Research paper

Immediate Effects of Thinning with a Small Patch Clearcut on Understory Light Environments in a *Cryptomeria japonica* Plantation in Central Taiwan

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【Summary】

Thinning is an important forest management practice; however, its effects on the microenvironment have rarely been investigated in tropical and subtropical ecosystems. We examined the effect of 25% (25 of 100 10 x 10 m subplots were clearcut) and 50% (1/2 of the subplots were cut) thinning on understory light environments characterized using hemispherical photography at a *Cryptomeria japonica* plantation, Taiwan's most common plantation species. Thinning had a greater effect on the variability than on the availability of understory light, with the former increasing 40 and 120% under 25 and 50% thinning intensities, respectively, and the variance increasing 2.4~9.9-fold. The > 40% increase in understory light availability following 25% thinning was much greater than the 25% increase in light at a forest in northeastern Taiwan following the 1996 category-3 typhoon Herb, which decreased variability of understory light. Typhoons are the most important natural disturbance in Taiwan. Thus, mechanical thinning at intensities > 25% increases light availability and variability to levels that rarely exist following typhoon disturbance. In addition, mechanical thinning of 0.01-ha patches as applied in this study led to an understory light environment that was decoupled from the pre-thinning condition. In contrast, typhoon disturbances are typically more evenly spread, resulting in positively correlated pre- and post-typhoon light environments. Long-term monitoring is required to understand differences in successional trajectories following mechanical thinning and typhoon disturbance.

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研究報告

小區塊皆伐式疏伐對台灣中部柳杉人工林林下光照環境的立即影響

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摘 要

疏伐是重要的森林經營手段然而其對熱帶及亞熱帶生態系微棲地環境影響的研究相當少。本研究利用半球面影像檢驗25%疏伐(100個小樣區伐除25個)及50%疏伐(1/2小樣區伐除)對台灣最常見的柳杉(*Cryptomeria japonica*)人工林林下光環境的影響。疏伐對林下光環境變異的影響更甚對林下光量的影響。林下光照量在25及50%疏伐後分別增逾40與120%，而變異數則增加了2.4到9.9倍。在25%疏伐後逾40%的林下光照增加遠超過1996年強烈颱風賀伯在東北部的森林所造成的25%增加量，而且在賀伯颱風侵襲後林下光環境的變異減少而非增加。颱風是台灣最常見的自然擾動，本研究結果顯示超過25%的疏伐將使林下光照量及其變動範圍提升到在颱風擾動下不易出現的程度。此外研究中所使用的0.01 ha區塊式疏伐使得林下微棲地的光照在疏伐前後相關性偏低，反之颱風擾動的影響較疏伐分散而全面，故林下微棲地的光照在擾動前後有顯著而高度的正相關。疏伐後森林的演替軌跡是否與颱風擾動後的回復有明顯差異需有長期監測才能完整評估。

關鍵詞：半球面影像技術、孔隙、光環境、疏伐。

江智民、林國銓、黃正良、王雪卿、林登秋。2012。小區塊皆伐式疏伐對台灣中部柳杉人工林林下光照環境的立即影響。台灣林業科學27(4):319-31。

INTRODUCTION

Mechanical thinning has long been applied as a forest management tool for timber production. In the US, thinning has also been applied to reduce fire hazards by controlling stem density and understory fuel loads (Covington and Moore 1994, Schoennagel et al. 2004). In addition, restoration efforts sometimes incorporate thinning to mimic historical disturbance regimes, manage forest successional trajectories (Brose et al. 1999, Albrecht and McCarthy 2006), and accelerate development of old-growth forest features (O'hara et al. 2010).

Changes in ecosystem structure via artificial thinning can improve tree growth by enhancing resource availability, especially light (Abbott and Loneragan 1983, Latham and Tappeiner 2002). Understory light is a key factor affecting the establishment and growth of seedlings and thus forest regeneration, because it is typically lower than optimal for plant growth. Thinning creates canopy gaps allowing more light to reach the forest floor and affects the angle of incidence of solar radiation, the timing and duration of sunflecks, the proportion of direct and diffuse solar radiation, and the heterogeneity of understory light environments. The role of canopy gaps and understory light on maintaining plant species richness was an active research topic for several decades (Whitmore 1989, Albrecht and McCarthy 2006, Fahey and Puettmann 2007). In Taiwan, experimental thinning was shown to enhance increments of basal area and volume of *Taiwania cryptomerioides* (Wang et al. 2006).

In addition to effects on understory light environments, thinning also changes the canopy structure and heterogeneity. Changes in the canopy structure affect important forest functions such as photosynthesis (Waring and Schlesinger 1985) and the suitability of the stand for wildlife (Allen et al. 2002, Craig et al. 2010). Thinning that promotes structural heterogeneity may lead to higher species richness and contribute to higher system stability (Latham et al. 1998). Canopy heterogeneity also affects the distribution of plants and animals inhabiting or visiting the canopy. For example, canopy openness was reported to be an important factor affecting the use of forests as overwintering sites of the monarch butterfly (*Danaus plexippus*) in California (Weiss et al. 1991) and the distribution of epiphytic bromeliads in a Mexican humid montane forest (Winkler et al. 2005).

Silvicultural practices in Taiwan are limited to forest plantations, which cover approximately 11.3% of the land area of Taiwan (TFB 1995). Due to public concern that arose from past over-exploitation and resulting problems with conservation of soil, water quality, and biodiversity, cutting of any intensity in natural forests has been prohibited, and since 1991, cutting in plantations must be offset by the planting of native tree seedlings (TFB 1995). As a result, there has been little cutting in Taiwan over the past 2 decades. Rising demand for timber and increased awareness of sustainable forestry practices have raised the pressure on those managing Taiwan's forest plantations to meet at least part of the domestic demand for timber while maintaining forest ecosystem services. Some small-scale (< 1-ha) studies have examined the effects of mechanical thinning on tree growth, litterfall decomposition, and soil processes in Taiwan (Wang et al. 2008). However, virtually none of the existing information has come from replicated experiments with more than 1 thinning intensity.

In 2006, an experimental thinning of a *Cryptomeria japonica* plantation in central Taiwan was initiated in an attempt to improve the structural heterogeneity and biodiversity of the forest (Sun 2007). The goals of this project included an evaluation of the impacts of thinning at 2 intensity levels on the growth and diversity of both overstory and understory plants, and crucial ecosystem processes (e.g., energy flows and nutrient cycling) (Sun 2007). This was the first large, replicated, comprehensive experimental thinning carried out in Taiwan, and the study included assessments of a wide variety of biotic and abiotic consequences (e.g., vertebrate and invertebrate diversity, recruitment of tree species, microclimate, decomposition, and soil respiration) of these forest management practices. Although the *C. japonica* plantation under investigation is located at a moderate elevation (1500~1700 m), the study aimed to produce recommendations for island-wide application (Sun 2007).

The objective of this study was to characterize changes in availability and heterogeneity of understory light following 25 and 50% thinning at a *C. japonica* plantation in central Taiwan. The results are critical for evaluating the consequences of artificial thinning on the microclimate that have major implications for the growth and diversity of understory plants because of the lack of such information in Taiwan.

MATERIALS AND METHODS

Study site and experimental design

The study was carried out at a *C. japonica* forest plantation located in central Taiwan, the Zenlun Experimental Forest, at 1500~1700 m in elevation with a mean slope of approximately 50%. Soil textures in this area were primarily sandy loam and loamy sand with > 68% sand and < 14% clay (Wang 2008). The natural vegetation in this area was clear-cut approximately 50 yr ago and replanted with *C. japonica*. Due to its high growth rate, *C. japonica* was a common species for forest plantation since its first introduction in 1891. The mean annual precipitation at the plantation is 3800 mm, and the mean monthly temperature is 17.5℃ (Wang et al. 2007). The mean tree height was approximately 17 m in 2006 (Chiu unpublished data).

In 2006, twelve 100×100-m plots were established at the Zenlun Experimental Forest following the design of large forest dynamic plots at the Center for Tropical Forest Science of the Smithsonian Tropical Research Institute (Losos and Leigh 2004). All woody plants of > 1 cm in diameter at breast height (dbh) were mapped, tagged, and identified to species (Losos and Leigh 2004, Sun 2007). The 12 plots were evenly and randomly assigned to 3 treatments: unthinned control, 25% thinning, and 50% thinning. The 25 and 50% thinning levels were chosen to represent moderate and heavy thinning regimes commonly used in forest management.

Each plot was divided into 100 10×10-m subplots, which were grouped into 25 20×20-m operating plots. Under the 25% thinning treatment, 1 of the 4 subplots in each operating plot was randomly assigned for clear-cutting. Under the 50% thinning treatment, 2 non-adjacent subplots were randomly assigned for cutting in each operating plot. In other words, all thinning-created gaps were 100 m^2 in area, with 1 of 4 subplots cut in the 25% treatment and 2 of 4 subplots cut in the 50% treatment (the 2 cut subplots were positioned diagonally). Thinning was carried out between 1 July and 10 October, 2007 by felling all trees in the assigned subplots. A post-thinning survey indicated that 25.0 and 52.3% of the basal area of *C. japonica* trees were felled in the 25 and 50% thinning treatments, respectively (Chiu unpublished data). All thinned trees were removed from the forest using cable skidders to mimic commercial practices in Taiwan. We established one 100-m transect perpendicular to the elevational contours at the center of each of the 12 plots 1 yr before thinning to monitor the pre-thinning light environment in the understory.

Measurements of understory light environments

Understory light environments were characterized using hemispherical photography (Rich 1990, Lin and Chiang 2002). Pre-thinning photographs were taken on May 4~5, 2007 and post-thinning photographs were taken on October 13~14, 2007. Photographs were taken at 1.5 m above the ground and at 5-m intervals through each transect resulting in a total of 20 measurements for each plot. The 5-m interval was chosen to avoid spatial autocorrelation in understory light availabilities (Becker and Smith 1990). Lin et al. (2003) showed that spatial autocorrelations of understory light indices were insignificant at intervals of ≥ 5 m in northeastern Taiwan.

Hemispherical photographs (2272×1704 pixels) were taken using a Nikon Coolpix 4500 digital camera (Nikon, Tokyo, Japan) equipped with a Nikon FC-E8 fisheye lens. In order to maximize the contrast between openings and foliage, all hemispherical photographs were taken at dawn or dusk or during overcast days when direct sunlight was absent. Photographs were analyzed to estimate direct (DSF) and indirect site factors (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 fully exposed location (Rich 1990). The DSF is estimated by superimposing solar tracks on digitized images, enabling the proportion of open pixels crossed by the sun's path to be calculated (Rich 1990). The ISF is determined by assessing the proportion of pixels classified as sky within the projected image of the hemisphere (Rich 1990). The DSF and ISF 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 1990).

All photographs were analyzed by 2 well-trained personnel to minimize bias in the selection of the threshold value that was used to classify an image into canopy (black) and sky (white) elements (Rich 1990, Lin and Chiang 2002, Wang and Lin 2006).

Statistical analysis

Both ISF and DSF were positively skewed, and their variances were susceptible to thinning treatment (see results below). Thus, a traditional mixed-model ANOVA was not suitable for comparing the pre-thinning and post-thinning light indices. Comparison of the central tendency and variance between treatments, and bi-variate correlation analyses were performed using permutation tests (Legendre and Legendre 1998). Schemes of the permutation tests were constructed to preserve the data structure reflecting the sampling and treatment plan (20 measurements of ISF and DSF per plot, 4 replicates for each of the 3 thinning treatments) so that a greater power for the statistical test was warranted (Anderson and ter Braak 2003, Jung et al. 2007). To test the thinning effect on changes in ISF and DSF, we first calculated their means in each 1-ha plot before and after thinning treatment. The difference in the plot mean before and after treatment was calculated for each plot. The mean of the difference (DIFF) for each of the 3 respective treatments (4 replicates for each treatment) was calculated and used as the test statistic. To create the null model of DIFF for each treatment, the procedure above was repeated 9999 times with permuted raw data of the selected index (ISF or DSF) in each permutation cycle. For each treatment, the level of significance (p value) in testing the difference between pre-thinning and post-thinning light indices was then calculated as the proportion of the simulated DIFF ($DIFF^{sim}$) more extreme than or as extreme as the observed DIFF ($DIFF^{obs}$):

p = (Number of $|DIFF^{sim}| \geq |DIFF^{obs}|$)/10,000.

In testing the thinning effect on the distribution (i.e., the variance) of the ISF and DSF, we first calculated the variance of the selected light index (among 20 measurements) in each 1-ha plot before and after thinning treatment. The ratio between post-thinning and pre-thinning variances in each plot was calculated. The mean of the variance ratio (F) of each of the 3 respective treatments (4 replicates for each treatment) was calculated and used as the test statistic. To create the null model of F for each treatment, the procedure above was repeated 9999 times with permuted raw

data of the selected index in each permutation cycle. For each treatment, the level of significance (p value) in testing the change in variance between pre-thinning and post-thinning light indices was then calculated as 2 times the proportion of the simulated F (F^{sim}) greater than or equal to the observed F (F^{obs}):
$p = 2 \times (\text{Number of } F^{sim} \geq F^{obs})/10{,}000$.

The coefficient of 2 in the formula above indicates a two-tailed test of variance difference.

We used Pearson's coefficient of correlation (r) to gauge the level of correlation between the pre-thinning and post-thinning light environments. The level of significance for r was estimated using the corPerm function of R statistical language (R Development Core Team 2010), developed by Dr. Pierre Legendre at Université de Montréal (P. Legendre, pers. Commun.). In this function, Pearson's correlation coefficient (r) was used as the test statistic for the bivariate correlation, and the null distribution of r was generated by recalculating r 9999 times with 1 of the 2 data vectors of interest permuted in each permutation cycle. (Legendre and Legendre 1998). The p values were calculated as the proportion of the simulated r (r^{sim}) more extreme than or as extreme as the observed r (r^{obs}):
$p = (\text{Number of } |r^{sim}| \geq |r^{obs}|)/10{,}000$.

All statistical analyses were performed using the R statistical package, vers. 2.12 (R Development Core Team 2010).

RESULTS

Thinning increased understory light availability

Thinning of both intensities (25 and 50%) significantly increased understory light availability ($p < 0.0001$), while no significant change was found for the control treatment (Table 1). The mean ISF increased 43% (from 0.173 to 0.247, Fig. 1a) after 25% thinning and 117% (from 0.160 to 0.347, Fig. 1a) after 50% thinning treatments (Table 1). Increases of similar magnitudes were found for the mean DSF, with 41% (from 0.172 to 0.243, Fig. 1b) and 124% (from 0.170 to 0.381, Fig. 1b) increases after 25 and 50% thinning treatments, respectively (Table 1). Illustrations of examples of the permutation tests are shown

Table 1. Summary of permutation test results of thinning effects on indirect (ISF) and direct site factors (DSF)

	DIFF	p	F value	p
ISF				
Control	-0.0034 (-1.99%)	0.6744	1.44	0.6340
25% thinning	0.0738 (42.70%)	< 0.0001	7.00	< 0.0001
50% thinning	0.1872 (116.67%)	< 0.0001	9.87	< 0.0001
DSF				
Control	-0.0111 (-6.37%)	0.1854	0.77	0.2986
25% thinning	0.0701 (40.79%)	< 0.0001	2.40	0.0194
50% thinning	0.2115 (124.05%)	< 0.0001	4.88	< 0.0001

ISF and DSF are the proportions of indirect (diffuse) and direct solar radiation reaching a given location, relative to a fully exposed location with no obstructions. DIFF indicates the change in mean light indices following thinning treatments. Values in parentheses indicate the percent change in light indices after thinning treatment. The F value represents the observed variance ratio of post-thinning and pre-thinning variances.

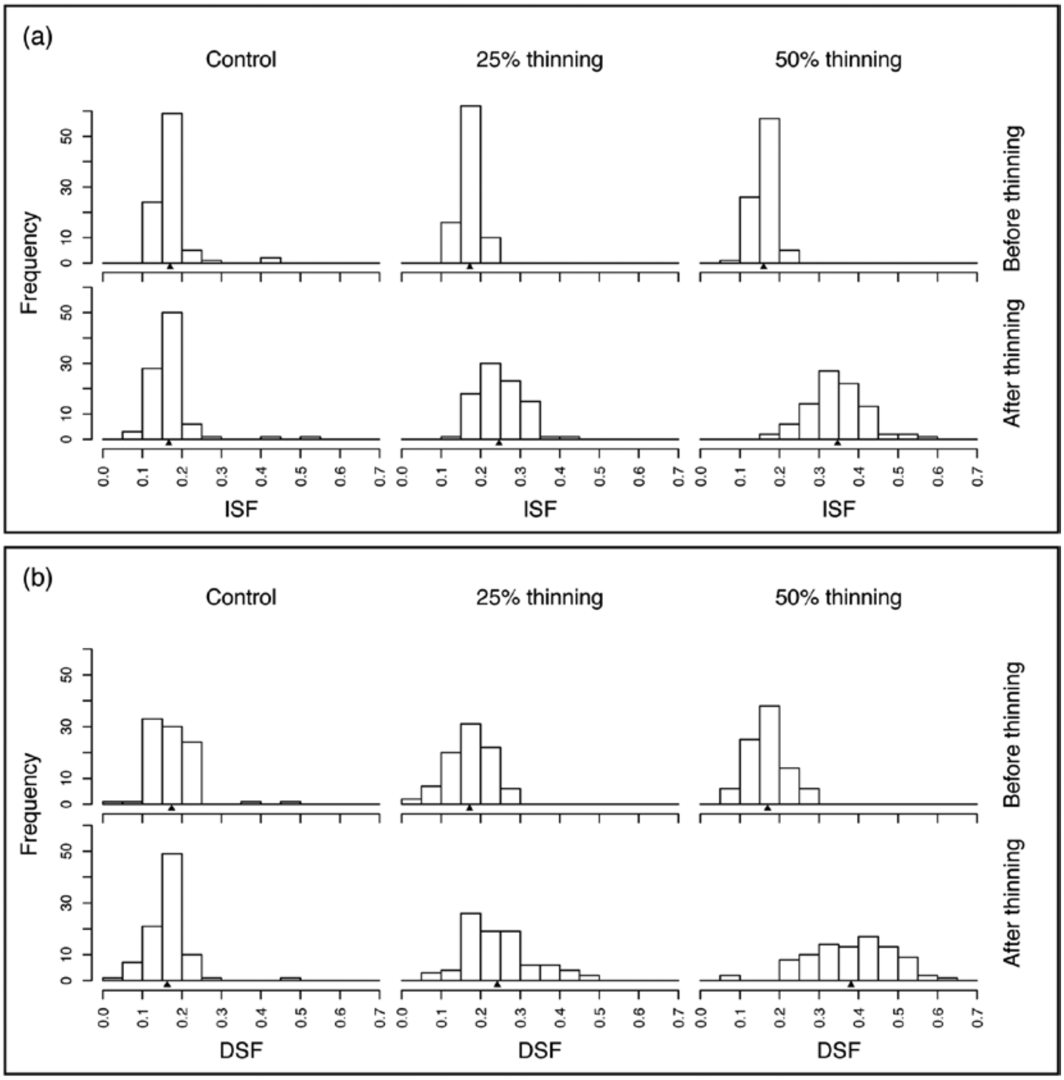

Fig. 1. Frequency distribution of (a) the indirect site factor (ISF) and (b) direct site factor (DSF) under control, 25% thinning, and 50% thinning treatments. The black triangle in each panel indicates the mean value.

in Fig. 2. The observed DIFF in control plots, indicated by a vertical dashed line, lay near the central part of the null distribution of DIFF (Fig. 2a), rendering a p value of 0.1854 (Table 1). In the 25% thinning plots, the observed DIFF lay toward the extreme upper tail of the null distribution (Fig. 2c). In fact, no simulated DIFF was greater than the observed DIFF of 0.0701, rendering a p value of 0 (indicated as < 0.0001 in Table 1).

Thinning increased the spatial heterogeneity of the understory light environment

In addition to increases in the availability of the 2 light indices following both levels of thinning treatment, the variation of

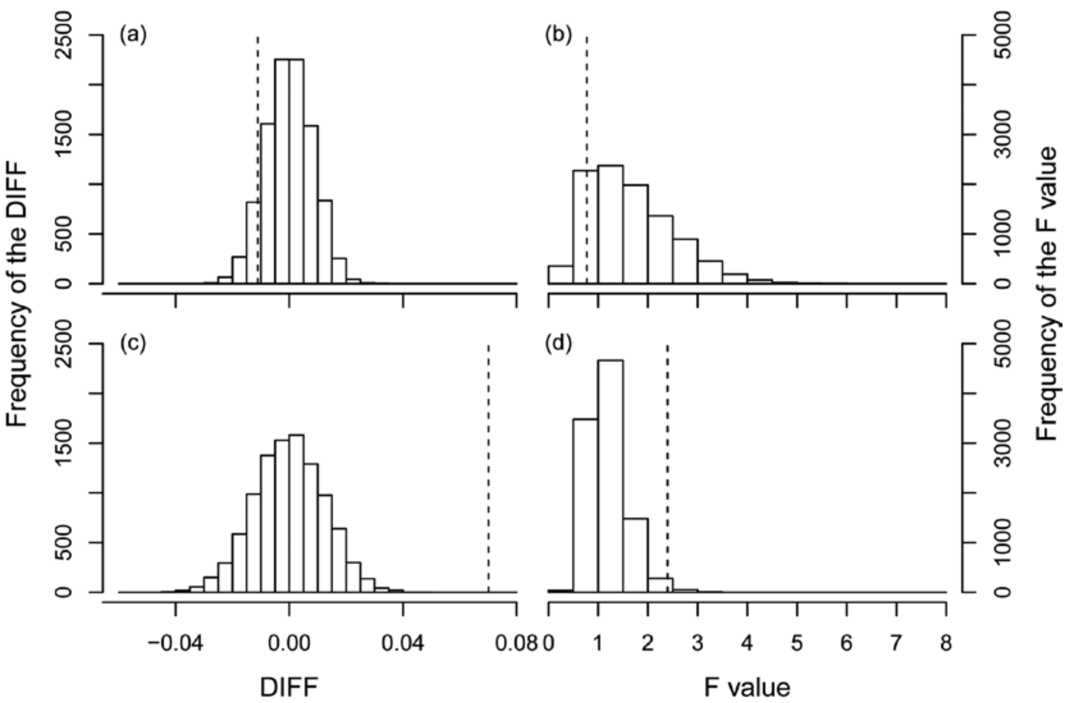

Fig. 2. Frequency distribution of the (9999+1) permutation test results: (a) the mean difference (DIFF) and (b) variance ratio (F) of the direct site factor (DSF) before and after the control treatment, (c) the mean difference (DIFF) and (d) variance ratio (F) of the DSF before and after the 25% thinning intensity. The vertical dashed line in each panel indicates observed values. Test results are shown in Table 1.

the understory light environment significantly increased (Fig. 1). The 25 and 50% thinning treatments significantly increased the variance of ISF by 7.0- and 9.9-fold, respectively, and DSF by 2.4- and 4.9-fold, respectively, while no significant change was found under the control treatment (Table 1). Under the control treatment, ranges of the ISF and DSF after thinning treatments were similar to that measured before treatment (Fig. 1). In contrast, the range of the ISF increased from 0.114 to 0.253 under the 25% thinning intensity and from 0.130 to 0.403 under the 50% thinning intensity (Fig. 1). A similar pattern of change was found for the DSF with an increase of the range in the DSF from 0.203 to 0.400 under the 25% thinning intensity and from 0.218 to 0.516 under the 50% thinning intensity (Fig. 1). Illustrated examples of the permutation test of variance are shown in Fig. 2. The observed variance ratio (F) for the DSF under the control treatment lies near the mode of its null distribution (Fig. 2b). In other words, the observed F value of 0.77 is typical of values under the null hypothesis (p = 0.2986; Table 1). Conversely, the observed F of 2.40 for the DSF under the 25% thinning treatment lay at the upper extreme of the null distribution (Fig. 2d), rendering a p value of 0.0194 (Table 1).

Thinning treatments decoupled the post-thinning from the pre-thinning understory light environments

Both the ISF and DSF in the control

treatment exhibited high correlations between pre-thinning and post-thinning measurements at the scale of individual observations (Fig. 3) with Pearson's coefficients of correlation (*r*) of 0.89 and 0.79, respectively (Table 2). For plots under 25 and 50% thinning treatments, both the ISF and DSF after thinning treatments shifted away from the 1: 1 relationship, showing increases in light availability and variability after both thinning treatments (Fig. 3, also see Fig. 1). With an increasing thinning intensity, the coefficients of correlation for both the ISF and DSF were reduced (Table 2). At the 50% thinning intensity, the correlation of the DSF between measurements before and after thinning was not significant ($p = 0.0835$, Table 2). The de-coupling of the ISF and DSF between pre-treatment and post-treatment measurements indicates inconsistent relative changes in understory light indices after thinning treatments among the sampling locations.

DISCUSSION

Thinning disproportionally increased understory light availability

The increase in understory light indices after artificial thinning is not surprising given that artificial thinning reduced the continu-

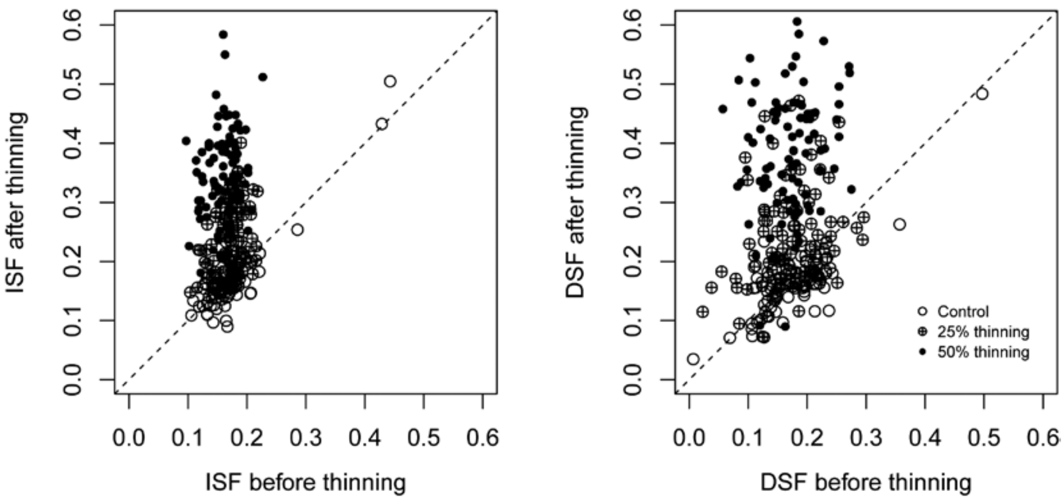

Fig. 3. Correlation of pre-thinning and post-thinning understory light availability under control, 25% thinning, and 50% thinning treatments. ISF, indirect site factor; DSF, direct site factor.

Table 2. Pearson's coefficient of correlation (*r*) and level of significance (*p*) for the relationship between 2 repeated measurements (before and after thinning) of the indirect (ISF) and direct site factors (DSF)

Treatment	ISF		DSF	
	r	*p*	*r*	*p*
Control	0.89	0.0001	0.79	0.0001
25% thinning	0.29	0.0073	0.26	0.0148
50% thinning	0.22	0.0393	0.18	0.0835

ity of the tree canopy, thereby allowing more light to reach the forest understory. Notably, enhancements in the understory light indices (by approximately 40 and 120%) were considerably greater than the 25.0 and 52.3% removal of basal area. Disproportionally large increases in understory light availabilities following artificial thinning were reported in several studies and illustrate the exponential increase in light transmittance with decreases in tree basal area (Hale 2001). This disproportional increase in understory light availability must be taken into consideration if artificial thinning is used to enhance understory light availability to a pre-determined level because reductions in tree basal area do not provide good estimates of increases in canopy transmittance (Hale 2003).

Thinning resulted in greater spatial heterogeneity of understory light availability

The much greater percent changes in the variances than the means of the ISF and DSF indicate that our thinning method, small patch clearcutting, had a more-dramatic effect on the variability than the availability of understory light. In addition, understory light availability after thinning treatments exhibited reduced correlations with pre-thinning levels. The divergent responses to artificial thinning among micro-sites with similar pre-thinning understory light indices resulted from the difference in distances to the thinned subplots. Due to the patchy and binary nature of the artificial thinning (i.e., each of the 10×10-m subplots was either completely cleared of trees or un-thinned), micro-sites near or on the edges of the thinned subplots exhibited large enhancements in understory light availability. In contrast, micro-sites further away were less affected. The effect of artificial thinning on the understory light availability at such micro-sites may even be smaller than the effect of tree growth between the 2 repeated measurements. As a result, the spatial pattern of understory light following thinning was decoupled from the pattern prior to thinning and showed a much greater spatial heterogeneity.

The variation in the DSF was greater than that of the ISF for both the pre-thinning and post-thinning measurements (Fig. 1). The higher variability of the DSF than ISF resulted from the differences in the nature of the 2 light indices. The ISF is a function of the total openness, and the DSF is a function of the openness within the sun's path. The spatial distribution of canopy openings affects the DSF but not the ISF. As a result, the ISF is less sensitive to the distribution of canopy disruptions than is the DSF. After 25% thinning, some micro-sites of the *C. japonica* plantation had a very low DSF (< 5%), despite the much-larger minimum ISF. This was likely due to a lack of canopy openings located along the sun's path. Low levels of direct light at these micro-sites might have impeded the growth of seedlings of shade-intolerant plants; however, the overall heterogeneity of understory light availability increased.

Management implications

Taiwan's reliance on foreign timber products has raised concerns regarding the long-term sustainability of timber supplies and the conservation of tropical forests. It is generally agreed that forest plantations with non-native tree species could be the first ones to be considered for logging to meet part of Taiwan's timber demands. Plantations in rough topography, however, should probably go through small-patch cutting, followed by natural regeneration to maintain ecosystem functions of soil and water conservation. In this study, we found that thinning with a patch size of 100 m^2 greatly increased the magnitude and heterogeneity of the understory light availability. Increased light availability in large gaps created by logging may promote forest regeneration through increased germination and growth rates (Yanai et al. 1998, Dickinson et al. 2000). Spatial heterogeneity enhanced by thinning allows plants of different successional stages and light preferences to coexist (Fahey and Puettmann 2007) and helps create diverse habitats for forest fauna (Suzuki and Hayes 2003, Wilson and Puttmann 2007). An assessment of the understory vegetation indicated general trends of increasing species richness with increasing means and standard deviations of both light indices approximately 2 mo after the thinning treatment (Hsieh unpubl. data). Rapid increases in the cover and diversity of plants in the understory is typical of many forest-thinning practices and is often attributed to increases in understory light availability (Ares et al. 2010). Our results suggest that the role of increases in light variability is probably overlooked and highlights the importance of immediate post-thinning asessments to obtain a thorough understanding of the effects of thinning on the forest understory environment.

Despite the fact that thinning is an effective tool for changing the understory light environment, thinning at both 25 and 50% intensities elevated understory light to levels that rarely occur following typhoons, the most common natural disturbance experienced by the island (Mabry et al. 1998, Lin et al. 2011). The increase in both the ISF and DSF in northeastern Taiwan following the 1996 strong typhoon Herb, the strongest typhoon of the last 3 decades (Longshore 2000), was approximately 25% (Lin et al. 2003) considerably lower than the 40% increase following 25% thinning. In addition, the patchy and binary pattern of mechanical thinning applied in this study led to an understory light environment that was decoupled from the pre-thinning condition and much more variable. This also differs from the effect of typhoon disturbance, which is primarily defoliation with few snapped boles or uprooted trees (Mabry et al. 1998, Lin et al. 2011). In other words, the effects of typhoon disturbance on understory light availability are relatively diffused, unlike the binary nature of mechanical thinning. Post-typhoon understory light availability was significantly greater than, but positively correlated with, pre-typhoon levels, and the variability was smaller than that before the typhoon disturbance (Lin T.C. unpubl. data). Thus, if artificial thinning is to be carried out in forests experiencing frequent typhoon disturbance, the regeneration pattern following such artificial thinning may greatly differ from natural regeneration following typhoon disturbances due to their very different effects on the availability and variability of understory light. Long-term monitoring of plant community dynamics following typhoons and thinning will be required to understand differences in their successional trajectories.

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