東海大學生命科學系

碩士論文

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Chiang, Jyh Min, Ph.D

不同程度的擾動環境下森林生態系樹形與林冠特徵之分化

Differentiation of tree architectural and crown traits in two hardwood forests under distinct disturbance regimes

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（中文）

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（英文）

Differentiation of tree architectural and crown traits in two hardwood forests under distinct disturbance regimes

經本委員會審定通過，特此證明。

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林宜靜

江智民

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致謝

時光荏苒，東海大學五年半的求學生涯即將隨著論文的付莘而告一段落。從懵懵懂懂、翹課、打電動、打球的死大學生，變成在茫茫書(paper)海中，一步一步織出一個有趣又富含邏輯的故事的研究生，這段過程要感謝許多人的幫忙。

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中文摘要

擾動如何影響生態系的特性是近年來生態研究者所關注的議題。颱風為影響臺灣森林生態系重要的擾動因子之一。過去 20 年颱風侵襲的資料顯示台灣不同地區長期以來累計不同程度的颱風擾動，這提供了良好的環境來探討不同程度的長期擾動環境對森林結構及植物適應策略的影響。近年來，研究者以植物的功能特徵作為探討大尺度生態問題的工具。植物功能特徵為相對易於廣泛量測的特徵如比葉面積、樹高、木質密度等。這些特徵可反映植物生長與生存的權衡。本研究比較颱風擾動頻繁與相對不頻繁的福山及蓮華池森林動態樣區內植物功能特徵組成，以三個層次探討長期颱風擾動環境對於森林生態系結構及植物適應策略的影響：(1) 物種層次：兩樣區之共同樹種是否因長期擾動環境不同而有特徵的分化？(2) 樣方層次：兩樣區之冠層高度是否因長期擾動環境不同而隨著地形有特定的空間分布？(3) 樣區層次：兩樣區之特徵組成是否因長期擾動環境不同而有不同的分化？本研究於兩個 25 公頃樣區內(每樣區含有 625 個 20 × 20m 之樣方)各選出重要指標累計前 70%的物種，每種約 40 棵，測量樹冠特徵(冠幅面積、長度及深度)和樹形結構(樹高、第一枝條高、木質密度)。以最大概似估計法推算特徵間的異速生長函數，使用共變數分析(Analysis of covariance)、最小化平方法(Generalized least square)及主成分分析(Principal component analysis)檢定特徵是否因長期擾動環境不同而有分化。結果顯示：(1)相同胸徑下位於福山的共同樹種有較矮的樹高，相同樹高下，位於福山的共同樹種有較大的冠幅。(2) 福山樣區的平均冠層高度小於蓮華池樣區，福山的冠層高度與地形凹凸度呈顯著負相關，蓮華池樣區的冠層高度與海拔高度呈顯著正相關。(3) 福山傾向於形成較大的冠幅及較矮胖的樹型，蓮華池的功能特徵組成則較為多樣。綜觀以上所述，植物為適應長期颱風擾動頻繁的福山樣區可能發展出的適應策略為：隨著地勢高低形成矮且一致的冠層高度，降低強風的傷害，因為沒有突出的樹冠及較為矮胖的樹型而形成寬廣的冠幅以提升光的攔截率。植物適應長期颱風擾動較不頻繁的蓮華池樣區所發展的策略較為多樣：如木質密度小、最大樹高高且細長的樹型，或木質密度大、較深的冠幅但較矮胖的樹型。此研究顯示，在不同程度的擾動環境下，種內特徵的分化、林冠結構的變化以及多樣化的群聚功能特徵組成能反映出森林面對不同擾動程度的適應策略。

關鍵字：擾動特性、異速生長函數、森林動態樣區、植物功能特徵、功能特徵組成

ABSTRACT

The impact of disturbance on the ecosystem characteristics has been an important topic in ecological studies. In Taiwan, typhoons are perhaps the most important disturbance agent in forest ecosystems. The meteorological records of typhoon raid during past 20 years show distinct typhoon disturbance regime in different regions of Taiwan. Such heterogeneity in disturbance regime provides ideal environment for investigating the importance of typhoon disturbance in shaping the community structure of forests. Recently, various plant functional traits are widely measured for investigating the large-scale ecological questions. Functional traits are generally easy to measure and thus make extensive measurements possible. Some common traits include specific leaf area, tree height and wood density. These traits can reflect trade-offs of various strategies for the growth and survival of plants. In order to understand how typhoons influence the structure of forest ecosystem, I will compare functional traits related to wind disturbance in two Forest Dynamics Plot (FDP): one at FuShan (FS) which has frequent typhoon disturbance and the other at LienHuaChih (LHC) where typhoon disturbance is relatively infrequent. My research questions are organized into: (1) Species level: are there any differentiations of functional traits between shared species of two plots under different disturbance regimes? (2) Quadrat level: do canopy heights of two sites exhibit differentiations that reflect different level of wind disturbance? (3) Site level: is there any difference in functional composition between two different disturbance regimes? I used the importance value (IV; %) to selected the most important species for each of the two 25ha plots (each plot has 625 20 × 20m quadrates) that constitute 70% of the total IV. For each species I selected approximately 40 trees to measure crown and architectural traits (e.g. crown area, crown depth, tree height and wood density). I used Maximum Likelihood method to model the allometric relationships between different trait values. Analysis of covariance (ANCOVA), generalized least square (GLS) model and principal component analysis (PCA) were used to test whether there were trait differentiations under different disturbance regimes. The results showed: (1) At a given diameter at breast height (DBH), shared species tended to have lower tree height in FS. At a given tree height, shared species tended to have greater crown area in FS. (2) Mean canopy height in FS was significantly lower than in LHC. Canopy height was negatively correlated with convexity in FS, but positively correlated with elevation in LHC. (3) FS tended to form higher maximum tree height and slender trunk, but functional composition in LHC was more diverse than in FS. The adaptation strategies in frequently disturbed FS tended to be conservative: lower but consistent canopy height can reduce the damage from high wind blow, and wider crown area can compensate the relatively low light condition. The adaptation strategies in less frequently disturbed LHC were diverse: ranging from lower wood density with slender tree form to higher wood density with greater crown depth, shorter and thicker tree form. This research indicated intraspecific trait differentiations, variation of canopy structure and diversity of functional composition can reflect different adaptation strategies between distinct typhoon disturbance regimes.

Keywords: disturbance regimes, allometric function, forest dynamic plot, plant functional trait, functional composition

CONTENTS

INTRODUCTION

The composition and functioning of many forest ecosystems are largely shaped by their disturbance regimes (Chapin et al. 1996). For example, different type of disturbance history such as clear cut or fire, may change the moisture and temperature regimes that influence the amount of carbon released by decomposition in temperate boreal forest (Hagemann et al. 2010). The spruce beetle can infect trees and become more susceptible to damages by windblown or fire burn, then cause the outbreak of tree death (Berg et al. 2006). Anthropogenic disturbance, such as trampling, may also alter the vegetation composition and characteristics, leading to plant community with high resistance and resilience to trampling disturbance (Bernhardt-Römermann et al. 2011). In subtropical region, typhoon is an important factor that alters the forest ecosystem community composition and functioning. The strong winds and heavy rains brought by typhoon may alter the forest canopy height (de Gouvenain and Silander 2003) and the nutrient cycling (Lin et al. 2003). Recently, Lin et al. (2011) found that forest in northeastern Taiwan, perhaps due to long history of frequent typhoon disturbance, has strong resistance and fast resilience to typhoon disturbance (Lin et al. 2011). Disturbance regimes of these ecosystems are important legacies that determine the current ecosystem structure and function.

Recently, plant functional traits have been widely used to link plant population dynamics, forest community composition and ecosystem functioning (Beale et al. 2010, Cornelissen et al. 2003, Swenson and Enquist 2007, Westoby et al. 2002). Plant functional traits are used to classify plant functional groups, predict ecosystem responses to environments and infer their impacts to ecosystem processes (Díaz et al. 2007, de Bello et al. 2010), most of the traits are relatively easy to measure and thus ecological questions of broader scales can be addressed through this approach (Cornelissen et al. 2003, Schwilk and Caprio 2011). Some of the commonly used traits are specific leaf area (SLA; cm^2/g), wood density, crown area, crown depth, tree height, and seed mass . These laminose, architectural and reproductive traits can reflect the trades-off between plant growth, survival, and reproduction (Cornelissen et al. 2003, Falster and Westoby 2003, Lambers et al. 2008). For example, plants with greater SLA have faster photosynthetic rate but with lower leaf life span and are susceptible to herbivores (Reich et al. 1997). Understory shade tolerant species may have dense branches with high wood density which facilitate the formation of wider and deeper crown to increase light interception. In contrast, although tall trees can sufficiently use canopy light, their mortality can be increased due to frequent and strong wind (Aiba and Nakashizuka 2009, Sterck et al. 2006). Wood density can reflect the trade-off between structural stability versus water transport efficiency (Preston et al. 2006, Wright et al. 2006). Furthermore, wood density is also considered a proxy trait for estimating growth, mortality, and photosynthetic rate (Chao et al. 2008, Chave et al. 2009, Ishida et al. 2008, Wright et al. 2006). Plant height is an integrative trait that reflects strategies of carbon allocation, reproduction, competition against its neighbors (Moles et al. 2009). Height of plant is allometrically correlated with other plant function traits such as wood density, relative growth rate, crown area, leaf arrangement, leaf area ratio, time to reproduction and seed mass (Poorter et al. 2008). These traits determine the way plant lives, grows, and reproduce.

In ecosystem or landscape ecology, functional traits can also be used as a tool to understand the community compositions and dynamics. By quantifying the spatial distribution of functional trait values, the opposing theories of species coexistence: the environment filtering vs. niche partitioning hypotheses are also examined (Ackerly and Cornwell 2007, Kraft et al. 2008). Plant functional traits can also be used to explain the variation of ecosystem processes (Berg et al. 2006). For example, community-weighted leaf traits such as SLA, leaf dry matter content (LDMC) and leaf nitrogen content (LNC) exhibited significant correlation with aboveground net primary productivity and litter decomposition (Vesk and Westoby 2004). Recent studies use plant functional traits to map the distribution of ecosystem services on the landscape to provide the land use and conservation planning (Lavorel et al. 2011, Lytle and Merritt 2004).

Taiwan is located in Northwest Pacific Ocean, which experience more tropical cyclones (category 3 or higher on the Saffir-Simpson scale) than other regions in the world (Lin et al. 2011). There are about 3.5 typhoons per year landed on Taiwan over the past 100 years. Most of the typhoon paths followed Southeast to Northwest direction. The central Mountain Range covers more than 50% of land area in Taiwan with more than 100 peaks higher than 3000 m above sea level. It forms the barrier for major typhoon paths and, as a result, spatial heterogeneity in typhoon disturbance regimes within the land area of Taiwan is formed and can greatly influence the structure of forests (Forsyth 2006). Previous studies have shown the spatial pattern of tree damage after hurricane strike is related to site exposure to hurricane and plant height (Flynn et al. 2010, Foster and Boose 1992, Xi et al. 2008). The complicated topography in Taiwan provides an ideal environment to investigate the relationship between plant adaptation strategies and disturbance regimes.

This study used plant functional traits (tree height, first branch height, wood density, crown area, crown depth and crown length) as indicators to reveal the differentiations of plant adaptation strategies in two forest ecosystems under distinct disturbance regimes in Taiwan. I organized our questions as follows: (1) are there any differentiations of functional traits between shared species under two disturbance regimes? (2) do canopy height of two sites exhibit differentiations that reflect different levels of wind disturbance? (3) is there any difference in functional groups between two different disturbance regimes. I expected that (1) at species level: shared species in frequently disturbed forest have conservative traits such as lower tree height or shallower crown area to reduce the impact of frequently disturbed; (2) at quadrat level: canopy height is lower at frequently disturbed forest, and canopy height will accompany with topographic factors to form sheltered and protected canopy.; (3) at site level: protective and less variable traits associations should be more important in FS to reduce frequently disturbed.

METHODS

Study sites, topography and typhoon characteristics

This study was conducted at forest dynamic plots which experienced different disturbance regime in different place of Taiwan (FIGURE 1). Both plots are dominated by broad-leaved evergreen forest. Fushan forest dynamic plot (FS; 24°45'40"N, 121°33'28"E) is a 25 ha (500 × 500 m) permanent plot which located in northeastern Taiwan. The elevation in FS ranges from 600 to 733 m above sea level, the average annual temperature and precipitation are 18.2℃ and 4271 mm respectively. According to meteorological records in FS whether station (24°45'19.4"N, 121°35'45.3"E, elevation = 634 m above sea level) from 1988 to 2009, the monthly mean of maximum wind speed and solar radiation are 11.8 m/s and 300 MJ/m^2 (Appendix 1), respectively. The first and second tree censuses were completed in 2004 and 2009, respectively. Each woody plants of which diameter at breast height (DBH; cm) greater than 1 cm were tagged, mapped and DBH measured. A total of 111,851 stems comprising 110 woody species were recorded in the second census. The vegetative type in FS can be categorized as the *Machilus-Castanopsis* zone of broadleaf forests in Taiwan (Su 1984). The most dominate canopy species in FS include *Limlia uraina*, *Castanopsis cuspidata*, *Engelhardia roxburghiana, Machilus thunbergii* and *Meliosma squamulata* (McEwan et al. 2011, Su et al. 2007).

LienHuaChih forest dynamic plot (LHC; 23°54'49"N, 120°52'43"E) is located in central Taiwan. The elevation in LHC ranges from 667 to 841 m above sea level, the average annual temperature and precipitation are 21℃ and 2211 mm, respectively. According to meteorological records in LHC whether station (23°56'N, 120°54'E, elevation = 666 m above sea level) from 1969 to 2007, the monthly mean of maximum wind speed and solar radiation are 3.2 m/s and 360 MJ/m^2 (Appendix 4). The first tree census was completed in 2008. All woody plants with DBH greater than 1 cm has been tagged, mapped and DBH measured. There were 144 woody species and 153,484 stems in LHC. The vegetative type in LHC is considered to be a *Lauro-Fagaceous* zone of broadleaf forests in Taiwan (Su 1984). The most dominate canopy species in LHC include *Cryptocarya chinensis, Schefflera octophylla, Pasania nantoensis, Engelhardia roxburghiana, and Cyclobalanopsis pachyloma* (Chang et al. 2010, McEwan et al. 2011).

The measurement of four topographic variables (elevation, convexity, slope and aspect) was completed at 2004 and 2008 in FS and LHC, respectively. The elevation in each quadrat was calculated by the mean of four corners within each quadrat. The convexity was calculated by the difference between focal quadrat and eight neighboring quadrats except for the quadrats on the edge of plots (Harms et al. 2001, Valencia et al. 2004). Slope and aspect was measured by the mean angular deviation from the horizontal and vertical plane, respectively, of each of the four triangular planes by connecting three out of the four corners in one quadrat.

I used typhoon warning period officially issued by the Central Weather Bureau of Taiwan to choose the typhoons of which storm radius come across FS and LHC. Two respective weather stations closest to FS and LHC, YiLan (24º46'56"N, 121º44'53"E) and SunMoonLake (23º53'00"N, 120º54'29"E) were selected. Meteorological data when typhoon stroke between 1958 to 2011 were analyzed. The number of typhoons stroke two plots of which intensities greater than category 1 on the Saffir-Simpson scale (Simpson and Richel 1981) were 1.722 and 1.815 typhoons per year in FS and LHC, respectively. Although less typhoon strokes were found in FS than in LHC, the mean of daily rainfall and maximum wind speed during typhoon stroke were both greater in FS than in LHC (Appendix 5). The respective means of daily rainfall during typhoon strokes were 44.04 and 41.08 mm/day in FS and LHC, while the means of maximum wind speed were 16 and 10.42 m/s in FS and LHC. Thus, different typhoon disturbance regimes were found in FS and LHC.

Tree selection and traits measurement

In order to investigate forest characteristics and adaptation strategies under different disturbance regimes, I selected species that add up to top 70% accumulated Importance Value (IV) in both plots (11 and 23 species in FS and LHC, respectively). I measured tree architectural and crown traits of 40 trees for each species. Architectural traits include tree height, first branch height and wood density. Crown traits include crown area and crown depth. I used telescopic measuring pole and laser rangefinder to measure tree height (the distance from the ground to the top leaf), first branch height (the height of first branch which diameter greater than 1cm and above ground than 1.3m) and the height of the lowest leaf. The height of the lowest leaf was used to further calculate the crown depth by the difference between tree height and lowest leaf height. The procedures for measuring wood density followed CTFS wood density protocol (http://www.ctfs.si.edu/data///documents/Wood_density_draft.pdf). I randomly selected 5 stems of each species then use increment borers to extract the wood cores. I used water displacement method to measure fresh wood volume, later I oven-dried the wood cores to constant weight at 80°C. The wood density was calculated by the dry weight divided by wood volume then weighted by wood segments length. The Crown area was determined by measuring the crown radii of 4 principal directions (north, east south and west). The north-south (d_1) and east-west (d_2) directions of projected crown length was used to calculate crown area by $0.25\,\pi\,d_1d_2$ (Poorter et al. 2006).

The analytical procedures for establishing of trait allometric relationships

The DBH-height relationship has been identified as asymptote (Poorter et al. 2006). In order to know whether there is trait differentiation under different disturbance regimes, I used maximum likelihood method (Goffe et al. 1994) to fit the allometric function of DBH and tree height (TH). I used the following function to fit the DBH-TH allometric relationship (Poorter et al. 2006),

$$H = H_{max} \times (1 - \log_e(-a \times DBH^b)) \ldots \text{ eqn 1}$$

where H is tree height, DBH is tree diameter at breast height, H_{max} is the modeled maximum tree height, variables a and b are parameters derived by model fitting procedure. After fitting species-specific DBH-TH allometric relationship, slenderness (SLD) of each species was defined as the tree height at DBH = 15 cm (Aiba and Nakashizuka 2009). Topographic factors, especially convexity, influence vegetative type and canopy height very well (Noguchi 1992, Su et al. 2010). In order to estimate the canopy height precisely, the allometric functions were developed separately for concave and convex quadrats. Species-specific and topography specific allometric functions were used to estimate the tree height of each individual stems of selected species under specific topography (convex or concave quadrate). The mean of 5 tallest trees of selected species in each quadrat was calculated to represent the canopy height of each quadrat in both plots. Quadrat-based canopy height was used to test whether the spatial pattern of canopy height can reflect the functional adaptation of plants under different disturbance regimes.

The fitting of TH-crown area (CA) allometric relationship was based on a power function: $CA = aH^b$. CA and H denote crown area (m^2) and tree height (m), respectively. Parameters a and b are species-specific constants derived from model fitting procedure. After fitting species-specific tree height-crown area allometric relationship, I defined the crown area at TH = 10 m as a species-specific and size-corrected traits (CA_{10}) for further analysis. The fitting of TH to first branch height (FBH) and crown depth (CD) were both based on a linear function: FBH (and CD) = aH+b. Parameters a and b are species-specific fitting constants. I also defined standardized FBH and CD at TH = 10 m (FBH_{10} and CD_{10}, respectively) of each species for further analysis.

Statistical analysis

I compared the species-specific allometric functions of shared species in two plots to test whether there was trait differentiation of the same species under two different disturbance regimes. To test whether there were significant differences in tree height-DBH function and crown area-DBH function, variables were log-transformed to approach linearity. Analysis of Covariance (ANCOVA) was then used to test the effects of DBH, site, and DBH × site interaction. The correlation between functional traits and topographic factors (elevation, slope, aspect, and convexity) were tested using Generalize Least Squares (GLS) model based on exponential method to account for spatial autocorrelation (Pinheiro and Bates 2000). For analyses at the site level, I used Principal Component Analysis (PCA) to investigate the trait associations, and Analysis of Similarities (ANOSIM) to test whether the functional compositions were different in two plots. Five functional traits for each individual species, including: H_{max}, tree height corrected crown area (CA_{10}), tree height corrected crown depth (CD_{10}), wood density (each species we calculated mean wood density of 5 stems as species-specific wood density; WD) and slenderness (height at DBH = 15cm; SLD) were incorporated in PCA and ANOSIM. All statistical analyses above were performed using R program (R version 2.10.1; R Development Core Team 2009).

RESULTS

Allometry

The allometric relationship in DBH-tree height was well-fitted in FS (R^2 ranged from 0.75 to 0.94; median = 0.84) and LHC (R^2 ranged from 0.44 to 0.96; median = 0.85). This gives a reliable prediction in tree slenderness and H_{max}. Tree slenderness (SLD) ranged from 8.5 (*Schefflera octophylla*) to 14.6 m (*Machilus zuihoensis var. mushaensis*) in FS and from 9.1 (*Syzygium buxifolium*) to 14.1 m (*Mallotus paniculatus*) in LHC (shrub species, including *Blastus cochinchinensis*, *Psychotria rubra* and *Euonymus laxiflorus* were not include in the analysis). H_{max} ranged from 10.8 (*Helicia formosana*) to 23 (*Machilus thunbergii*) m in FS and from 4.6 (*Pasania konishii*) to 23.2 (*Schefflera octophylla*) m in LHC.

The fitting results in tree height-crown area, tree height-first branch height and tree height-crown depth relationships were quite variable. The results of tree height-crown height allometric relationship in FS (R^2 range from 0.31 to 0.93; median = 0.63) and LHC (R^2 range from 0.06 to 0.96; median = 0.56) are quite variable. The crown area at tree height = 10 m ranged from 16.4 (*Helicia formosana*) to 30 (*Litsea acuminata*) m^2 in FS and from 4.8 (*Tricalysia dubia*) to 29 m^2 in LHC (*Pasania nantoensis*).The results of tree height-first branch height allometric relationship in FS (R^2 range from 0.33 to 0.91; median = 0.67) and LHC (R^2 range from 0.11 to 0.9; median = 0.58) were quite variable. The first branch height at tree height = 10 m ranged from 3.6 (*Limlia uraiana*) to 5.4 m (*Pyrenaria shinkoensis*) in FS and from 2.6 (*Helicia formosana*) to 5.3 m (*Ardisia quinquegona*) in LHC. The results of tree height-crown depth allometric relationship in FS (R^2 range from 0.04 to 0.85; median = 0.72) and LHC (R^2 range from 0.49 to 0.91; median = 0.71) were also variable. The crown depth at tree height = 10 m ranged from 4.0 (*Machilus zuihoensis* var. *mushaensis*) to 6.1 (*Helicia formosana*) m in FS and from 3.9 (*Ardisia quinquegona*) to 7.1 (*Helicia formosana*) m in LHC.

Species level: comparison of plant functional traits between two plots

We found some trait differentiations of shared species between two plots.

For the overall ANCOVA model of which all species were pooled, DBH vs. tree height and tree height vs. crown area were log-transformed to attain linearity (TABLE 1). The allometric relationship of traits between shared species in two plots showed that species in FS tend to have lower tree height, wider crown area, lower first branch height and shallower crown depth than in LHC (FIGURE 2A). Among four allometric relationships, the interaction effect of ln(DBH) × plot and ln(tree height) × plot can significantly explain the variation of tree height and crown area between two plots. Take one shared species, *Schefflera octophylla*, as example, in DBH-tree height relationship, we found at a given DBH, tree height is greater in LHC than in FS (FIGURE 3A). For the analysis separated by species, three of seven shared species (*Limlia uraiana*, *Litsea acuminata* and *Schefflera octophylla*) showed significant plot × ln(DBH) interaction effect, which indicated significantly different slope of the allometric equation between two plots (TABLE 2).

For the analysis separated by species in tree height-crown area relationship, none of the selected species showed significant effect (TABLE 2). Nevertheless, take *Limlia uraiana* species as example, we still found a tendency that at a given tree height, crown area is greater in FS than LHC (FIGURE 3B). In TH-FBH relationship, the only significant plot × tree height interaction effect was found in *Schefflera octophylla* species (TABLE 2). At a given tree height of *Schefflera octophylla*, the first branch height tended to be greater in FS than in LHC (FIGURE 3C). In tree height-crown depth relationship, none of the selected species exhibited significant differentiation between plots. Nevertheless, two species, *Limlia uraiana* and *Castanopsis cuspidata*, exhibited marginally significant plot × tree height interaction and plot effect, respectively. Take *Castanopsis cuspidate* species as example, we found at a given tree height, crown depth was slightly shallower in FS than in LHC (FIGURE 3D).

We found two of seven shared species (*Schefflera octophylla* and *Helicia formosana*) have significantly greater wood density in LHC than in FS (Wilcoxon rank sum test, $P = 0.007$ in both species; FIGURE 4).

Quadrat level: the spatial patterns of quadrat-based canopy height in two plots

We found a distinct spatial pattern of canopy height in FS. The canopy height in FS was lower at the ridge top than in other flat or quadrats which located in low elevation (FIGURE 5A); however this pattern was not found in LHC. Canopy height was lower in two of the valleys but higher at the upper slopes near the ridge tops in LHC (FIGURE 5B). We also found mean canopy height in LHC tended to be higher than in FS (Wilcoxon rank sum test, $P = 0.0001$; FIGURE 5C), and the variation of canopy height in two plots can be explained by different topographic factors. Canopy height was negatively correlated with elevation in FS ($P = 0.001$; TABLE 3 & FIGURE 6A), but was negatively correlated with convexity ($P = 0.002$; TABLE 3 & FIGURE 6B) and positively correlated with slope in LHC ($P = 0.024$; TABLE 3 & FIGURE 6C).

Site level: patterns of functional composition in two plots

The PCA results reveal the different functional compositions in two plots (FIGURE 7). Most of species in FS tended to have greater crown area accompanied by stout tree form and lower wood density. Two exceptions were found in *Machilus zuihoensis* var. *mushaensis* and *Helicia formosana*. The former had slender stem with great H_{max} and the later had deep crown, high wood density, accompanied with stout tree form. The functional compositions in LHC are more diverse than in FS (FIGURE 7). The functional compositions comprise traits characteristic of both pioneer and shade tolerant species: one group of species tend to have greater H_{max} and slender tree form, some species tend to have greater wood density accompany with greater crown depth And other species in middle part of PCA plot didn't show a clear trait association. The result of ANOSIM test also indicates that the functional composition between two plots are significantly different (ANOSIM test, $P = 0.002$).

DISCUSSION

Species level: the intraspecific trait differentiations between two plots

We found shared species in FS tend to have lower tree height, greater crown area, higher first branch height and shallower crown depth than in LHC. In DBH-tree height relationship, we found 3 of 7 shared species (*Limlia uraiana*, *Litsea acuminata*, *Schefflera octophylla*) in FS had lower tree height at greater DBH. Numerous studies indicate that tree height is negatively correlated with wind speed (Chao et al. 2010, Chen et al. 1997). Results of this study are consistent with the previous studies from which tree heights were found to be lower in forests with frequent wind disturbance (Martin and Ogden 2006). Lower tree height is beneficial for trees at areas with frequent wind disturbance in reducing the risk of bole snap, uprooting, branch damage, and so on. In tree height-crown area relationship, none of shared species showed the differentiation of crown area between two plots. In overall ANCOVA model, shared species in FS tended to have greater crown area than in LHC. This unexpected result can be explained by a relatively consistent and low canopy height in FS that trees can shelter each other. In addition, greater crown area can compensate the relatively low incident solar radiation (monthly mean = 300 MJ/m^2 in FS and 360 MJ/m^2 in LHC, respectively). In tree height-first branch height relationship, only *Schefflera octophylla* in FS have greater first branch height at greater tree height, but neither interaction nor plot effect was detected in overall ANCOVA model. Greater first branch height, together with orthotropic growth form, larger leaves and longer petioles, are thought to be an indicator for adaptation for low light condition (King 1998). Trees of the same species in FS where light availability is relatively low tend to have greater first branch height. In overall tree height-crown depth relationship, none of shared species showed the differentiation of crown depth between two plots. Shared species in FS tended to have shallower crown depth, but this differentiation was not significant in overall ANCOVA model. Shallower crown depth is thought to be an adaptation for plants to avoid self-shading that can ensure sufficient light interception in a dim forest (Aiba and Nakashizuka 2009, Poorter et al. 2006).

Wood density was found to be negatively correlated with annual precipitation and soil fertility (Swenson and Enquist 2007, ter Steege et al. 2006). In this study, two of seven shared species (*Schefflera octophylla* and *Helicia formosana*) had greater wood density in LHC than in FS. This pattern might be explained by annual precipitation and soil fertility because both annual precipitation and soil fertility were lower in LHC than in FS, (Liao 2006, Lin 2010).

Quadrat level: the spatial pattern of canopy height can reflect the conditions in wind exposure

The results in quadrat level were consistent with our expectation. Typhoon occurrence is found to be negatively correlated with canopy height in a global analysis (de Gouvenain and Silander 2003). This perhaps explains why the mean canopy height is lower in severely disturbed FS forest than gently disturbed LHC forest. Numerous studies indicate that tree height is influenced by high wind blow, especially for canopy trees which have great risk in bole snap, branch damage and uprooting due to wind blow (Brokaw and Grear 1991, Martin and Ogden 2006, Peterson 2000, Peterson and Rebertus 1997, Webb 1958). According to my analysis of the meteorological records, the mean of maximum wind speed in FS and LHC are 11.8 and 3.2 m/s, respectively. The lower canopy height in FS compared to LHC was likely influenced by higher mean of maximum wind speed. In addition to the difference of canopy height, we also found different spatial pattern of canopy height between two plots. Canopy height was negatively correlated with elevation in FS. This suggests higher canopy in low elevation quadrats but lower in exposed ridge quadrats in FS. This result is consistent with the general findings that lower tree height may be an adaptive consequence to avoid the damage from frequent wind blow (Chao et al. 2010, Forsyth 2006, Jaffe 1973, King et al. 2009, Lawton 1982, Martin and Ogden 2006).

In LHC, canopy height was negatively correlated with convexity but positively correlated with slope. This suggests greater canopy height in protective concave and/or steep quadrats. The topography-driven floristic composition (Chang, unpublished data) in LHC might have resulted in the spatial pattern of the forest structure. Vegetative type at the side of ridge top with steep and concave topography was grouped to *Schellefra octophylla-Cryptocarya chinensis* type, which is regarded as a pioneer-dominant vegetative type.and greater canopy height was found. Although vegetative type at the ridge top is grouped to wind-resistant *Syzygium buxifolium* - *Pasania nantoensis* type, GLS result did not show a positively correlated pattern between canopy height and elevation. Vegetation types in valleys are variable and grouped as *Machilus kusanoi*

- *Cryptocarya chinensis* - *Neolitsea konishii* or *Schellefra octophylla-Cryptocarya chinensis-Cinnamomum subavenium-Tricalysia dubia* in LHC. Canopy height did not show a clear pattern in valleys: two of the valleys show a pattern that canopy height was positively correlated with convexity (in southwest and northwest valleys); but in other valleys canopy height was positively correlated with convexity (e.g. northeast and southeast valleys). Rainfall with high intensity in LHC may have led to frequent tree damage and recruitment in the valleys (Chang, unpublished data). The low canopy height at some valleys of LHC can be caused by the frequent setting back of the vegetation succession due to frequent small-scale landslides. Together, the ambiguous spatial pattern of canopy height in LHC need more research to reveal complex interactions between canopy height, topography and disturbance.

Site level: different functional compositions may reflect different adaptation strategies under different disturbance regimes

PCA and ANOSIM results indicate that trait associations were different between FS and LHC. Most of the species in FS (8 of 10) tended to have greater crown area, shallower crown depth and lower wood density accompany with stout tree form and greater H_{max}. In order to be well adapted to the wet, humid, high wind blow and low-light conditions of the FS forest, species expand their crown horizontally rather than vertically to increase light interception rate and avoid self-shading. This finding is consistent with previous studies that species live in a low light condition tend to form single layer of tree crown to increase light interception without the risk of self-shading (Horn 1971, Poorter 1999). Stout tree forms, lower canopy height while accompanied with greater H_{max} can increase tree survival under high wind blow. A pioneer species *Machilus zuihoensis* var. *mushaensis* with slender tree form and greater H_{max} and *Helicia formosana* with greater wood density and crown depth accompanied with stout tree form were also well adapted in FS. These two species were widespread in a wet, humid and foggy environment. The generalist habits of the two species may contribute to the possession of traits not fully consistent with other coexisting species.

The trait associations in LHC were more diverse than in FS. Functional trait associations ranged from fast growing pioneer species to slow growing shade tolerant species. Pioneer species in LHC such as *Mallotus* *paniculatus*, *Cinnamomum subavenium* and *Schima superba* have low wood density that facilitates fast growth to reach the top of canopy, hence pioneer species in LHC have slender tree form with great H_{max}. Shade tolerant species such as *Tricalysia dubia*, *Pasania konishii* and *Syzygium buxifolium* have high wood density accompanied with deep crown can increase the light interception in understory. Denser wood is associated with lower growth rate (Chave et al. 2009), hence shade tolerant species with greater wood density and crown depth have stout tree form.

The possibility of monsoon effect

Besides the stochastic wind blow caused by typhoon disturbance, chronic and predictable wind blow from northeastern monsoon can potentially affect forest structures in Taiwan. For example, the vegetation at the Kenting dynamic plot in southern Taiwan is characterized by short and dense stems (Wang et al. 2004) . Although this study contains only two sites from which the determination of the wind disturbance modes (typhoon vs. monsoon) cannot be made, the seasonal patterns of litterfall can perhaps imply their relative importance in affecting the canopy structure. In Kenting plot, a distinct peak of litterfall was found in winter when northeastern monsoon was prevailing (Liao et al. 2006). FS is located in northeastern Taiwan, which experience typhoon disturbance in summer and constant wind blow from northeastern monsoon in winter. The seasonal pattern of litterfall in FS did not show a distinct peak in winter (Lin 2009), Indicating relatively limited impact of monsoon in shaping the canopy structure in FS. In LHC, neither summer nor winter exhibited peaks of litterfall (Chiang and Lin unpublished data), indicating insignificant effect of wind disturbance from typhoons and monsoon.

CONCLUSION

We suggest the difference of plant functional composition between two plots may reflect different adaptation strategies under distinct typhoon disturbance regime. Functional composition is simple in severely disturbed FS where species tend to form lower tree height and consistent canopy height. In order to compensate the light interception, species form wider but shallower crown to increase light interception without self-shading. Due to lower and consistent canopy height, trees would shelter each other to avoid the damage from high wind blow. The greater potential tree height (H_{max}) of species in FS also indicates that squatter tree form and wider but shallower crown might imply structural adaptation for in frequently disturbed forest.

LHC forest experienced different disturbance regimes from FS. Unlike FS, the spatial pattern of canopy height in LHC show a ambiguous pattern that canopy height was higher in most of the concave quadrats but lower in two of the valleys. Unlike FS where strong winds may have caused the under-dispersion of function traits, more diverse functional composition, consisting both pioneer species (lower wood density and crown area with slender tree form) and shade tolerant species (greater wood density and crown area with stout tree form) were found in LHC. It is unlikely that the relatively mild wind disturbance experienced in LHC had strong effects on trait dispersion.

In this study, we demonstrated complex interactions between functional traits, topography, and disturbance regimes. Much uncertainty remains and can potentially be reduced by incorporating more functional traits, such as leaf traits, vessel area, vessel density, regeneration traits (e.g. seed mass, seed number), and demography data, and more abiotic factors such as soil water content, organic carbon. Such comprehensive dataset will be required to achieve mechanistic understandings of plant adaptation strategies under heterogeneous and frequently disturbed environment.

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FIGURES

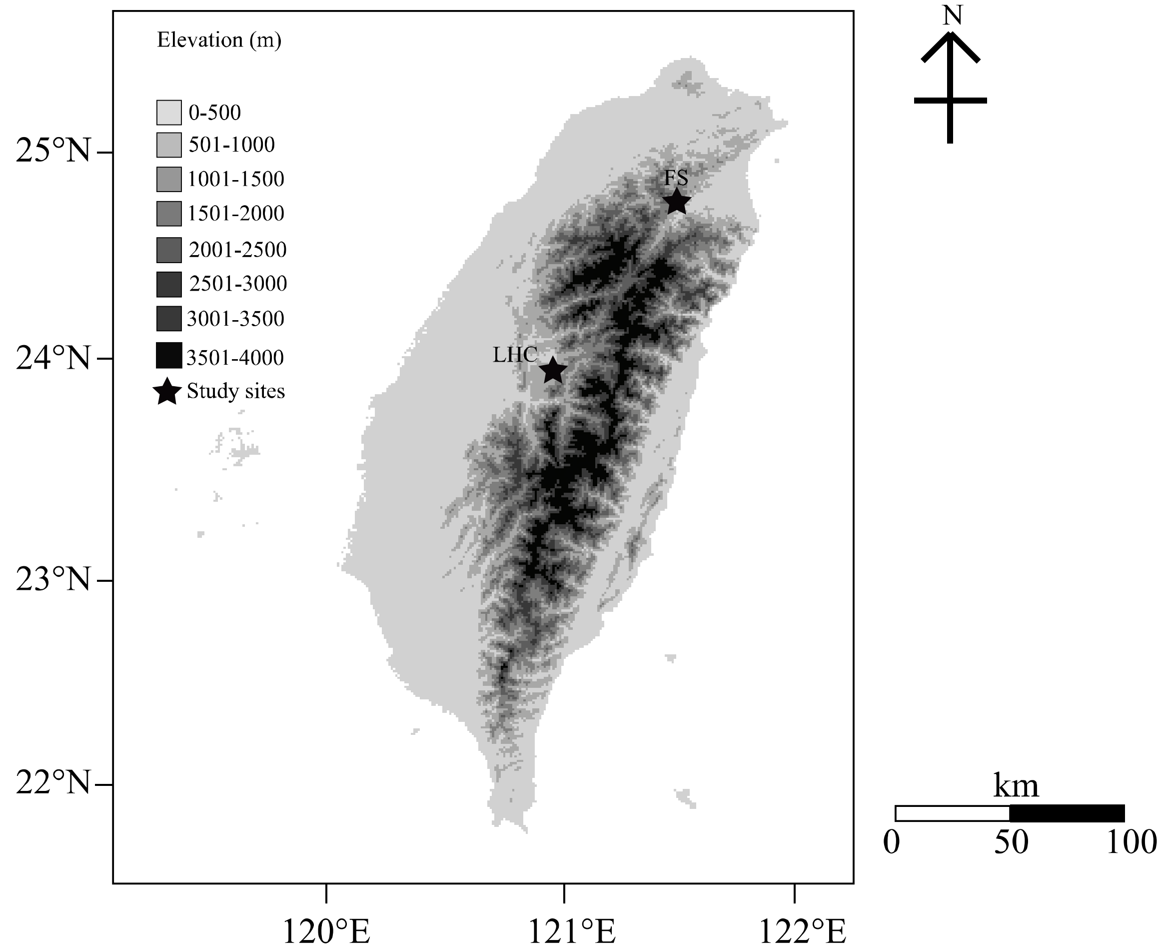


FIGURE 1. The location of Fushan (FS) and Lienhuachih (LHC) in Taiwan.

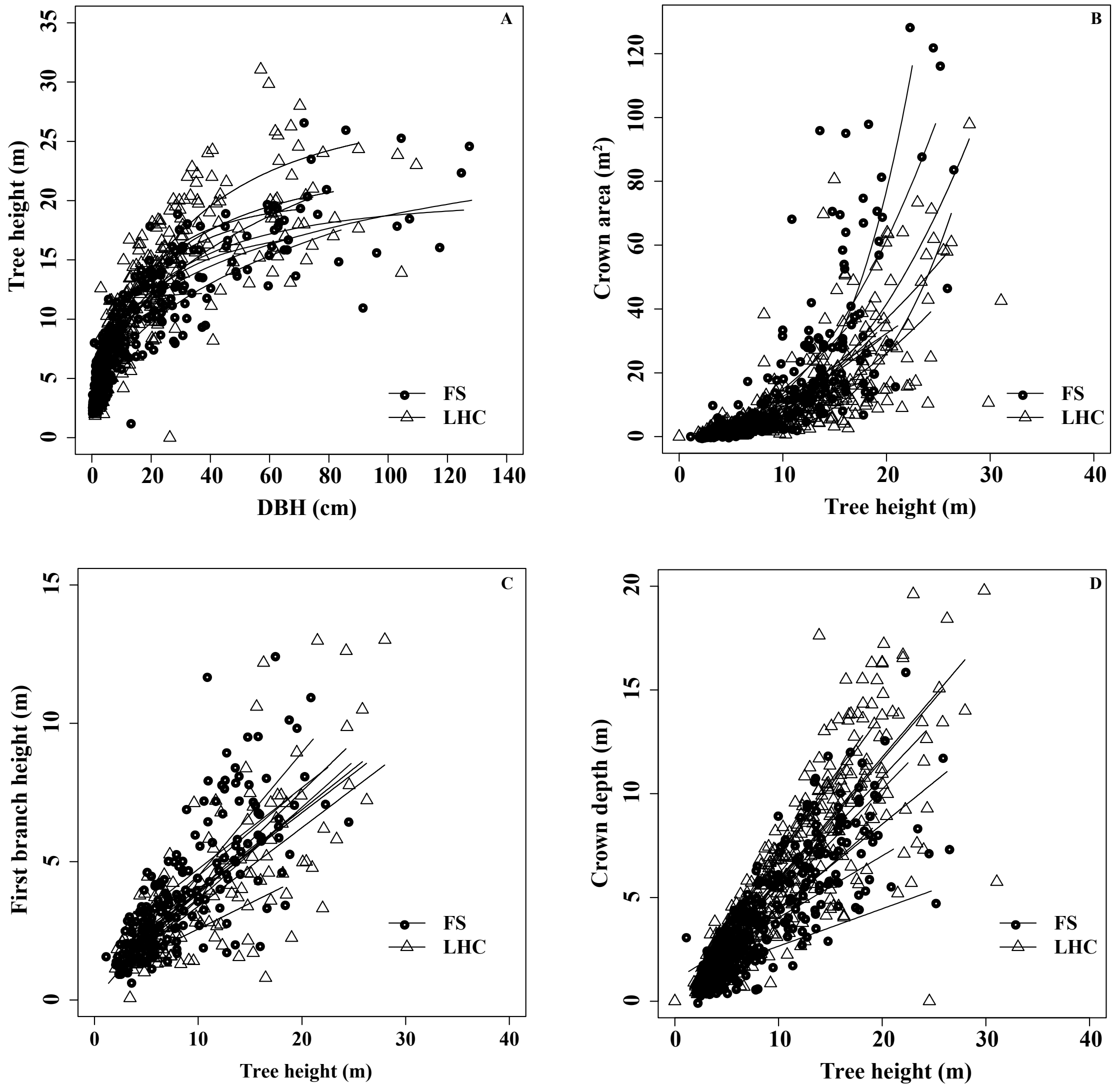


FIGURE 2. The allometric relationship of traits between shared species in two plots.

Circles and triangles indicate species in FS and LHC. Each line represents each species' allometric functions between DBH and tree height (A), tree height and crown area (B), first branch height (C) and crown depth (D) in FS (solid line) and LHC (dashed line).

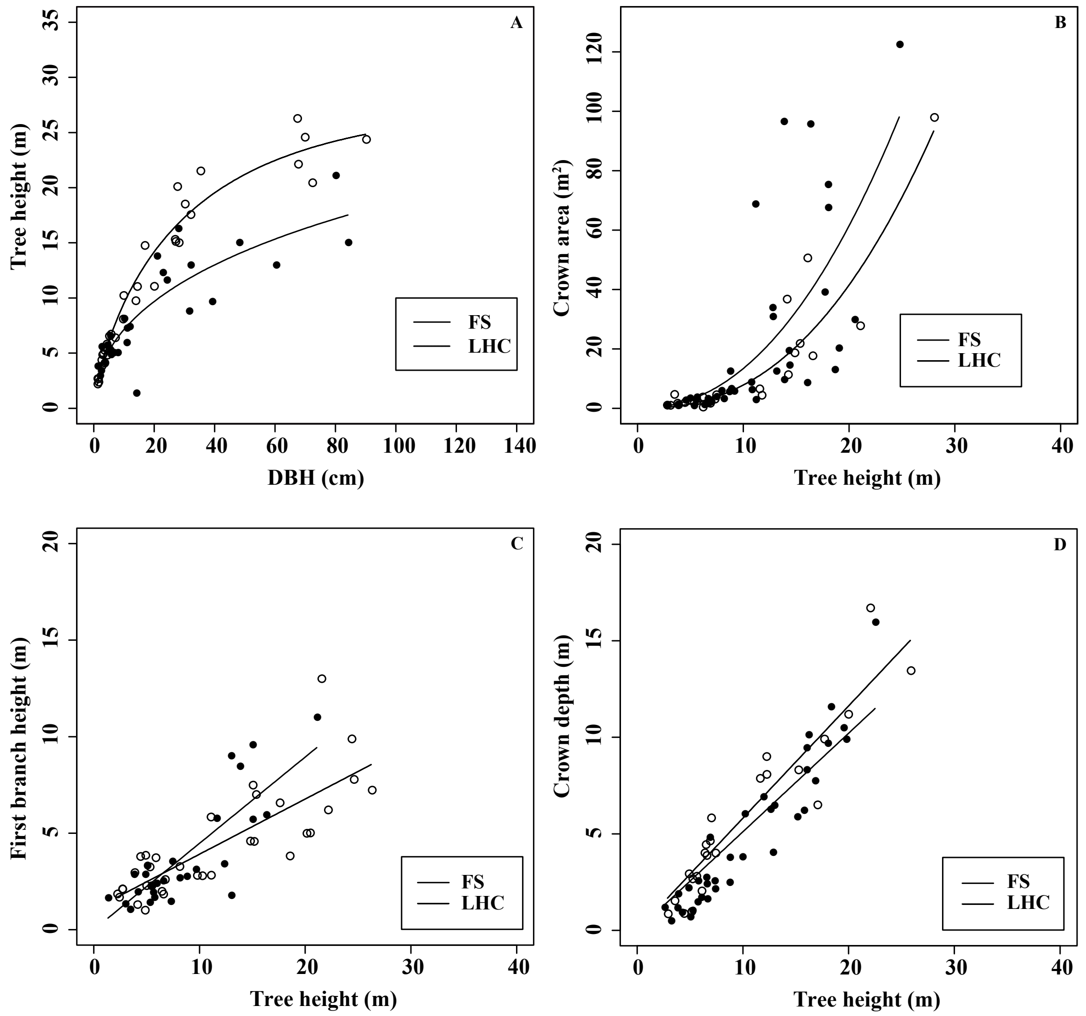


FIGURE 3. The allometric relationship of traits between shared species in two plots.

Solid and open circles are data in FS and LHC, the lines indicate the allometric equation fitted by maximum likelihood method. (A) The relationship between DBH and tree height of *Schefflera octophylla* in FS and LHC. R^2 is 0.75 in FS and 0.96 in LHC (B) The relationship between tree height and crown area of *Limlia uraiana* in FS and LHC. R^2 is 0.48 in FS and 0.85 in LHC. (C) The relationship between tree height and first branch height (FBH) of *Schefflera octophylla* in FS and LHC. R^2 is 0.68 in FS and 0.65 in LHC. (D) The relationship between tree height and crown depth of *Castanopsis cuspidata* in FS and LHC. R^2 is 0.85 in FS and 0.87 in LHC.

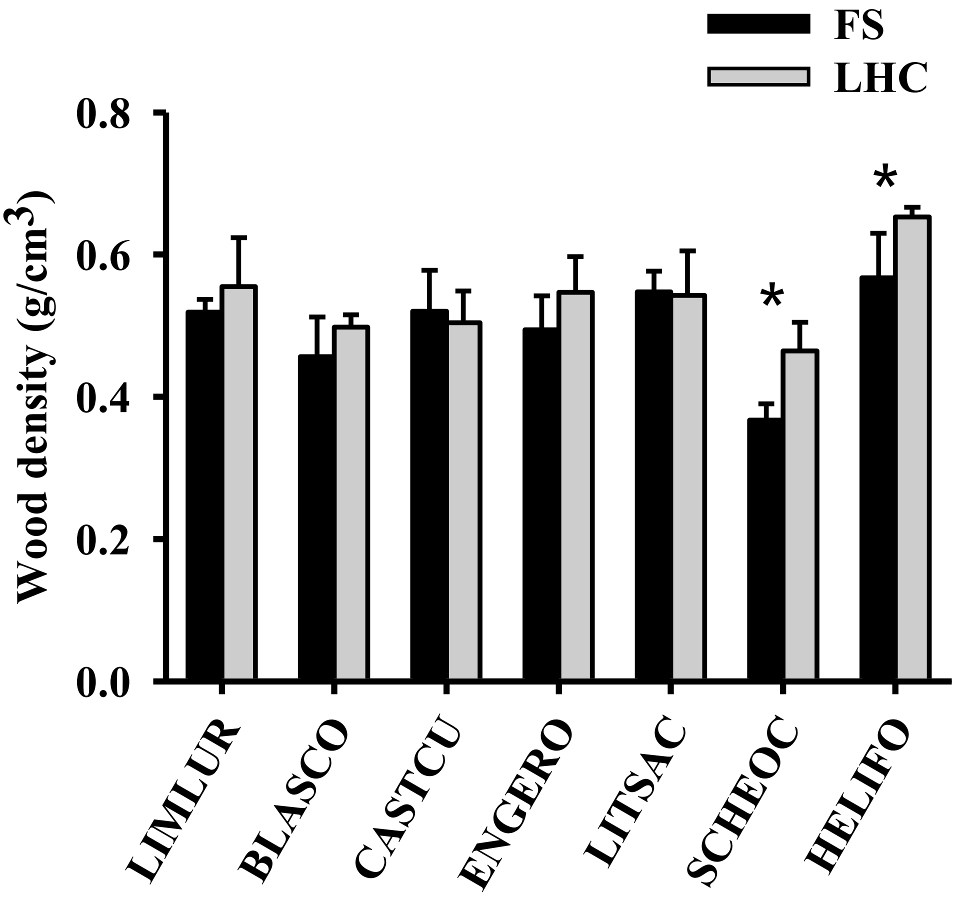


FIGURE 4. The barplot of wood density in two plots.

Species in FS and LHC are represented with black and white bar respectively. Species abbreviation showed in Appendix 1. The bar showed the mean ± 1 SD. The asterisk showed the significant difference (Wilcoxon rank sum test, $P = 0.007$ both in SCHEOC and HELIFO).

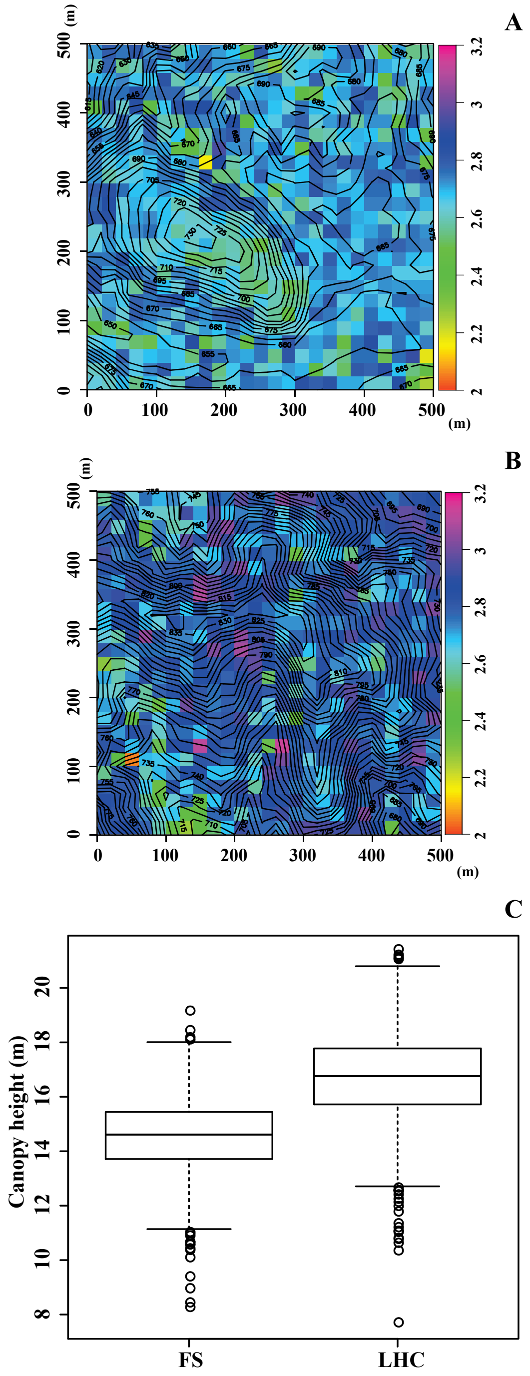


FIGURE 5. Spatial distribution of canopy height in FS and LHC. The size of each pixel is at 20 by 20 meters. Canopy height were both log transformed in FS (A) and LHC (B). The boxplot of quadrat-based canopy height in FS and LHC (n = 625 quadrats for each plots) is shown in (C).

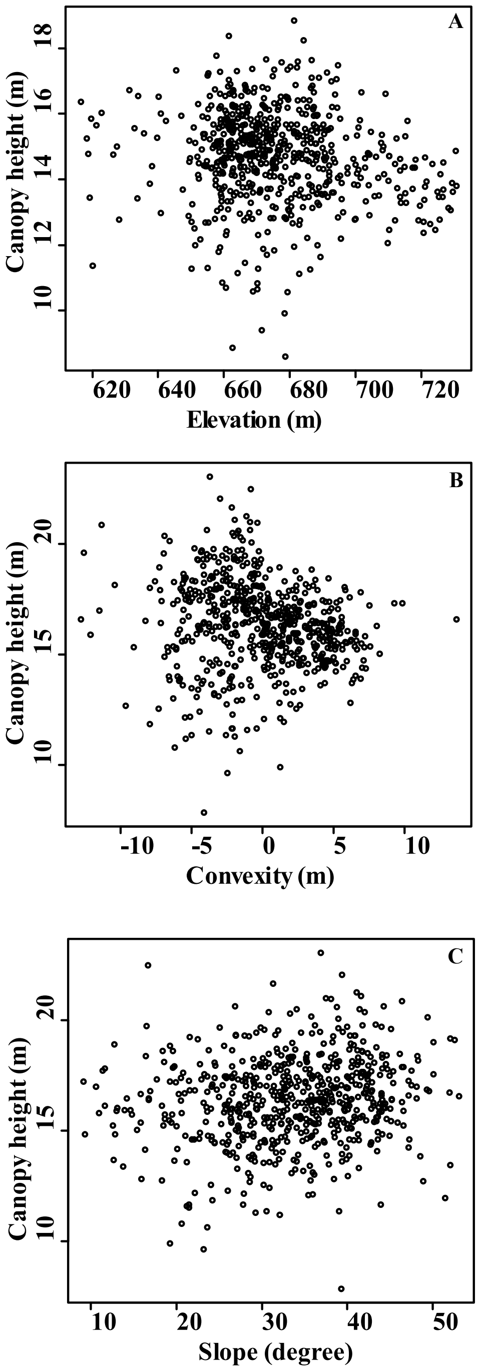


FIGURE 6. The scatter plot between canopy height and elevation in FS (A). The relationship between canopy height, convexity and slope in LHC were drawn in (B) and (C).

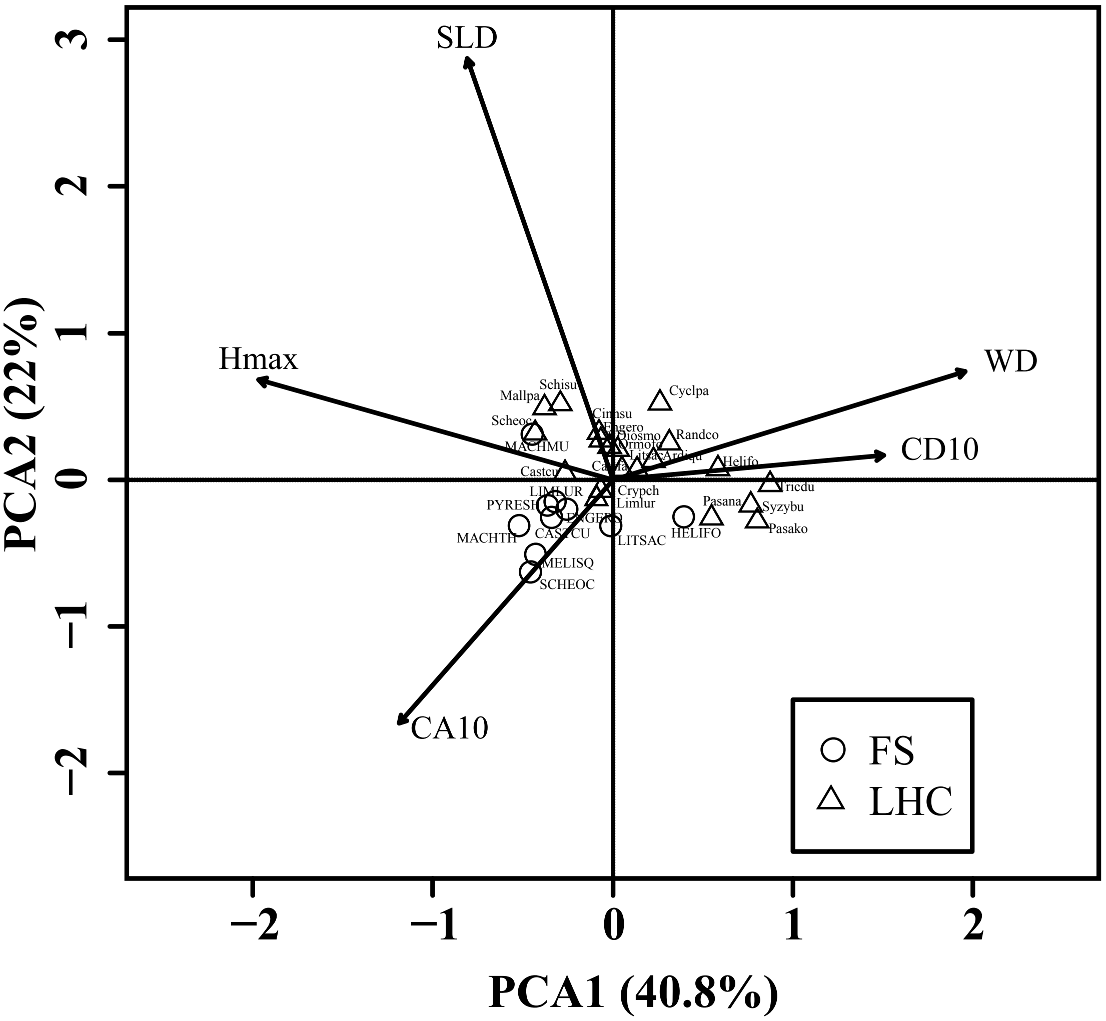


FIGURE 7. The PCA result of functional composition in two plots. Circle and triangle indicate species in FS and LHC. Shrub species (BLASCO in FS; Blasco, Euonla, and Psycru in LHC) were removed in this analysis. Abbreviations: SLD, slenderness; H_{max}, maximum tree height; CA_{10}, crown area at tree height = 10 m; WD, wood density; CD_{10}, crown depth at tree height = 10 m. The abbreviations of species names are shown in Appendix 1.

TABLES

TABLE 1. Four allometric relationships of shared species under ANCOVA model between two plots.

The numbers represent the parameter estimate value of trait effect (DBH to TH; TH to CA, FBH and CD), plot effect (FS and LHC) and interaction between trait and plot. Asterisks represent: *, P < 0.05; **, P < 0.01; ***, P < 0.001. Marginally significant effect is code as $^{\#}$.

	DBH VS TH	TH VS CA	TH VS FBH	TH VS CD
trait	**0.4078*** **	**2.0784*** **	**0.3564*** **	**0.4932*** **
plot	-0.0934$^{\#}$	0.3325	-0.2539	0.3929
interaction	**0.0842*** **	**-0.2761* **	-0.0459	0.0464

DBH: diameter at breast height (cm); TH: tree height (m); CA: crown area (m^2); FBH: first branch height (m); CD: crown depth (m). *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$. $^{\#}$: marginally significant.

TABLE 2. Species specific allometric relationships between DBH vs. TH, TH vs. CA, TH vs. FBH, and TH vs. CD.

ANCOVA model were used to test whether there is trait differentiation between two plots. The number represents the estimated value of plot effect and interactions. Species abbreviations are: LIMLUR, *Limlia uraiana*; BLASCO, *Blastus cochinchinensis*; CASTCU, *Castanopsis cuspidata*; ENGERO, *Engelhardia roxburghiana*; LITSAC, *Litsea acuminata*; SCHEOC, *Schefflera octophylla*; HELIFO, *Helicia formosana*.

Species		DBH VS TH	TH VS CA	TH VS FBH	TH VS CD
LIMLUR	plot effect	**-0.259***	0.819	-1.261	-0.108
	interaction	**0.095***	-0.422	-0.014	$0.148^{\#}$
BLASCO	plot effect	0.259	-0.384	0.927	-1.115
	interaction	-0.021	0.267	-0.168	0.409
CASTCU	plot effect	0.009	$0.985^{\#}$	-0.877	$1.383^{\#}$
	interaction	0.034	$-0.476^{\#}$	0.004	-0.034
ENGERO	plot effect	0.002	0.126	-0.964	0.547
	interaction	0.047	-0.230	0.041	0.063
LITSAC	plot effect	$-0.208^{\#}$	0.529	-0.403	-0.009
	interaction	**0.116***	-0.399	0.022	0.092
SCHEOC	plot effect	-0.086	-0.079	1.275	-0.604
	interaction	**0.149***	-0.121	**-0.181***	0.106
HELIFO	plot effect	0.061	-0.253	0.184	0.068
	interaction	-0.017	0.123	$-0.129^{\#}$	0.047

*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$. $^{\#}$: marginally significant.

TABLE 3. The GLS models of canopy height in FS and LHC plots.

	Value	S.D.	t-value	*P*-value
FS				
Elevation	-0.013	0.004	-3.161	**0.001**
Convexity	0.043	0.030	1.433	0.152
Slope	0.007	0.006	1.218	0.223
Aspect	0.342	0.427	0.799	0.424
LHC				
Elevation	0.003	0.004	0.700	0.484
Convexity	-0.084	0.027	-3.038	**0.002**
Slope	0.024	0.010	2.250	**0.024**
Aspect	-0.319	0.535	-0.595	0.551

APPENDIX

Appendix 1. The growth forms and importance values (IV) of selected species in this study. The capital code means the shared species in two plots.

Site	**Code**	**Scientific name**	**Growth form**	**IV**
FS	LIMLUR	*Limlia uraiana*	Canopy	15.1068
	HELIFO	*Helicia formosana*	Subcanopy	11.7071
	BLASCO	*Blastus cochinchinensis*	Shrub	7.7920
	CASTCU	*Castanopsis cuspidata*	Canopy	6.9355
	ENGERO	*Engelhardia roxburghiana*	Canopy	5.6907
	Machth	*Machilus thunbergii*	Canopy	4.6156
	Melisq	*Meliosma squamulata*	Canopy	4.5751
	Pyresh	*Pyrenaria shinkoensis*	Subcanopy	4.3470
	LITSAC	*Litsea acuminata*	Canopy	3.8337
	Machmu	*Machilus zuihoensis* var. *mushaensis*	Canopy	3.5029
	SCHEOC	*Schefflera octophylla*	Canopy	2.3480
LHC	Randco	*Randia cochinchinensis*	Subcanopy	7.1353
	Crypch	*Cryptocarya chinensis*	Canopy	5.5194
	BLASCO	*Blastus cochinchinensis*	Shrub	5.3712
	SCHEOC	*Schefflera octophylla*	Canopy	5.1807
	Pasana	*Pasania nantoensis*	Canopy	4.7689
	ENGERO	*Engelhardia roxburghiana*	Canopy	4.6483
	Cyclpa	*Cyclobalanopsis pachyloma*	Canopy	3.2339
	Cinnsu	*Cinnamomum subavenium*	Canopy	3.1085
	HELIFO	*Helicia formosana*	Subcanopy	3.1076
	Diosmo	*Diospyros morrisiana*	Subcanopy	2.8816
	Tricdu	*Tricalysia dubia*	Subcanopy	2.7813
	Schisu	*Schima superba*	Canopy	2.7808

	Mallpa	*Mallotus paniculatus*	Canopy	2.7774
	Psycru	*Psychotria rubra*	Shrub	2.6718
	Euonla	*Euonymus laxiflorus*	Shrub	2.5876
	Syzybu	*Syzygium buxifolium*	Subcanopy	2.4212
	Castfa	*Castanopsis fargesii*	Canopy	2.3530
	Ardiqu	*Ardisia quinquegona*	Shrub	2.0910
	Pasako	*Pasania konishii*	Subcanopy	1.9231
	Ormofo	*Ormosia formosana*	Canopy	1.9113
	LIMLUR	*Limlia uraiana*	Subcanopy	1.0715
	CASTCU	*Castanopsis cuspidata*	Canopy	1.1809
	LITSAC	*Litsea acuminata*	Canopy	1.4298

Appendix 2. The fitting R^2 of allometric functions in two plots.

Site	**Code**	**DBH - Tree Height**	**Tree Height - Crown Area**	**Tree Height - First Branch Height**	**Tree Heigh - Crown Depth**
FS	**BLASCO**	0.78	0.31	0.33	0.04
	CASTCU	0.9	0.82	0.59	0.85
	ENGERO	0.87	0.78	0.5	0.78
	HELIFO	0.78	0.56	0.55	0.8
	LIMLUR	0.82	0.48	0.35	0.63
	LITSAC	0.83	0.57	0.67	0.79
	Machmu	0.84	0.64	0.71	0.64
	Machth	0.85	0.75	0.74	0.68
	Melisq	0.92	0.93	0.82	0.81
	Pyresh	0.94	0.63	0.91	0.72
	SCHEOC	0.75	0.39	0.68	0.49
	mean	0.843636	0.623636	0.622727	0.657273
	minimum	0.75	0.31	0.33	0.04
	maximum	0.94	0.93	0.91	0.85
	median	0.84	0.63	0.67	0.72
LHC					
	Ardiqu	0.93	0.96	0.9	0.62
	BLASCO	0.44	0.06	0.11	0.72
	CASTCU	0.84	0.76	0.66	0.87
	Castfa	0.89	0.54	0.48	0.83
	Cinnsu	0.92	0.65	0.72	0.73
	Crypch	0.88	0.83	0.82	0.88
	Cyclpa	0.89	0.6	0.61	0.88
	Diosmo	0.76	0.54	0.27	0.74
	ENGERO	0.87	0.59	0.48	0.61
	Euonla	0.72	0.42	0.61	0.52
	HELIFO	0.76	0.53	0.52	0.91
	LIMLUR	0.86	0.85	0.47	0.84
	LITSAC	0.86	0.56	0.6	0.91
	Mallpa	0.88	0.68	0.67	0.49
	Ormofo	0.95	0.65	0.83	0.7
	Pasako	0.85	0.26	0.47	0.72
	Pasana	0.84	0.63	0.37	0.9

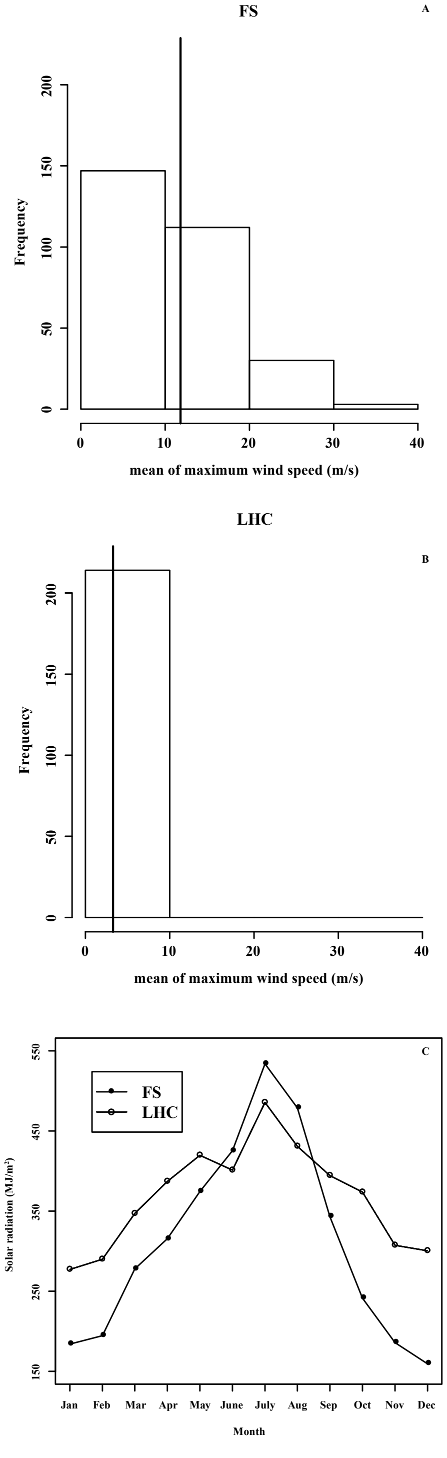
	Psycru	0.67	0.2	0.13	0.56
	Randco	0.83	0.53	0.7	0.76
	SCHEOC	0.96	0.85	0.65	0.52
	Schisu	0.91	0.57	0.58	0.7
	Syzybu	0.73	0.31	0.17	0.71
	Tricdu	0.76	0.31	0.19	0.75
	mean	0.826087	0.56	0.522174	0.733478
	minimum	0.44	0.06	0.11	0.49
	maximum	0.96	0.96	0.9	0.91
	median	0.85	0.56	0.58	0.71

Appendix 3. The fitting result of each species' allometric function. The parameters are listed below each relationship.

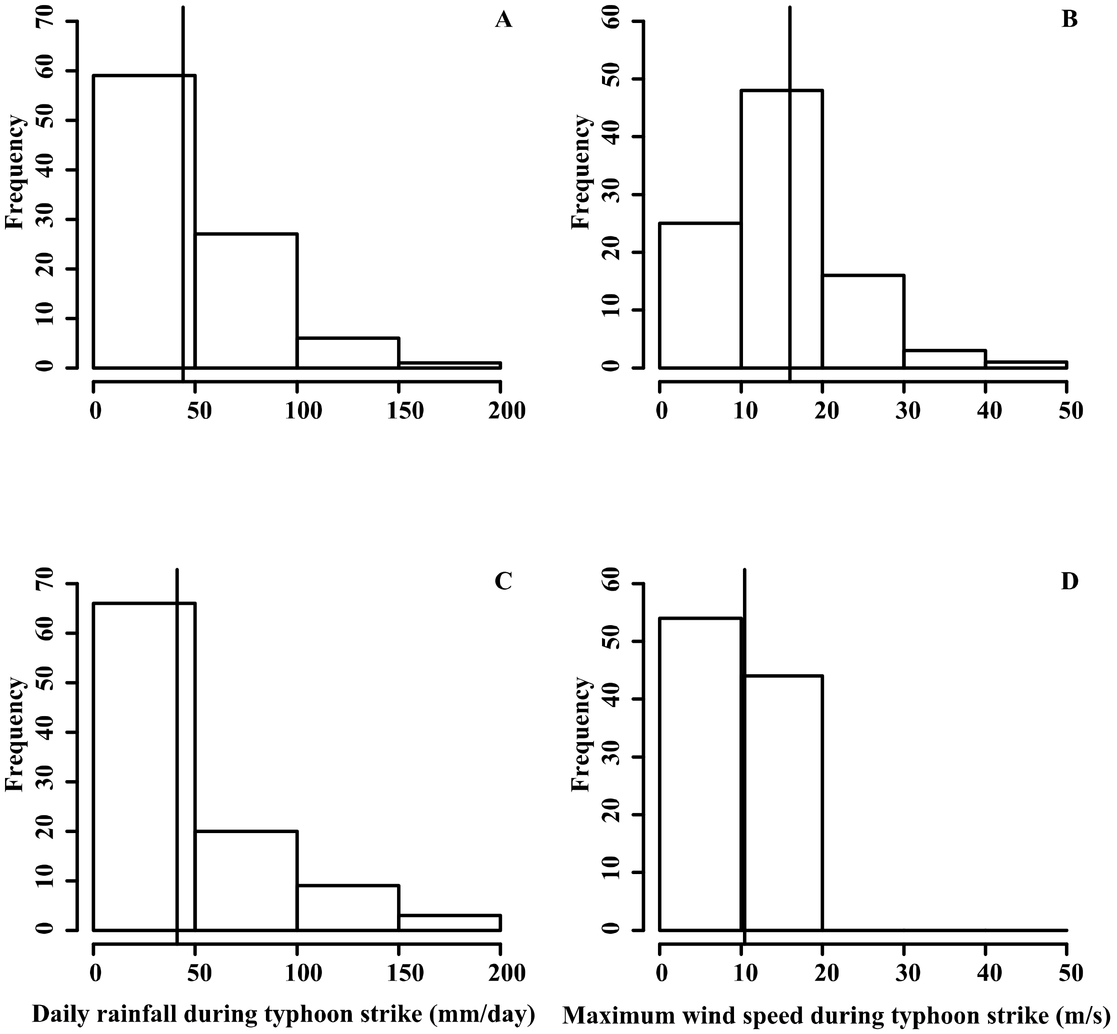
Site	**Code**	**DBH - Tree Height**			**Tree Height - Crown Area**		**Tree Height - First Branch Height**		**Tree Heigh - Crown Depth**	
		a	b	H_{max} (m)	a	b	a	b	a	b
FS	**BLASCO**	0.200464	0.778417	5.022293	0.36244	1.225509	0.338138	0.263537	0.170241	0.883683
	CASTCU	0.138484	0.63948	19.27863	0.00227	3.482676	0.294292	1.786282	0.510604	1.76E-73
	ENGERO	0.125409	0.725921	16.76286	0.108301	1.935517	0.319656	1.287158	0.437237	1.81E-48
	HELIFO	0.201442	0.7923	10.79427	0.223685	1.586798	0.314133	0.535396	0.610471	1.86E-116
	LIMLUR	0.115656	0.386534	20.05327	0.108067	1.936298	0.333834	0.290124	0.447736	1.46E-13
	LITSAC	0.263246	0.781992	12.61467	0.274911	1.732284	0.289092	1.125036	0.572881	2.07E-11
	Machmu	2.60E-08	10.3954	14.55821	0.046484	2.294195	0.405967	1.12602	0.389862	0.027399
	Machth	0.054367	0.526853	23.42071	0.06916	2.201791	0.364885	1.097761	0.434027	8.07E-29
	Melisq	0.035329	0.642253	21.56736	0.022763	2.609417	0.364441	0.82488	0.456483	4.98E-54
	Pyresh	0.083383	0.668107	16.61637	0.183092	1.77683	0.541625	4.50E-60	0.382881	0.141373
	SCHEOC	0.050338	0.484783	17.52411	0.552542	1.358017	0.447306	3.93E-19	0.298178	1.039449
LHC	**Ardiqu**	0.042557	0.649096	14.54815	0.107098	1.702766	0.533575	1.72E-29	0.318574	0.730647
	BLASCO	0.94262	1.575335	4.784259	1.029343	0.522925	0.170356	1.188949	0.53132	2.49E-27
	CASTCU	0.125175	0.661674	19.62134	0.207418	1.729712	0.297793	0.919967	0.581328	7.39E-30
	Castfa	0.13696	0.822743	16.78627	0.119313	1.963424	0.262479	1.320298	0.626856	2.96E-29
	Cinnsu	0.049965	0.636732	19.21374	0.163154	1.497886	0.384229	0.595509	0.545257	0.132451
	Crypch	0.090062	0.690153	16.08062	0.047391	2.252281	0.418272	0.125856	0.563603	0.266413

	Cyclpa	0.127859	0.805829	18.58443	0.014471	2.592009	0.253221	1.688039	0.609088	1.60E-85
	Diosmo	0.227548	0.724544	14.16024	0.196117	1.551989	0.176731	2.544945	0.472102	1.25E-52
	ENGERO	0.120079	0.774529	17.69377	0.051662	2.078525	0.361201	0.320551	0.528592	0.222516
	Euonla	0.054583	0.606596	7.042138	0.198226	1.131994	0.554731	1.15E-95	0.328491	0.290656
	HELIFO	0.174487	1.030043	11.63181	0.57877	1.178422	0.185701	0.709887	0.706508	9.40E-16
	LIMLUR	0.063334	0.48866	19.84488	0.030647	2.407309	0.283898	0.550464	0.588123	9.00E-35
	LITSAC	0.13627	0.70952	15.30595	0.235943	1.63951	0.310764	0.729766	0.692415	1.56E-84
	Mallpa	0.128572	0.766379	18.80325	0.703186	1.157785	0.499455	4.10E-26	0.365335	2.35E-17
	Ormofo	0.043567	0.673085	20.09043	0.646651	1.17043	0.44867	0.206446	0.599631	0.128042
	Pasako	0.225143	0.966475	4.649269	0.921203	0.977418	0.262221	0.929058	0.556972	6.73E-14
	Pasana	0.152833	0.6396	15.29413	0.056811	2.301967	0.156464	1.478258	0.680982	4.35E-32
	Psycru	0.271804	0.436798	5.400012	0.302096	1.31063	0.2113	0.88941	0.440076	4.87E-13
	Randco	0.173599	0.729933	14.06399	0.095453	1.722924	0.322967	1.198612	0.509795	2.68E-219
	SCHEOC	0.072048	0.768445	23.20843	0.00049	3.632096	0.285856	1.052496	0.405371	0.42412
	Schisu	0.075214	0.879377	23.08216	0.273395	1.511866	0.437998	0.028012	0.538544	0.098449
	Syzybu	0.242592	0.95854	8.544595	0.372392	1.183195	0.191691	1.399044	0.556873	5.60E-115
	Tricdu	0.066611	0.424535	8.246459	0.593583	0.775587	0.20858	1.537342	0.592577	7.35E-43

Appendix 4. The meteorological data during typhoon strike from 1988 to 2007 in FS (24°45'19.4"N, 121°35'45.3"E, elevation = 634 m above sea level) and LHC (23°56'N, 120°54'E, elevation = 666 m above sea level) weather stations. The mean of maximum wind speed in FS (A) and LHC (B) are 11.8 and 3.2 m/s, respectively. The monthly mean of solar radiation (C) are about 300 and 360 MJ/m^2 in FS (field circles with solid line) and LHC (open circles with solid line), respectively.



Appendix 5. The meteorological data of typhoons strike during 1958 – 2011 in YiLan (24°46'56"N, 121°44'53"E; A and B) and SunMoonLake (23°53'00"N, 120°54'29"E; C and D) weather station. The vertical line indicate mean of daily precipitation during typhoons strike in YiLan (A) and SunMoonLake (C) station. The vertical line indicate mean of maximum wind speed during typhoons strike in YiLan (A) and SunMoonLake (C) station.



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