should be aware of intra-site spatial variability before making inter-site comparisons.

That understory light indices significantly differed among aspects within the same spatial scale at FEF, with the difference in the DSF being more pronounced, is of ecological significance. ISF is mainly affected by canopy openness, whereas the DSF is a function of canopy openness and the location of the openings relative to the sun path (Rich 1990). Consequently, the DSF is more sensitive to topographical position. Understory microsites under large canopy openings will certainly have large values for the ISF, but if most of the openings are not located in the sun path or are shaded by the topography, then the DSF will be very low. Because diffuse light under forest canopies may be too weak for photosynthesis, brief but direct light (sunflecks) is critical for the growth of understory plants. Sunflecks contribute 60~90% of the total daily PPFD to plants in the understory of tropical rain forests, driving up to 65% of total daily carbon gain (Pearcy 1983, Pearcy and Calkin 1983, Chazdon 1988, Pfitsch and Pearcy 1989). The observed differences in DSF values among aspects may lead to differences in the growth and composition of understory vegetation including seedlings and, therefore, the subsequent development of the forest canopy.

The higher variability of light indices among aspects within a spatial scale as compared to the overall variability between the 2 spatial scales has important implications for sampling design. To scale up measurements of understory light regimes from limited locations to broader scales in a tropical moist forest, Becker and Smith (1990) used two 1-km-long transects. Our results indicate that if we had used this same approach and the transects were located on the same slope or with the same aspect, then much of the spatial variability would have been missed. Thus, at FEF as well as in many mountain forests around the world, topographic effects should be given high priority when considering the sampling of understory light. Trichon et al. (1998) used hemispherical photography for inter-site comparisons of canopy structure. They took measurements in 60~100 adjoining subplots located in 0.6~1.0-ha plots at each site, which were more than 30 km apart from each other. Since their study sites had low topographical variability, results from the selected plots may have effectively characterized the sites. Yet, at FEF, an area of 0.6~1.0 ha usually has only 1 aspect and cannot cover the spatial heterogeneity occurring even at the watershed level.

The senior author conducted a study comparing understory light regimes in 3 stands adjacent to the current study site (Lin WX et al. 2002) and found that differences in understory light levels were greater among transects with different aspects than among the 3 forest types. In areas with rough topography, adequate coverage of the topographic variation is more important than extending transects into larger spatial coverage. Yet, use of extended transects is better than isolated plots. At FEF, coverage of understory vegetation varied from 22% on the ridge to 71% on the slope and to 72% near the valley (Lin TT, unpubl. data). Much of the variation might be attributable to differences in understory light availability, and long transects extending from the ridge to the valley have a better chance of covering the spatial heterogeneity over that distance. Given the high topographic variations at FEF, the approach of Clark et al. (1996) using fifteen 100-m long transects would be more likely to provide adequate coverage of spatial heterogeneity than would the approach of using a few long transects or plots.

For analysis of relationships among understory light regimes, canopy structure, and seedling establishment and growth, intensive sampling at a fine scale (plots) can achieve the same goal as sampling on a broad scale. In contrast, when comparing light regimes between forests of different sites/regions, spatial heterogeneity within each site must be carefully addressed. Our studies indicate that when spatial heterogeneity is topographically related, intra-site variability might be greater than inter-site variability. Consequently, expanding the spatial extent of sampling does not necessary improve the coverage of spatial heterogeneity if the topographical influence is not carefully addressed, and using 10~20 randomly located transects is preferable to a few large plots or long transects.

One limitation to our discussion of understory light patterns at the 2 spatial scales is that our landscape level transects were not set up randomly. One might argue that the comparison of light levels between the 2 spatial scales is not valid because aspects which have major influences on understory light levels are not comparable between the 2 spatial levels. Because all our transects ran perpendicular to the topographic contours and extended from the ridge to the valley, the running direction of the creek within the watershed largely determined the aspects of the transects. A recent study on changes in the normalized difference vegetation index at 3 spatial levels carefully analyzed the topography of 44 first-order watersheds at FEF (Kang 2005). The results indicated that the directions of first-order streams are highly variable. At WS1 the creek runs from north to south and then turns to the southeast. Yet, based upon the analysis of Kang (2005) this is not true for most of the first-order watersheds at FEF. Setting up landscape-level transects in the same aspects as at WS1 would not represent the general patterns at the landscape level. That our landscape level transects have more-variable aspects reflects the variable nature of aspects at the landscape level. Thus, our comparison of watershed and landscape level light availability based upon the current transect setup is probably more appropriate than if we set up transects at the landscape level with aspects similar to those at WS1. Our discussion of the impact of aspect on understory light availability is based upon comparisons made between transects with the same aspects but at 2 spatial scales. Therefore, although setting up transects randomly would certainly improve our confidence in the observed patterns, our current setup is unlikely to have provided distorted results.

CONCLUSIONS

Distribution of the direct site factor (DSF), an estimate of direct solar radiation, did not differ between the 2 spatial levels, but distribution of the indirect site factor (ISF), an estimate of indirect solar radiation, did. The distribution was toward the high light end at the landscape level relative to the watershed level.

At both spatial scales, understory light indices significantly differed among aspects suggesting that studies of understory light environments must take topographic influences into consideration. Expanding the spatial extent of sampling does not necessary improve the coverage of spatial heterogeneity if such topographic influences are not carefully addressed; using 10~20 randomly located transects is preferable to a few large or long transects.

Spatial variability of the DSF was more prominent than that of the ISF. Because brief but direct solar radiation is critical to the growth of many understory plants, differences in the DSF may lead to differences in growth and composition of understory vegetation including seedlings and, therefore, subsequent development of the forest canopy.

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