Research paper

Growth and Photosynthetic Responses of Understory Saplings of Three Hardwood Species to Small Patch Thinning in a *Cryptomeria japonica* Plantation

Yau-Lun Kuo,[1,3] Fan-Hsuan Tseng,[1] Yeh-Lin Yang[2]

【Summary】

The growth and photosynthetic responses to different light environments created with small patch thinning in a *Cryptomeria japonica* plantation in central Taiwan of 3 hardwood species, *Lasianthus fordii Hance*, *Eurya loquaiana* Dunn., and *Helicia formosana* Hemsl., were investigated. Three different light environments included a gap site in a thinned stand, a non-gap site next to the gap site, and an unthinned control site. The respective average light intensities received by understory saplings were 27, 15, and 4% of full sunlight in the gap, non-gap, and control sites. For *H. formosana* and *E. loquaiana*, the light-saturated photosynthetic rates (A_{sat}) were all significantly higher in the gap and non-gap sites than in the control site, showing obvious physiological acclimation. This acclimation was not detected in saplings of *L. fordii.* For *H. formosana* and *E. loquaiana*, the mean annual diurnal photosynthetic rates (A_{mean}) were all significantly higher in the gap and non-gap sites than in the control site, whereas for *L. fordii*, no significant differences in A_{mean} were found among the 3 sites. There were significant linear relationships for all 3 species between the A_{mean} and light intensity, with *H. formosana* having the highest slope. The mean chlorophyll fluorescence value (Fv/Fm) of *H. formosana* was ≥ 0.75 in the gap site, which indicates no sign of photoinhibition, while Fv/Fm values of *L. fordii* indicated mild photoinhibition in the gap and non-gap sites. One year after the thinning operation, in the gap site, *H. formosana* had the highest relative rate of height growth, while *E. loquaiana* had the highest relative rate of leaf area growth. For *H. formosana* and *E. loquaiana*, both the height and leaf area growth had significant positive relationships with light intensity. In spite of their shade-tolerance, saplings of *H. formosana* and *E. loquaiana* possessed the ability to acclimate to elevated light intensities without suffering photoinhibition. With increasing light intensities, these 2 species raised their photosynthetic rates and growth. In contrast, saplings of *L. fordii* did not perform as well when exposed to elevated light intensities.

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Received May 2013, Accepted August 2013. 2013年5月送審 2013年8月通過。

Key words: acclimation, diurnal photosynthesis, light environments, photoinhibition, relative growth rate.

Kuo YL, Tseng FS, Yang YL. 2013. Growth and photosynthetic responses of understory saplings of three hardwood species to small patch thinning in a *Cryptomeria japonica* plantation. Taiwan J For Sci 28(3):113-28.

研究報告

柳杉人工林林下三種闊葉稚樹生長及光合作用對小區塊疏伐的反應

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摘 要

本研究探討台灣中部地區的柳杉人工林，在疏伐後的三處不同光環境下，琉球雞屎樹、山龍眼及細枝柃木三種闊葉樹稚樹的生長及生理表現。三處環境包括疏伐孔隙區、疏伐林分的非孔隙區及未疏伐林分的對照區。此三種稚樹在上述三處環境白天分別可接受到約27、15及4%的相對光量。山龍眼及細枝柃木在光量較高的孔隙及非孔隙兩區，其光飽和光合作用率均會顯著高於生長在對照區的同種植株，有明顯的生理馴化表現，而琉球雞屎樹則無此表現。藉由一年12次的光合作用日變化測定，得知細枝柃木及山龍眼生長於孔隙及非孔隙兩區的植株，光合作用日變化年平均值皆顯著高於對照區的同種植株。相反的，琉球雞屎樹該數值在三處環境間則無顯著差異。這三種樹種所有植株的光合作用日變化年平均值，與各植株接受到的光量間，都有極顯著直線正相關，但山龍眼該迴歸式的斜率最高。山龍眼在孔隙區植株，葉綠素螢光反應Fv/Fm值在0.75以上，未遭光抑制，而琉球雞屎樹在該環境則會遭輕微光抑制。疏伐後一年，在孔隙區樹高相對生長率最大的是山龍眼，而葉面積相對生長率最大的是細枝柃木。山龍眼與細枝柃木所有植株的樹高及葉面積相對生長率，與各植株接受到的光量間，均具有極顯著直線正相關，而琉球雞屎樹則否。本研究發現此三種植物雖然都是耐陰的樹種，但山龍眼及細枝柃木在生理上有馴化高光的能力，在疏伐形成的孔隙環境不易遭光抑制，且較能有效利用疏伐後提高的光資源，提高光合作用率，因而有較高的相對生長率。琉球雞屎樹在生理不具馴化高光能力，在孔隙環境不能顯著增加生長。

關鍵詞：馴化、光合作用日變化、光環境、光抑制、相對生長率。

郭耀綸、曾繁絢、楊月玲。2013。柳杉人工林林下三種闊葉稚樹生長及光合作用對小區塊疏伐的反應。台灣林業科學28(3):113-28。

INTRODUCTION

Light availability is a key environmental factor affecting the growth and survival of understory seedlings. The intensity of incident light reaching a forest floor exhibits tremendous heterogeneity both temporally and spatially (Chazdon et al. 1996). Light heterogeneity can affect instantaneous net photosynthetic rates and long-term carbon gains, and consequently the biomass of plants. When a forest encounters events of natural disturbance (e.g., typhoons) causing defoliation or uprooting that form gaps in the canopy, light levels are normally elevated in the understory such that understory plants have increased photosynthetic rates and growth (Yamashita et al. 2000, Kuo et al. 2007, Souza et al. 2010). However, not all understory plants benefit from the sudden increase in light through canopy gaps. Some understory shade-tolerant species may suffer photoinhibition from the sudden strong light, which is unfavorable to their growth (Houter and Pons 2005). Artificial thinning, a tending practice in silviculture, can also increase the light intensity in the understory (Zhu et al. 2003, Boucher et al. 2007). Thinning operations remove part of the canopy of a stand, increasing the amount and duration of incident light reaching the forest floor and indirectly triggering microenvironmental changes in air and soil temperatures, relative humidity, and soil water (Zhu et al. 2003, Wang et al. 2008, Chiang et al. 2012). The extent of thinning impacts depends on the intensity and method of thinning as well as the plant species.

In 2005, under sponsorship of the National Science Council of Taiwan, long-term research plots were set up in *Cryptomeria japonica* plantations near Zenlun, Nantou County, Taiwan (Sun 2008), and since then, a large project has been carried out to investigate the effects of alternative thinning regimes on the community structure and ecosystem functions of forest plantations. Thinning with the complete removal of a small patch of *C. japonica* trees was applied between June and September 2007. Within these patches, elimination of the upper canopy created gaps in which the incident light was greatly increased. Understory plants growing at sites adjacent to the cleared patch (i.e., non-gap sites) where the upper canopy trees were still intact, received less light than those in gap sites. However, compared to plants growing in unthinned plots, those growing in non-gap sites could periodically receive higher amounts of direct and diffuse light through nearby gaps during the day. To understand the responses of natural recruits to environmental changes after thinning, differences in physiological activities and growth under 3 contrasting environments (gap, non-gap, and unthinned control) of preexisting saplings of *Lasianthus fordii Hance*, *Eurya loquaiana* Dunn., and *Helicia formosana* Hemsl. were studied. The objectives of this study included: (1) comparing light availability in the 3 sites (gap, non-gap, and unthinned) after a thinning operation; (2) examining the net photosynthesis, chlorophyll concentration, and chlorophyll fluorescence of saplings of *L. fordii*, *E. loquaiana*, and *H. formosana* in 3 different environments; and (3) examining sapling growth responses of the 3 species to elevated light resources after the thinning operation. Results of this study can help understand the effectiveness and mechanisms of artificial thinning operations on the growth of understory plants.

MATERIALS AND METHODS

Study site

The study site is located in Zenlun forests (120°54’N, 23°43’E), Nantou, Taiwan, at elevations of 1300~1500 m, with east- and northeast-facing slopes of 6° to 31°. The mean annual temperature is about 15.6℃, and the mean annual precipitation is 2370 mm, with a wet season from April to September and a relatively dry winter (Chen et al. 2011). The *C. japonica* plantation, established in 1974, has an area of about 78 ha with a stand density of 1050 stems ha^{-1}. The average tree height and diameter at breast height were 17 m and 25 cm, respectively, and the stand volume was about 450 m^3 ha^{-1} at the time of this study (Chiu et al. 2011a).

This study was part of an experimental site designated for the project “Effects of alternative thinning regimes on the community structure and ecosystem functions of plantation forests” sponsored by the National Science Council of Taiwan. Four large blocks were set up by means of a completely randomized block design in February 2006. In each block, three 1-ha (100 × 100-m) plots were established for treatment with different thinning operations: 0% (un-thinned control), 25% thinning, and 50% thinning. Therefore, this study had a total of 12 plots (plots #1~#12). A preliminary survey of the biotic and abiotic environments of the plots was carried out before the thinning operation began. Thinning with clear-cutting operation of a small patch was systematically carried out between June and September 2007. Each 1-ha plot was divided into 25 operating plots (each of 20 × 20 m), and each operating plot was further divided into 4 subplots (each of 10 × 10 m). For the 25% thinning regime, all *C. japonica* trees in 1 of the 4 subplots (the one at the southwestern corner) were felled (Fig. 1). For the 50% thinning regime, 2 of the 4 subplots (those at the southwestern and northeastern corners) were felled. With these thinning regimes, 25 gaps (for 25% thinning) or 50 gaps (for 50% thinning) were created and distributed evenly throughout the site. This study selected plots #7 (a plot with 25% thinning) and #6 (an adjacent unthinned plot of plot #7) as the major investigation plots. In the 25% thinning plot, each species was studied in 2 different environments, a gap site (with a high level of incident light) and a non-gap site (with an overhead canopy and a lower level of incident light). In addition, the amount of incident light was compared in 3 different environments: gap, non-gap, and un-thinned control.

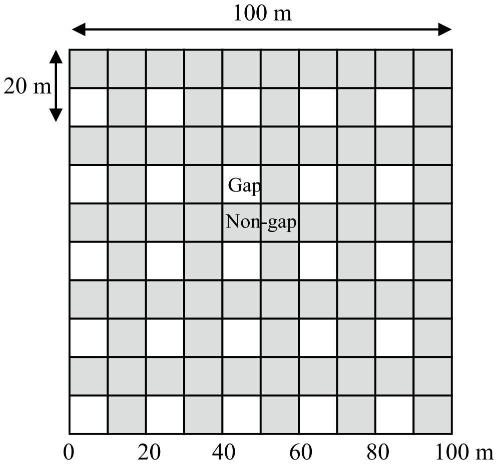

Fig. 1. A schematic diagram of the distribution of gap and non-gap sites in a 25% thinned plot. The 25 white squares (□) denote gap sites, each with an area of 100 m^2, and gray squares (▨) denote non-gap sites.

Studied species

Three hardwood species, *L. fordii*, *E. loquaiana*, and *H. formosana*, which existed before the thinning operation in the *C. japonica* plantations, were selected for this study. These 3 species ranked the first, fourth, and sixth in terms of the numbers of natural recruits of woody plants in the plantations before the thinning operation. In particular, saplings of *L. fordi* numerically accounted for 52.2% of the woody plants in the entire stand (Sun 2011). After thinning, 5 saplings of each species were selected for further investigation in each of the 3 different light environments (a total of 15 saplings selected for each species) in December 2007. Heights of sampled saplings of *L. fordii*, *E. loquaiana*, and *H. formosana*, ranged 22~54, 20~120, and 27~77 cm, respectively.

Measurements of light environments

In the 3 light environments, 2 d of monitoring of the diurnal light intensity was done in March, May, and June 2008. Four quantum sensors (LI-190SA, LI-COR, Lincoln, NE, USA) and a data logger (LI-1400, LI-COR) were randomly placed 60 cm above the ground in the stands. Data were recorded every 15 min. At the same time, another light sensor and data logger were set up at a nearby weather station in the Zenlun Nursery to record diurnal variations in full light. The relative light intensity (% full light) was accordingly calculated for the 3 light environments. The instantaneous light intensity at the top of each sampled sapling was also recorded every 2 h from 08:00 to 16:00 for 1 d in March, May, and August 2008. Similarly, data collected at the nearby weather station at the same time were used to calculate the relative instantaneous light intensity.

Growth characteristics of saplings

Tree height was measured and the number of leaves was counted for each selected sapling once every 2 mo from December 2007 to February 2009. Because existing saplings of the same species in the 3 environments were not the same size to begin with, their relative growth rate of height (RGR-H) in a year was used for comparisons in this study. The RGR-H was calculated as ((final height – initial height) ÷ initial height) × 100%. To assess variations in the whole-plant leaf area of each species, we picked 30 leaves for each species from nearby non-selected saplings under the 3 light environments. An area meter (LI-3000A, LI-COR) was used to calculate the mean leaf area of a single leaf. Then the mean was multiplied by the number of leaves counted in each selected sapling to evaluate variations in leaf area of a single plant in a year. Similarly, the relative growth rate of the whole-plant leaf area (RGR-A) was used for comparisons and calculated by ((final leaf area – initial leaf area) ÷ initial leaf area) × 100%.

Measurements of physiological activities

Diurnal course of photosynthesis

Net photosynthesis of each selected sapling was measured under field light conditions with a portable photosynthesis system (CIRAS-2, PP-Systems, Hitchin, UK) once a month from December 2007 to November 2008. Fully expanded and mature leaves were chosen for these measurements. The measured CO_2 concentration was set to 400 ppm without adjustment for other measuring conditions. On each measurement day, net photosynthetic rates of each sapling were measured every 2 h from 07:00 to 17:00/18:00 (from May to August 2008, when daytime was longer). Due to an unexpected construction event that blocked access to our study site in February 2008, we used the data collected in February 2009 instead to represent the physiological performance of saplings in February. The diurnal mean of each season (spring, summer, autumn, and winter) and the annual mean of photosynthetic rates for each species were calculated.

Photosynthetic light responses

Photosynthetic light responses of each sampled sapling under the 3 light environments were measured with a portable LI-6400 (LI-COR) photosynthesis system, in June and July 2008. Newly mature leaves were chosen for these measurements. The measured CO_2 concentration was set to 400 ppm, the leaf temperature to 25℃, and the relative humidity to 60~70%. In the beginning, a chosen leaf was illuminated with 500 μmol photon m^{-2} s^{-1} for 5 min to fully induce its photosynthetic apparatus. Then, starting from a light intensity of 1500 μmol photon m^{-2} s^{-1} and gradually lowering it to 0 (light off) through 17 light levels, the net photosynthetic rate of the leaf was monitored at each light level. For saplings in the unthinned plot, which usually received lower light levels, photosynthetic rates were measured from a high light intensity of 1000 to 0 μmol photon m^{-2} s^{-1} through 15 light levels. A light response curve was plotted using the net photosynthetic rate vs. light intensity. For photosynthetic rates measured under 30 μmol photon m^{-2} s^{-1}, a linear regression analysis was used. The regression equation was used to estimate the light compensation point (LCP) and the dark respiration rate (R_d). In this study, 95% of the highest net photosynthetic rate was regarded as the light-saturated photosynthetic rate (A_{sat}) of each leaf, and the corresponding light intensity was the light saturation point (LSP).

Chlorophyll fluorescence and concentration

Chlorophyll fluorescence and concentration of sampled saplings in the 3 environments were investigated in July, August, and December 2008. Chlorophyll fluorescence was measured with a chlorophyll fluorescence analyzer (Mini-PAM, Heinz Walz GmbH, Effeltrich, Germany). The measurement began by holding the test leaf with a custom-made clip to a dark adapting process for 30 min before measuring its minimum (Fo) and maximum fluorescence (Fm). Then the highest photosynthetic efficiency (Fv/Fm, where Fv = Fm - Fo) after dark adaptation for this leaf was calculated. One mature leaf of each sampled sapling of the 3 species was measured at 08:00~09:00 in the morning. A chlorophyll meter (SPAD-502, Mionta Co., Osaka, Japan) was employed to assess the chlorophyll concentration index (Chl) for each species. Five mature leaves of each sampled sapling were used for this assessment.

Data analysis

Analysis of variance (ANOVA) procedures of the SPSS statistical package (IBM, Armonk, NY, USA) were performed to identify whether there were significant differences among mean photosynthetic rates, 4 photosynthetic characteristics, chlorophyll fluorescence, chlorophyll concentrations, RGR-H, and RGR-A of the 3 species. If a significant difference existed ($p < 0.05$), then Duncan's multiple-range test was used to further explain the differences.

RESULTS

Mean light intensity

The mean diurnal incident light levels of 6 measurement days were 250, 125, and 40 μmol photon m^{-2} s^{-1} in the gap, non-gap, and control sites, respectively, equivalent to the relative light intensities of 34, 19, and 6%, respectively, with the average full light in the open field of 700 μmol photon m^{-2} s^{-1}. The instantaneous light intensities received by the sampled saplings ranged 130~400, 80~230, and 14~60 μmol photon m^{-2} s^{-1} in the gap, non-gap, and control sites, respectively. The mean photosynthetic photon flux density (PPFD) and mean relative light (% full light) for each species in the 3 environments are listed in Table 1. The relative light intensities received by saplings at the 3 sites averaged 27, 15, and 4%, respectively.

Diurnal net photosynthetic rates

Twelve diurnal courses of net photosynthetic rates were monitored during the study period. Results showed that the net photosynthetic rates of all species fluctuated with the light intensity. An example measurement taken on August 1, 2008, a cloudy day, is shown in Fig. 2. The highest incident light available to saplings in the gap site, that reached 200 μmol photon m^{-2} s^{-1}, occurred at 09:00~12:00, when the saplings concurrently exhibited higher net photosynthetic rates. During the same time period, saplings at the other 2 sites received < 100 μmol photon m^{-2} s^{-1} of light intensity, and their photosynthetic rates were not as high as those in the gap site. Photosynthetic rates of saplings usually declined in the afternoon due to lower light intensities caused by frequent foggy conditions. We also compared diurnal mean photosynthetic rates of each season among the 3 sites for each species (Fig. 3). For *L. fordii*, the means of summer and autumn were significantly lower at the control site than those at the other 2 sites, whereas no significant differences in the means of spring or winter were detected among the 3 sites. For *E. loquaiana*, the means of all 4 seasons were significantly higher at the gap site than those in the control site. For *H. formosana*, the means of 3 seasons (spring, summer, and autumn)

Table 1. Mean photosynthetic photon flux density (PPFD) and mean relative light (RL) measured at the top of sampled saplings of the 3 studied species growing at 3 sites (gap, non-gap, and un-thinned control sites)

Species	Mean PPFD (μmol photon m^{-2} s^{-1})			Mean RL (% full light)		
	Gap	Non-gap	Control	Gap	Non-gap	Control
Lasianthus fordii	223	121	34	26.3	14.6	4.4
Eurya loquaiana	237	148	29	27.1	17.1	3.6
Helicia formosana	224	103	21	26.9	12.4	2.7

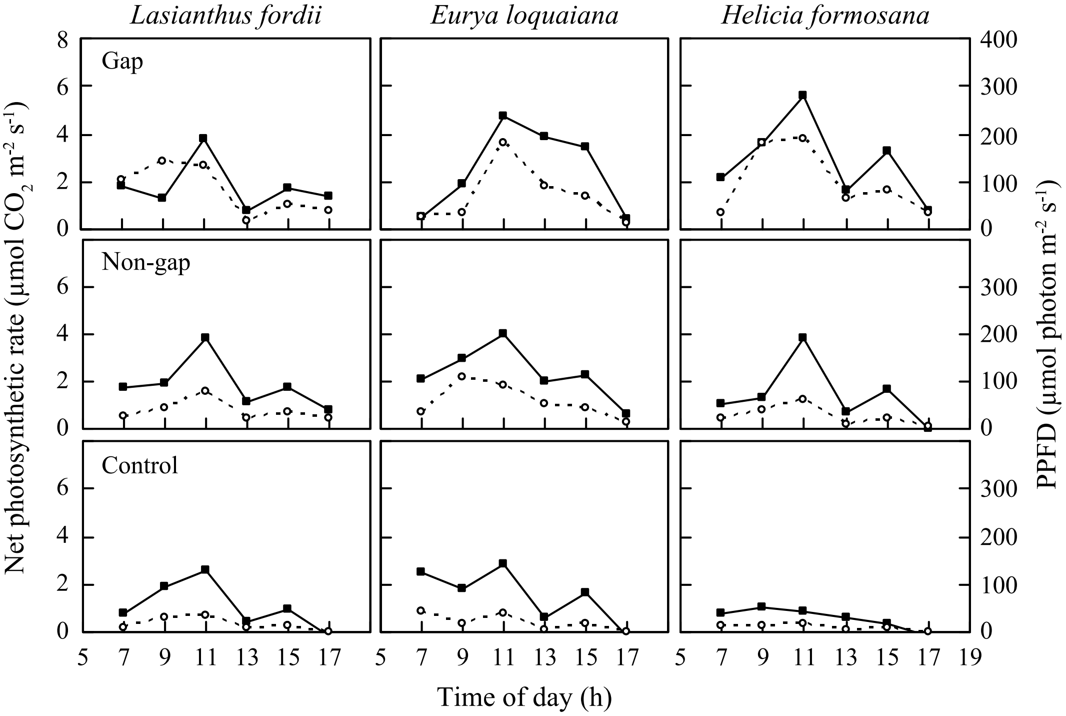

Fig. 2. Diurnal courses of net photosynthetic rates (■) and photosynthetic photon flux density (PPFD, ○) of the 3 studied species growing in gap, non-gap, and control sites. Measurements were taken on 1 August 2008.

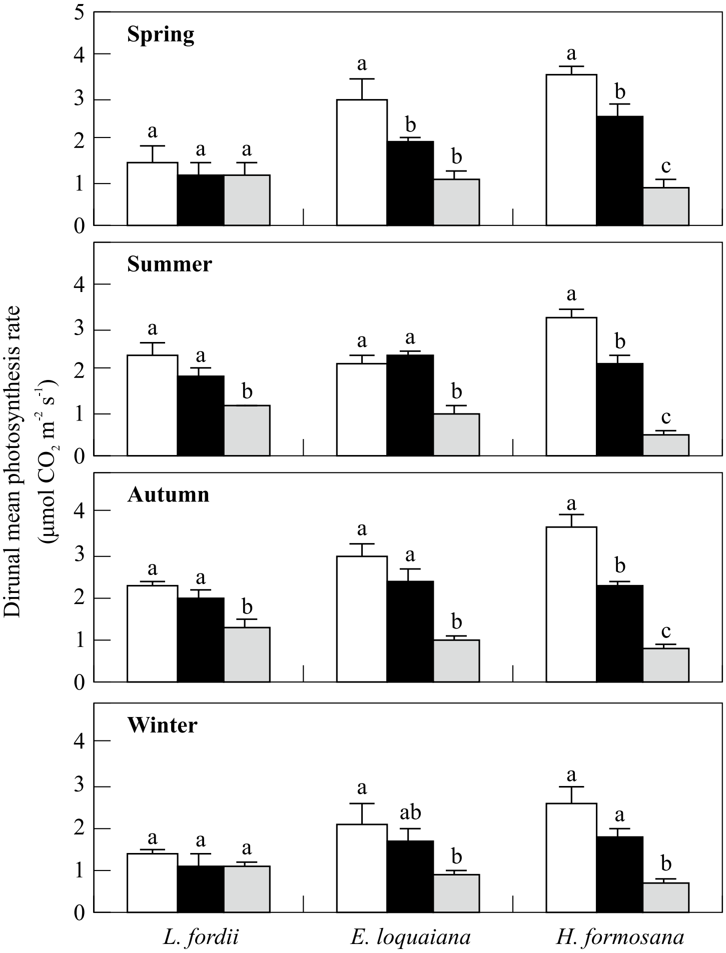

Fig. 3. Comparisns of diurnal mean photosynthetic rates of *Lasianthus fordii*, *Eurya loquaiana*, and *Helicia formosana* in gap (□), non-gap (■), and control (□) sites in each season. Histograms labeled with different letters significantly differ at the 5% level by Duncan's multiple-range test.

significantly differed among the 3 sites, with the highest at the gap site and the lowest at the control site. Combining the photosynthetic rates obtained from the 12 courses, annual mean diurnal photosynthetic rates (A_{mean}) of each studied species in the 3 sites were calculated and compared (Fig. 4). For *E. loquaiana* and *H. formosana*, A_{mean} was significantly higher at the gap site than that in the control site, while for *L. fordii*, no significant differences were detected among the 3 sites (Fig. 4A). At the gap site, *H. formosana* had a significantly higher A_{mean} than did *L. fordii*, while in the control site, *H. formosana* had a significantly lower A_{mean} than the other 2 species (Fig. 4B). For all 3 species, significantly positive relationships were found between the A_{mean} of the 15 sampled saplings growing in the 3 sites and the relative light intensity (Fig. 5). The slope yielded by the regression analysis was the largest for *H. formosana* (0.091), and the smallest for *L. fordii* (0.029).

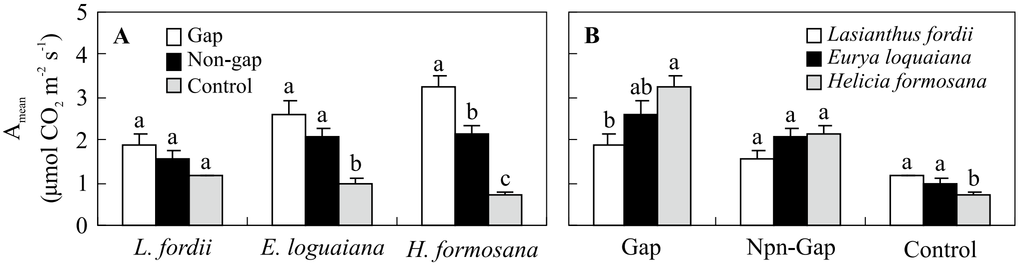

Fig. 4. Annual mean diurnal photosynthetic rates (A_{mean}) of tested saplings, comparing the same species at 3 different sites (A) and 3 different species at the same sites (B). Histograms labeled with different letters significantly differ at the 5% level by Duncan's multiple-range test.

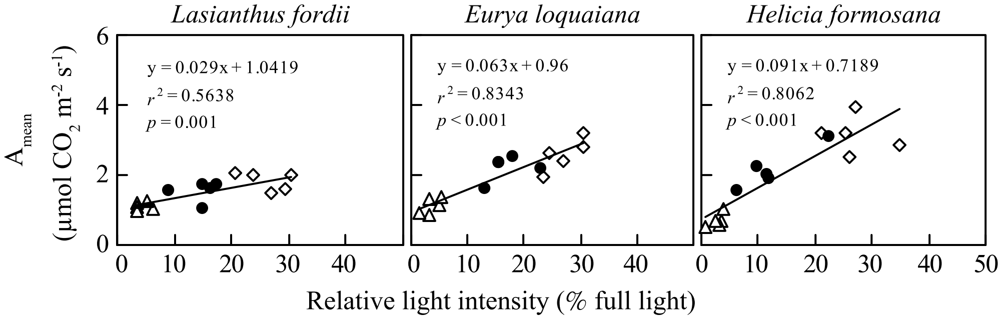

Fig. 5. Relationships between annual mean diurnal photosynthetic rates (A_{mean}) of sampled saplings and the relative light intensity (% full light) measured at gap (◇), non-gap (●), and control (△) sites for the 3 studied species.

Photosynthetic light response

The photosynthetic light response curves presented by saplings of the 3 species exhibited different patterns at the 3 sites (Fig. 6). For *L. fordii*, the light response curves were similar among the 3 sites. In contrast, the other 2 species had different light response curves among the 3 sites, with the net photosynthetic rates higher in the gap site than in the control site. Four photosynthetic characteristics, A_{sat}, LSP, LCP, and R_d, of the 3 studied species in the 3 sites are listed in Table 2. A_{sat} values of *H. formosana* and *E. loquaiana* in the gap site reached 8.4 and 7.3 μmol CO_2 m^{-2} s^{-1}, respectively, while it was only 4.2 μmol CO_2 m^{-2} s^{-1} for *L. fordii*. In addition, A_{sat} values of *H. formosana* and *E. loquaiana* were significantly higher in gap and non-gap sites than in the control site. In contrast, A_{sat} values of *L. fordii* did not significantly differ among the 3 sites. LSP values of the 3 species were all < 600 μmol photon m^{-2} s^{-1} at the control site, but were significantly higher (850~1160 μmol photon m^{-2} s^{-1}) at the gap site. In the gap site, the LSP value of *H. formosana* was significantly higher than that of *L. fordii.* In the other 2 sites, however, no significant differences in LSP values were found among the 3 species. For all 3 species, LCP and R_d values were significantly higher in the gap and non-gap sites than in the control site. Comparisons of the 3 species within the same sites showed that *L. fordii* had significantly higher LCP and R_d values than *H. formosana* and *E. loquaiana*.

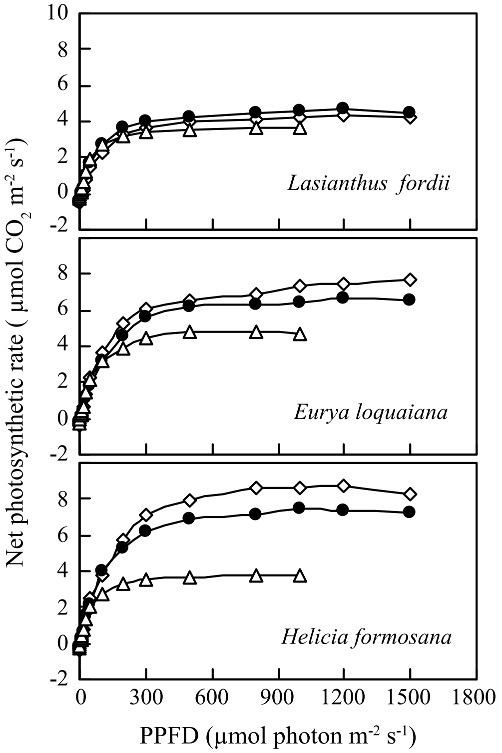

Fig. 6. Photosynthetic light response curves of the 3 studied species in gap (◇), non-gap (●), and control (△) sites (n = 5). PPFD, photosynthetic photon flux density.

Chlorophyll concentration index and chlorophyll fluorescence value

One year after the thinning operation (August to September 2008), the Chl concentration and fluorescence of sampled saplings were examined (Table 3). For *L. fordii*, the Chl concentration was significantly lower at the gap site than at the other 2 sites. For *E. loquaiana*, Chl concentrations were significantly lower in the gap and non-gap sites than at the control site. For *H. formosana*, Chl concentrations did not significantly differ among the 3 sites. For *L. fordii* and *E. loquaiana*, Fv/Fm values were significantly lower (< 0.75) at the gap and non-gap sites than at the control site. For *H. formosana*, all Fv/Fm values were > 0.75, with significantly lower values at the gap site than the control site (Table 3).

Growth performance of sampled saplings

For *E. loquaiana* and *H. formosana*, the RGR-H significantly differed among the 3 sites, being highest in the gap site and lowest in the control site, while for *L. fordii*, the RGR-H did not significantly differ among the 3 sites (Fig. 7A). Comparing the 3 species within the same environment, *H. formosana* had a significantly higher RGR-H than *L. fordii* at the gap site, while *L. fordii* had the highest RGR-H at the control site (Fig. 7B). For *L. fordii*, the RGR-A was significantly higher at the non-gap site than at the control site, while for *E. loquaiana* and *H. formosana*, RGR-A values were significantly higher at the gap site than at the other 2 sites (Fig. 8A). Comparisons of the 3 species within the same environment showed that *E. loquaiana* had the highest RGR-A (500%) at the gap site (Fig. 8B).

We found that RGR-H and RGR-A values of the 15 saplings of *L. fordii* did not significantly increase with the amount of light received by plants in any of the 3 different light environments (Fig. 9A, D). However, significant positive relationships were found of both RGR-H and RGR-A values with the amount of light for *E. loquaiana* and *H. formosana* (Fig. 9B, C, E, F). Regressions using the RGR-H against the relative light intensity showed that *H. formosana* had the highest slope, and *L. fordii* the smallest. Regressions using the RGR-A against the relative light intensity showed that *E. loquaiana* had the highest slope, and *H. formosana* the smallest.

DISCUSSION

Thinning operations in plantations are traditionally aimed at regulating the stand density and promoting the growth of residual

Table 2. Light-saturated photosynthetic rate (A_{sat}), light saturation point (LSP), light compensation point (LCP), and dark respiration rate (Rd) of the 3 studied species growing at 3 sites (*n* = 5, mean ± SE)

	Site		
	Gap	Non-gap	Control
A_{sat} (μmol CO_2 m^{-2} s^{-1})			
Lasianthus fordii	4.2±0.2$^{a\ 1)\ B}$	4.4±0.4$^{a\ B\ 2)}$	3.5±0.3$^{a\ B}$
Eurya loquaiana	7.3±0.3$^{a\ A}$	6.3±0.4$^{a\ A}$	4.6±0.2$^{b\ A}$
Helicia formosana	8.4±0.5$^{a\ A}$	7.2±0.5$^{a\ A}$	3.7±0.3$^{b\ B}$
LSP (μmol photon m^{-2} s^{-1})			
Lasianthus fordii	850±65$^{a\ B}$	770±59$^{a\ A}$	523±23$^{b\ A}$
Eurya loquaiana	960±103$^{a\ AB}$	825±33$^{a\ A}$	567±14$^{b\ A}$
Helicia formosana	1160±89^{aA}	912±71$^{b\ A}$	580±12$^{c\ A}$
LCP (μmol photon m^{-2} s^{-1})			
Lasianthus fordii	11.9±1.4$^{a\ A}$	11.4±1.5$^{a\ A}$	3.8±0.5$^{b\ A}$
Eurya loquaiana	6.1±0.3$^{a\ B}$	7.4±0.6$^{a\ B}$	1.9±0.3$^{b\ B}$
Helicia formosana	5.4±0.7$^{a\ B}$	5.6±0.8$^{a\ B}$	1.2±0.2$^{b\ B}$
R_d (μmol CO_2 m^{-2} s^{-1})			
Lasianthus fordii	0.49±0.04$^{a\ A}$	0.55±0.05$^{a\ A}$	0.29±0.03$^{b\ A}$
Eurya loquaiana	0.35±0.02$^{a\ B}$	0.39±0.03$^{a\ B}$	0.22±0.02$^{b\ B}$
Helicia formosana	0.37±0.03$^{a\ B}$	0.44±0.02$^{a\ B}$	0.22±0.04$^{b\ B}$

1) Values in a row with different lower-case letters significantly differ among sites at the 5% level by Duncan's multiple-range test.

2) Values in a column with different capital letters significantly differ among species at the 5% level by Duncan's multiple-range test.

Table 3. Chlorophyll concentration index (Chl) and chlorophyll fluorescence value (Fv/Fm) of the 3 studied species growing in gap, non-gap, and control sites (*n* = 5, mean ± SE)

Species	Chl			Fv/Fm		
	Gap	Non-gap	Control	Gap	Non-gap	Control
Lasianthus fordii	47.1±1.8$^{b1)}$	52.3±1.1^{a}	55.8±1.1^{a}	0.69±0.01^{b}	0.71±0.01^{b}	0.76±0.02^{a}
Eurya loguaiana	49.8±0.9^{b}	50.4±0.5^{b}	55.9±2.2^{a}	0.71±0.01^{b}	0.73±0.01^{b}	0.80±0.02^{a}
Helicia formosana	50.4±0.9^{a}	50.4±0.6^{a}	50.9±2.3^{a}	0.75±0.01^{b}	0.78±0.01^{ab}	0.79±0.02^{a}

1) Values in a row with different letters significantly differ at the 5% level by Duncan's multiple-range test.

trees. The method of thinning from below (or low thinning) is the most common thinning method used in Taiwan (Wang et al. 2008, Chiu et al. 2011b), in which individual trees are removed from the stand. A different method once utilized in *C. japonica* plantations of Chilan Mountain, northern Taiwan, was mechanical thinning with the removal

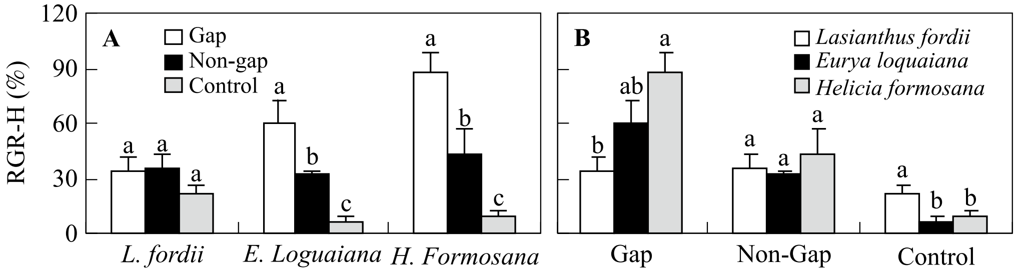

Fig. 7. Relative growth rates of height (RGR-H) of sampled saplings at the end of our experiment, comparing the same species at 3 different sites (A) and 3 different species at the same site (B). Histograms labeled with different letters significantly differ at the 5% level by Duncan's multiple-range test.

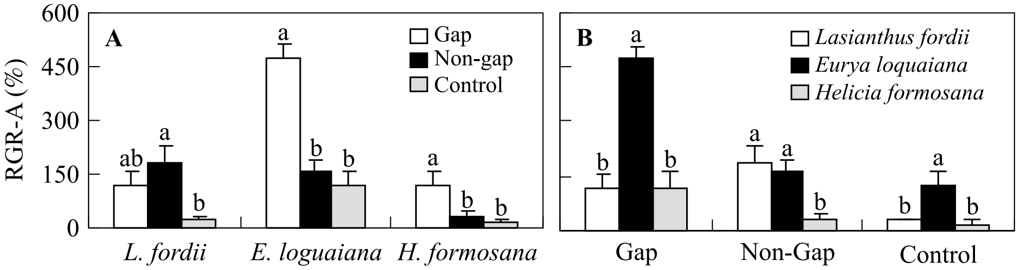

Fig. 8. Relative growth rates of leaf area (RGR-A) of sampled saplings at the end of our experiment, comparing the same species at 3 different sites (A) and 3 different species at the same site (B). Histograms labeled with different letters significantly differ at the 5% level by Duncan's multiple-range test.

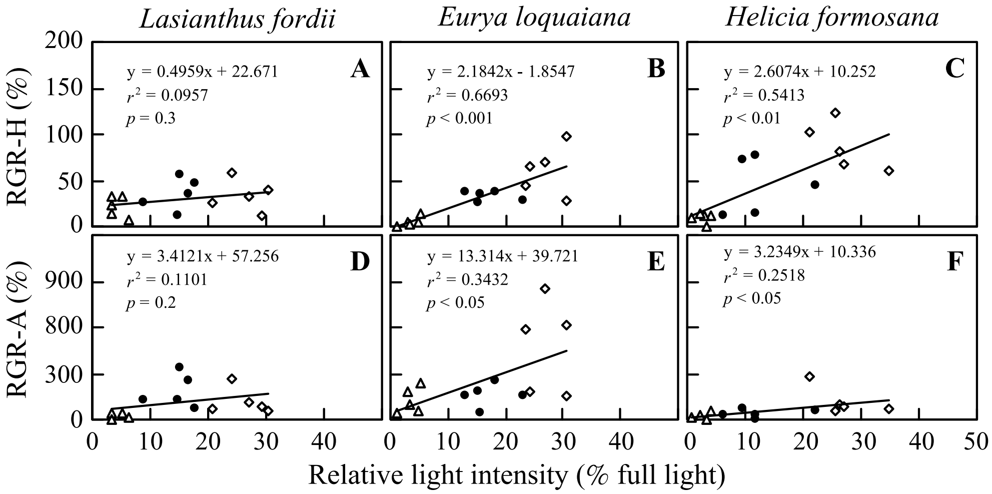

Fig. 9. Relationships of relative growth rates of height (RGR-H) and relative growth rates of leaf area (RGR-A) with relative light intensities (% full light) measured in gap (◇), non-gap (●), and control (△) sites for the 3 studied species.

of several rows of trees in a strip (Lo-Cho et al. 1997, Lin et al. 2010). The latter method is also called group thinning because a group of adjacent trees are felled during the operation. The thinning operation used in this study could be classified as group thinning; but instead of cutting rows, small patches were clear-cut. Patches, each consisting of about 10 trees, were clear-cut, creating small gaps (each 100 m^2) distributed systematically throughout a 1-ha *C. japonica* stand. In the created gap site, saplings of the 3 studied species on average received 27% of the relative light intensity, much higher than the relative light intensity (4%) received by saplings at the unthinned site (Table 1). Even with the overhead canopy of *C. japonica* trees, saplings growing in non-gap sites adjacent to the gaps still received higher amounts of direct or diffuse light through the nearby openings than those in the unthinned site. This study showed that saplings in the non-gap site received 12~17% of relative light, 4~5-fold greater than the light availability in un-thinned control sites. In addition to increased light availability, the spatial heterogeneity of the understory was also enhanced by this small-patch clear-cutting method (Chiang et al. 2012). This created highly variable microenvironments promoted the regeneration of shade-intolerant woody plants and increased understory biodiversity (Sun 2011).

All 3 studied species already existed in the understory of the *C. japonica* plantations before the thinning operation. Although all 3 species are shade-tolerant species, they had different physiological responses to the elevated light intensity caused by thinning. On most measurement days, the diurnal mean photosynthetic rate of *H. formosana* was significantly higher at gap sites than at the non-gap site, the latter was also significantly higher than at the control site (Fig. 4). Significant positive relationships between the A_{mean} and light availability received by the saplings were found for all 3 species (Fig. 5). However, the slope of the regression equation was greater in *H. formosana* (0.091) than in *E. loquaiana* (0.063) and *L. fordii* (0.029), which suggests that the former 2 species, *H. formosana* and *E. loquaiana*, are more capable of utilizing the approximate 27% of relative light available in a gap (Table 1). The performances of the 4 photosynthetic characteristics (A_{sat}, LSP, LCP, and R_d) of the 3 species also support the aforementioned inference. A_{sat} values of *H. formosana* and *E. loquaiana* at the gap site reached 8.4 and 7.3 μmol CO_2 m^{-2} s^{-1}, which were both significantly higher than the A_{sat} of *L. fordii* (4.2 μmol CO_2 m^{-2} s^{-1}); LSP values of *H. formosana* and *E. loquaiana* at the gap site were also higher than that of *L. fordii.* Furthermore, both A_{sat} and LSP values of *H. formosana* and *E. loquaiana* in gap and non-gap sites were all significantly higher than those of the same species at the control site (Table 2). With increases in A_{sat} and LSP values with the elevated light intensity, a type of physiological acclimation (Naidu and DeLucia 1998, Souza et al. 2010), *H. formosana* and *E. loquaiana* could increase rates of carbon fixation and substantially increase their growth rates in response to the thinning operation. By contrast, *L. fordii* showed less-significant physiological acclimation to the elevated light availability.

For shade-tolerant species originally growing in a low-light understory, their photosynthetic apparatus in the leaves may experience photoinhibition after a sudden increase in incident light caused by thinning (Chazdon 1992, Yamashita et al. 2000, Houter and Pons 2005). This photoinhibition could result in a decrease in the photosynthetic rate (Critchley 1998). Whether a plant suffers any photoinhibition and to what extent depends on its intrinsic shade-tolerance or photosynthetic capacity. It was pointed out that shade-tolerant species with a low photosynthetic capacity are more susceptible to photoinhibition (Mulkey and Pearcy 1992, Chazdon et al. 1996). In this study, saplings at gap sites received only an average 27% of full light during the day, and they might be exposed to intense light similar to that in an open field at noon of a sunny day after thinning. Among the 3 studied species, *L. fordii* had the lowest photosynthetic capacity (Table 2) and possibly suffered photoinhibition. The Fv/Fm value of a healthy leaf is about 0.80 or slightly lower, while any value < 0.725 is indicative of photoinhibition due to the stress of high light (Critchley 1998). Fv/Fm values were significantly lower for saplings growing at the thinned plots (both gap and non-gap sites) than those growing at unthinned plots, but most values were > 0.725 with the exception of *L. fordii* (Table 3). Fv/Fm values of *L. fordii* at gap and non-gap sites were 0.69 and 0.71, respectively, indicating that these saplings were experiencing mild photoinhibition. In contrast, respective Fv/Fm values of *H. formosana* at gap and non-gap sites were 0.75 and 0.78, meaning that these saplings were experiencing no stress due to high light levels. Especially in the case of *H. formosana*, the Chl concentration was very similar between higher-light and lower-light environments (Table 3), meaning that the strong light did not damage the chlorophyll. Furthermore, if shade-tolerant species originally growing in low-light environments possess the ability to acclimate to elevated light intensities and raise their photosynthetic potential accordingly, they can utilize the excess light energy for photochemistry and greatly reduce the possibility of photoinhibition (Lovelock et al. 1994).

Growth performances of saplings of the 3 species supported what we found concerning their physiology. Relative growth rates of height and leaf area of saplings of *E. loquaiana* and *H. formosana* significantly increased with an increased light intensity, but not so for *L. fordii* (Figs. 7, 8). The linear regressions of RGR-H vs. light intensity yielded the highest slope in saplings of *H. formosana*, indicating the height growth of *H. formosana* was very sensitive to an increased light intensity. A previous study (Kuo et al. 2007) reported similar species differences in responses of the RGR-H to increased light resources for 6 tree species in the understory of a forest in Kenting, southern Taiwan, with *Melanolepis multiglandulosa* and *Diospyros maritima* being the most sensitive to and *D. philippensis* and *Pisonia umbellifera* the least sensitive to the increased light. RGR-A values of both *E. loquaiana* and *H. formosana* also significantly increased with increased light, and the slope yielded in the regression of the RGR-A vs. light intensity was larger in *E. loquaiana* (13.31, Fig. 9E) than in *H. formosana* (3.23, Fig. 9F), suggesting greater sensitivity of the leaf area growth in the former species to increased light. Particularly at the gap site, the RGR-A of *E. loquaiana* reached 500%, compared to a less impressive increase of 120% in the other 2 species (Fig. 8B). For a plant growing in a gap environment, a rapid increase in leaf area can improve the carbon gain of the entire plant, and thus benefit growth (Popma and Bongers 1988). While saplings of *E. loquaiana* and *H. formosana* significantly increased growth with enriched light availability in high-light environments such as gaps (Figs. 7A, 8A), saplings of *L. fordii* had significantly higher RGR-H values than the other 2 species in low-light environments as at the control site (Fig. 7B). These results implied that *H. formosana* and *E. loquaiana* may be more competitive than *L. fordii* after the thinning operation.

CONCLUSIONS

Spatial heterogeneity in light availability in the understory of *C. japonica* plantations was created after thinning operations in the stand. The 3 preexisting hardwood species, *L. fordii*, *E. loquaiana*, and *H. formosana*, in the plantations are all shade-tolerant species. Saplings of *H. formosana* and *E. loquaiana* possessed better physiological acclimation to elevated light, including higher net photosynthetic rates, lower vulnerability to photoinhibition of their photosynthetic apparatus, and higher relative growth rates. In contrast, saplings of *L. fordii* showed little acclimation to elevated light and suffered mild photoinhibition, and their growth did not improve. *Helicia formosana* and *E. loquaiana* would be more competitive than *L. fordii* after the thinning operation.

ACKNOWLEDGEMENTS

This study was supported by grants (NSC96-2621-Z-020-001 and NSC97-2621-M-020-001) from the National Science Council, Taiwan. We also thank the Taiwan Forestry Research Institute and Taiwan Forestry Bureau for providing accommodations and logistical support. We appreciate the attentive editing by the reviewers as well.

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