Seedling Composition and Facilitative Effects of the Herbaceous Layer in a Monsoon-Affected Forest in Nanjenshan, Southern Taiwan

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ABSTRACT: Tree seedlings play an important role in forest regeneration. To understand the factors that control seedling establishment, we (1) compared the composition patterns of tree seedlings and their corresponding overstories, (2) examined the relationships between seedling composition and environmental factors and (3) evaluated the interaction (competition or facilitation) between seedlings and herbaceous layer in a wind-stressed forest in Nanjenshan, southern Taiwan. In the study plot, seedling abundance of canopy, subcanopy and shrub species (with true leaves and < 1 cm diameter at breast height) and coverage of herbaceous species (including herbaceous species, climbers and tree ferns ≤ ca. 1 m in height) were investigated on three transects with a total of 180 contiguous 5 × 5 m quadrats. Clustering classification and ordination methods were used to reveal the tree seedling composition patterns and the relationships between seedling composition and environmental factors. Correlation coefficients were computed between herbaceous coverage and seedling abundance among herb-seedling species pairs and between tall (≥ 1 m high)/short (< 0.5 m high) herbs and seedlings pairs to test the herb-seedling interaction. The spatial distribution of tree seedlings presented a perfect match to the overstory vegetation pattern. There was a strong relationship among seedling composition, herbaceous composition and topographic features, especially exposure to monsoon winds. Because of the absence of strong correlations between herbaceous structure/species and seedling abundances, the strong linkage in spatial patterns between seedling and herbaceous compositions suggests that certain plant species in the study plot have similar responses to the monsoon exposure. Our results also indicated that seedlings < 1 cm in diameter were strongly influenced by wind stress, similar to the response of the overstory composition, and that the facilitative/competitive effects of the herbaceous layer on tree seedlings were relatively weak.

KEY WORDS: forest regeneration, interspecific interaction, ordination, understory vegetation, vegetation layers.

INTRODUCTION

Tree seedlings usually defined as plants (< 1 m high), play an important role in forest regeneration (Swaine, 1996). Understory seedlings replace dead trees and replenish forest gaps, thereby maintaining forest structure. However, most forest investigations have neglected seedling composition patterns, despite their importance for forest regeneration (Lieberman, 1996).

The abundance and distributions of seedlings are constrained by the seed fecundity of parent trees and environmental requirements (Lepage et al., 2000). Seedling availability necessitates adequate seed fecundity and a sufficiently close seed source. In natural forests, the seed scarcity was uncommon; instead, the presence of dispersal limitation is evident in the spatial distributions between seedlings and parent trees (Ribbens et al., 1994; Clark et al., 1998; Masaki et al., 2005). For example, artificial gaps in Sabah many kilometers from the closed stand of old secondary forest contain almost no local pioneer species (notably *Macaranga* spp. *Mallotus* spp., *Trema* spp.) (Kennedy and Swaine, 1992). Narrow distributions and limited numbers of seedlings may result from the lack of suitable habitat for germination and survival (Clark et al., 2007).

In many studies, tree seedling distributions have been strictly correlated with abiotic environmental factors, such as micro-topography (Beatty, 1984; Shimamura et al., 2006), soil properties (Gauch and Stone, 1979) and solar radiation (Bray, 1956; Canham et al., 1994; Bebber et al., 2002). Enoki and Abe (2004) found that the sapling (small trees with 30-200 cm high) distributions of most species in a subtropical forest correlated with a topographical gradient from concave to convex areas or with a gradient of fertility. In addition, sunlight exposure appears to be an important factor influencing newly emerged seedling survival and distribution because scarcity of light in the understory reduces carbon assimilation and may lead to seedling mortality (Augspurger, 1984; Johnson and Smith, 2005).

In addition to seed limitations and environmental requirements, tree seedlings are also influenced by the understory layer, which is a stratum containing herbs, small shrubs and tree ferns (George and Bazzaz, 1999). Tree seedlings compete with the herbaceous layer for light, water and nutrients under the tree canopy (Royo and Carson, 2008). A dense herbaceous layer is inimical to seed germination and seedling survival(Denslow et al., 2006; Royo and Carson, 2006). High herbaceous coverage reduces the light quality and the availability of

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sunflecks near ground level (Denslow et al., 1991; Nilsen et al., 2001; Lei et al., 2006). Both tall and short herbaceous covers exacerbate belowground competition with seedlings for soil nutrients and water (Putz and Canham, 1992; Dillenburg et al., 1993; Messier, 1993). Therefore, an inverse correlation between herb coverage and seedling density has been repeatedly reported in the literature (Maguire and Forman, 1983; Royo and Carson, 2008). In temperate and tropical forests, tree regeneration has been reported to be suppressed by herbaceous species (Denslow et al., 1991; Lieffers et al., 1993; Royo and Carson, 2006).

While the negative effect of intact vegetation on seedling growth is well documented, a facilitative interactions in the plant community have also received considerable attention over the past two decades (Brooker et al., 2008). The presence of herbaceous vegetation can have positive effects on seedling survival through changes in abiotic environment or community structure. In arid environments with strong sunlight, the survival of highly shade-tolerant but bright light-intolerant seedlings was facilitated by the presence of neighboring herbs (Desteven, 1991; Berkowitz et al., 1995). In addition, dense herbaceous vegetation can have indirect positive effects on seedling survival by reducing invasion of small herbivores, thus increasing the survival rate of newly emerged tree seedlings (Song, 2007). Under extreme environmental conditions (*e.g.*, alpine and desert), herbaceous species and small shrubs help nurse tree seedlings as well as benefit seedling establishment. For example, in a semi-arid steppe, an adult individual of the tussock grass *Stipa tenacissima* protected a sapling *Pinus halepensis* from drought (Maestre et al., 2001; Maestre et al., 2003). The cushion of *Azorella monantha,* which buffered substrate and air temperature and enhanced soil moisture and nutrient content, harbored native and invasive species (*e.g.*, the Andean cauliflower *Nastanthus agglomerates* and the filed chickweed *Cerastium arvense*, respectively) at the upper limit of vegetation in the high Andes of central Chile (Cavieres et al., 2005; Cavieres et al., 2007).

The forests of Nanjenshan in southern Taiwan are strongly affected by both chronic monsoon and typhoons and characterized by an extremely high density (> 10000 ha^{-1}), low tree height (< 6 m) and a high degree of canopy openness (> 12 %) (Sun, 1993; Yeh, 2006; Chao et al., 2007). The mechanisms of tree regeneration and diversity maintenance in this wind-stressed forest have attracted much attention (Li, 1995; Kuo and Fan, 2003). However, surveys of seedling composition are still lacking, despite the recognized importance of seedlings for forest regeneration. Trees face various limiting factors that act as filters for species survival during the process of seedling establishment; therefore, the composition and distribution of trees vary among different establishment stages. To identify the factors underlying seedling establishment, we compared the composition patterns of tree seedlings and their corresponding overstories, and examined the relationships between seedling composition and environmental factors. We also tested the competitive and facilitative interactions between herb and seedling species under wind stress. We sought to determine (1) whether seedling composition patterns are related to the overstory composition, (2) which exogenous factors strongly affect seedling composition and (3) whether herbaceous species facilitate or compete with woody seedlings in a subtropical monsoon forest.

MATERIALS AND METHODS

Study site

Lanjenchi Forest Dynamics plot (22°3'N, 120°51'E) is located in the Nanjenshan Reserve of the Kenting National Park on the eastern slope of the Central Mountain Range near the Pacific Ocean in southern Taiwan (Fig. 1). The climate is coastal and tropical with a mean annual temperature of 22.3°C (recorded from 1994 to 1998) and a mean monthly temperature ranging from 18°C in January to 26.1°C in July. Of the total annual precipitation (3,793 mm), 72% occurred between June and October, usually as a result of typhoons. The forest in the Nanjenshan reserve have been classified as monsoon rain forest (Su and Su, 1988) or *Machilus-Castanopsis* forest in the vegetation classification system of Taiwan (Su, 1984). The overstory is composed of evergreen oak-laurel species. The distribution patterns of overstory plant communities are closely associated with the wind stress gradient caused by the interaction between micro-topography and the northeast monsoon (Chen et al., 1997; Chao et al., 2010).

The 3-ha Lanjenchi Forest Dynamics Plot (100 m × 300 m) was established in 1989 (Fig. 1). The plot has moderate relief with slopes mostly between 10 and 30% and elevation from 300 to 350 m above sea level. The plot is separated into two ridge crests by a small north-south oriented creek. The exposed geological strata consist of interbedded sandstone and shale of the Miocene age (Chen et al., 1997).

Field sampling

Field work on understory vegetation was carried out from July to October in 1991. Three transects containing 60 contiguous 5 × 5 m quadrats (180 quadrats in total) were established (Fig. 1). All seedlings

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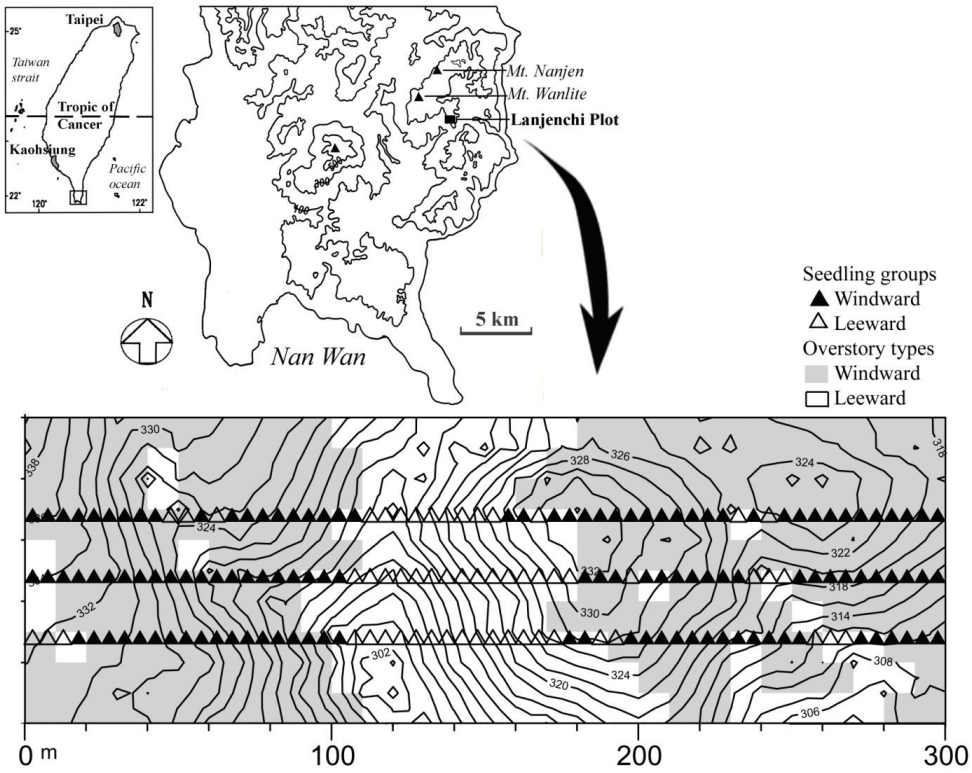


Fig. 1. Location of the 3-ha Lanjenchi plot in southernmost Taiwan (22°3'N and 120°51'E). Two groups of quadrats (5 × 5 m each) based on cluster analysis of seedling composition are indicated by different symbols: windward type (▲) and leeward type (△). Types of quadrats (10 × 10 m) classified by TWINSPAN with overstory vegetation data from Chao et al., (2010) are also shown on the contour map: the windward type (*Lithocarpus amygdalifolius-Illicium arborescens* forest) is in gray and leeward type (*Helicia formosana-Schefflera octophylla* forest) is in white.

(including canopy, subcanopy and shrub species with true leaves and < 1 cm in diameter at breast height) and herbaceous species (including herbaceous species, palms and tree ferns ≤ 1 m in height) within each quadrat were identified and recorded. The coverage of each herbaceous species was measured by the line intercept method along two transect lines that were set 1 m from the northern and southern borders of each quadrat. Nomenclature, life forms of understory species and individual heights of herbaceous species are presented according to the definitions in *Flora of Taiwan* (Huang, 1993-2000). We also took hemispherical photographs to determine the degree of canopy openness which is regarded as a good indicator of understory photosynthetic active radiation (Canham, 1988). Photographs were taken one meter above the center of each quadrat in summer 1991 using a Minolta 7.5 mm lens on Minolta X700 camera equipped with Kodak T-Max ASA-400 film.

Analysis

To reveal spatial patterns of seedling composition, cluster analysis (Goodall, 1978) was performed to classify quadrats into community groups. A data matrix of quadrats and seedling abundances was used in the cluster analysis. The Sorensen (Bray-Curtis) distance (Faith et al., 1987) and flexible beta linkage methods (Lance and Williams, 1968) were used to build a dendrogram. To examine the correlations between seedling composition patterns and overstory composition or topographical position, the results of the clustering classification were projected onto a topographical map and merged with the spatial distribution of overstory types reported by Chao et al. (2010). To construct groups within the seedling composition patterns, the species abundance was averaged for each group and significance was determined by Bonferroni tests for multiple comparisons.

Detrend canonical analysis (DCA) was used to identify the relationships between seedling composition and environmental factors (Hill and Gauch, 1980). The explanatory variables used in the DCA included aspect, elevation, slope, quadrat position, monsoon exposure, canopy openness and herbaceous composition. Herbaceous species composition patterns were evaluated by transformed principal component analysis (transformed PCA) proposed by Legendre and

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Gallagher (2001). The procedures are identical to those traditional PCA but use Hellinger-transformed species data (Legendre and Gallagher, 2001). A data matrix of quadrats and herbaceous coverage was used in transformed PCA. The herbaceous coverage for each species was calculated as the total intercept length of the species divided by the investigation length of a quadrat (10 m). The first-axis scores of the transformed PCA were used for the index of herbaceous composition in the DCA. Aspect values were converted into deviations from southwest and ranged from 0° (SW) to 180° (NE). The elevation of each quadrat was the mean elevation of its four quadrat corners. The quadrat position was defined as the difference in elevation between the focal quadrat and its nearest ridge. The index of monsoon exposure was determined using the angle between the zenith and the skyline in the northeastern direction. The index of canopy openness was characterized using hemispherical photography, following the field protocol of Robison and McCarthy (1999). Images were digitally analyzed using a self-developed Visual Basic program to determine percentage of open sky relative to canopy cover. To calibrate fish-eye distortion of the image, we divided the photograph into four parts with concentric circles, and the percentage of sky area in each part was weighted by its corresponding hemispherical surface area. The adjusted proportion of sky area was defined as canopy openness.

Pearson and Spearman correlations were used to examine the relationship between herbaceous coverage and seedling abundance. We assumed that when the herbaceous layer had a competitive effect on seedlings they would show a significantly negative correlation; on the other hand, when the herbaceous layer had a facilitative effect on seedlings they would show a significantly positive correlation.

Regarding the effects of the herbaceous structure on seedlings, the herbaceous species were classified into two groups: tall herbs (individual height > 1 m) and short herbs (individual height < 0.5 m). We suggest that these two herb groups may utilize different mechanisms to inhibit or facilitate on seedling growths. Tall herbs can act as light or wind shelters, thereby impeding seedling growth or protecting seedlings from wind damage. However, short herbs may only compete with seedlings for soil water and nutrients. The correlations between tall herb coverage and seedling abundance were computed using the quadrats in which the coverage of tall herb was greater than the residual herbaceous coverage, whereas the correlations between short herbs and seedling abundance were estimated using the quadrats in which the short herbs covered a greater area than the residual herbs.

For species-species interactions, we computed correlations among all pairs of herbaceous and seedling species. Sampling within closed distances might reveal spatial autocorrelations and lead to misunderstandings in statistical tests (Legendre, 1993; Thomson et al., 1996). Hence, the correlations were computed with the selected quadrats based on their autocorrelation scales (Fan and Hsieh, 2010). For example, if a variable showed a significant autocorrelation within 10 m that indicated that the sample values between two adjacent 5 × 5 m quadrats were related, the correlation was re-calculated with re-selected quadrats at a distance interval of one quadrat. If the autocorrelation scale was within 15 m, the correlation was calculated with the quadrats at a space interval of two quadrats. The larger autocorrelation scales were deduced by analogy. Before computing the correlation coefficients, the selected quadrats containing zero abundance values of the given herbaceous or seedling species were eliminated. After a selection of quadrats at space intervals from the 180 total quadrats, more than two sets of data were available for calculating correlation coefficients. The significant correlations were counted only when the sample size was larger than five pairs and when more than two data sets showed the same trend of significant correlation.

RESULTS

A total of 16,925 seedling individuals from 102 tree and shrub species, representing 76 genera and 37 families, were found in the selected seedling transects (Appendix I). The average density of tree seedlings was 3.76 m^{-2}. The most abundant species, with more than 500 individuals were, in order of decreasing abundance, *Illicium arborescens*, *Osmanthus marginatus*, *Psychotria rubra*, *Daphniphyllum glaucescens oldhamii*, *Beilschmiedia tsangii*, *Ilex cochinchinensis* and *Lasianthus wallichii*. Among the dominant seedling species, *Psychotria rubra* and *Lasianthus wallichii* were shrubs and *Illicium arborescens* and *Ilex cochinchinensis* were subcanopy species. They were also dominant species of the overstory vegetation in Nanjenshan (Chao et al., 2010).

Cluster analysis (percent chaining = 1.55) indicated that the 180 quadrats could be divided into two main groups associated with topography (Fig. 1). The spatial pattern of seedling communities was similar to that of the overstory vegetation described by Chao et al. (2010) (Fig. 1). The windward community, dominated by seedlings of *Illicium arborescens*, *Osmanthus marginatus* and *Psychotria rubra*, was mainly found on the windward slopes. The other species with more than 1,000 seedlings ha^{-1} were *Daphniphyllum glaucescens* ssp. *oldhamii*, *Ardisia cornudentata*, *Melastoma candidum*, *Microtropis japonica*, *Beilschmiedia tsangii*,

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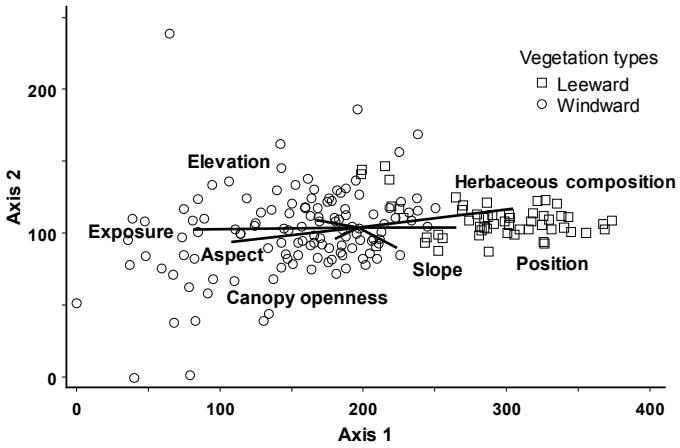


Fig. 2. DCA ordination diagram of seedling data from 180 quadrats with respect to environmental variables (aspect, elevation, slope, position (quadrat position), exposure (monsoon exposure), canopy openness and herbaceous composition (transformed PCA axis 1 score of herbaceous composition)).

Antidesma hiiranense, *Castanopsis carlesii*, *Ilex cochinchinensis* and *Litsea acutivena.* These 12 species accounted for 60% of the total seedling abundance in the windward understory. The leeward community, dominated by seedlings of *Lasianthus wallichii*, *Psychotria rubra* and *Ilex cochinchinensis,* was distributed along creeks and on the leeward slopes. The other abundant species in this type were *Beilschmiedia tsangii*, *Helicia formosana*, *Archidendron lucidum*, *Lasianthus fordii*, *Illicium arborescens*, *Litsea acutivena* and *Callicarpa remotiflora*. These ten species accounted for 62% of the total seedling abundance in the leeward understory. There were seven shrub species among the 16 dominant species of the two seedling groups.

The DCA ordination results showed a close relationship between the seedling community and topographic or habitat environmental variables (Fig. 2). The first two DCA axes together explained 16.3 % of the total variance in seedling composition in the understory dataset. The first axis reflected a gradient of monsoon exposure (r = -0.76). Quadrats with low scores on axis 1 were those on the windward slopes (high values of monsoon exposure). In contrast, quadrats with the highest scores on the axis 1 were found on the leeward slopes or creek sides. Among the physical environmental factors assessed, monsoon exposure, which showed high correlations with aspect and quadrat position (r = 0.58 and -0.79, respectively), had the greatest influence on seedling composition. Seedling composition also had a high correlation with herbaceous species composition (r = 0.73). There was a high negative correlation between monsoon exposure and the particular composition of herbaceous species (r = -0.45).

There was no significant correlation between herbaceous coverage and seedling abundance (Pearson correlation (r): -0.45-0.32, p = 0.058-0.807). When herbaceous species were divided into two groups (tall and short herbs), neither type of herbaceous coverage showed any significant correlation with the total abundance of seedlings (p = 0.064 and 0.458, respectively) or the seedling abundance of each species (data not shown). In terms of species-species interactions, a total of 2,160 species-species pairs with sample size n > 5 were available for computing correlation coefficients. Most pairs of herb-seedling species showed no significant correlation. Only 68 of the 2,160 species-species pairs revealed significant correlations. Among the significantly correlated pairs, most of the relationships were positive (56 species pairs) and associated with very low abundances (Table 1). The only two species pairs with relatively high abundance were *Diplazium donianum* and *Illicium arborescens*, which showed a negative correlation (Fig. 3a) and *Diplazium dilatatum* and *Helicia formosana*, which showed a positive correlation (Fig. 3b).

DISCUSSION

One of the most striking results of this study was that the spatial distribution of tree seedlings presented a nearly perfect match to the pattern of overstory composition (Fig. 1). Another notable result of our study was that seedling composition showed a strong correlation with the herbaceous species composition (Fig. 2). The reasons for the strong linkage among forest strata (*i.e.*, overstory, seedling and herb layer) can be deduced from the following points: (1) the result of biotic interactions between strata via certain mechanisms (*e.g.*, competition or facilitation) (Lopez et al., 2007) or (2) a phenomenon resulting from direct influences of physical environmental factors on each forest stratum (Gilliam and Roberts, 2003). Because of

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Table 1. Summary of Pearson and Spearman correlations between herbaceous and seedling species pairs. Only the species pairs with significant correlations ($p < 0.05$) are shown. The seedling species names in bold show significantly negative correlations; species names in italics indicate positive correlations. Underlining means that a significant relationship was found only by the Spearman correlation and asterisks represent significance only according to Pearson method; all other pairs were significnat according to both methods.

Herbaceous species (coverage %)		Seedling (density ha^{-1})		
		Abundant (>900 ha^{-1})	Medium (400-900 ha^{-1})	Rare (<400 ha^{-1})
Medium (> 1%)	*Diplazium donianum*	**Illicium arborescens***		
	Diplazium dilatatum		*Helicia formosana**	
Rare (1-0.5%)	*Blechnum orientale*	*Melastoma candidum**		
	Dianella ensifolia			*Eurya nitida* var. *nanjenshanensis**, *Ilex maximowicziana**, *Machilus thunbergii*
	Dryopteris sordidipes			*Prunus phaeosticta*
	Elatostema lineolatum var. *major*		**Callicarpa remotiflora**	**Callicarpa remotiserrulata**
	Hemigramma decurrens		*Lasianthus cyanocarpus*	*Symplocos congest*, **Sapium discolor**
	Pronephrium triphyllum		**Helicia formosana, Neolitsea buisanensis**	*Ardisia sieboldii**, **Diospyros eriantha,** *Machilus thunbergii**, *Mallotus paniculatus**, *Schima superba* var. *kankoensis*, *Syzygium euphlebium**
	Psychotria serpens		*Ardisia quinquegona**	
	Scleria terrestris		*Syzygium buxifolium*	**Euonymus pallidifolia,** *Ficus formosana**
Very rare (<0.5%)	*Alpinia pricei*			*Beilschmiedia erythrophloia*, *Eurya nitida* var. *nanjenshanensis**, *Ilex uraiensis*, *Mallotus paniculatus**, *Sarcandra glabra**
	Calanthe speciosa		*Callicarpa remotiflora*	
	Cephalantheropsis gracilis	*Castanopsis carlesii**		*Glochidion rubrum*
	Dioscorea japonica var. *pseudojaponica*			*Elaeocarpus sylvestris**, *Tricalysia dubia**
	Farfugium japonicum var. formosanum		*Schefflera octophylla**	
	Liparis henryi		*Helicia formosana**, *Syzygium buxifolium**	*Adinandra formosana*, *Callicarpa remotiserrulata**, *Euonymus pallidifolia**, **Ilex maximowicziana,** *Lithocarpus amygdalifolius**, *Prunus phaeosticta**
	Oplismenus compositus			*Cyclobalanopsis longinux**
	Oplismenus hirtellus	*Castanopsis carlesii*		*Machilus obovatifolia**, *Machilus zuihoensis*, *Pasania harlandii**, *Sloanea formosana*
	Piper kawakamii			*Beilschmiedia erythrophloia**, *Castanopsis stellato-spina*, *Diospyros eriantha**, *Euonymus pallidifolia**, *Glochidion rubrum**, *Machilus zuihoensis**, *Symplocos shilanensis*
	Pothos chinensis	*Castanopsis carlesii**	*Neolitsea hiiranensis*, *Lasianthus cyanocarpus**	*Castanopsis stellato-spina*, *Cinnamomum rigidissimum*, *Clerodendrum cyrtophyllum**, *Lasianthus obliquinervis**, *Schima superba* var. *kankoensis**
	Pronephrium cuspidatum		**Helicia formosana, Neolitsea hiiranensis**	*Astronia formosana*, **Elaeocarpus sylvestris**

the absence of a strong correlation between herbaceous structure and seedling abundances in Lanjenchi (Table 1), we suggest that the strong linkage between spatial patterns of seedling composition, overstory composition and herbaceous composition might be attributed to similarity between partucular species' responses to exogenous factors like monsoon exposure.

Tree and herbaceous species can have differen responses to various environmental factors (Cantlon, 1953). Previous studies reported that graminoid abundances were greater on drier, less fertile slopes, while fern cover was high on wet slopes but declined after wind disturbance (Cantlon, 1953; Small and Mccarthy, 2002; Halleck et al., 2004). Both seedlings and adult trees might respond to wind stress inNanjenshan. Tree species differentiated between windward and leeward slopes, and could be categorized by forest physiognomy (Sun et al., 1998), leaf structure (Su, 1993), and tree physiology (Wang, 1995). Overstory trees of leeward and windward species

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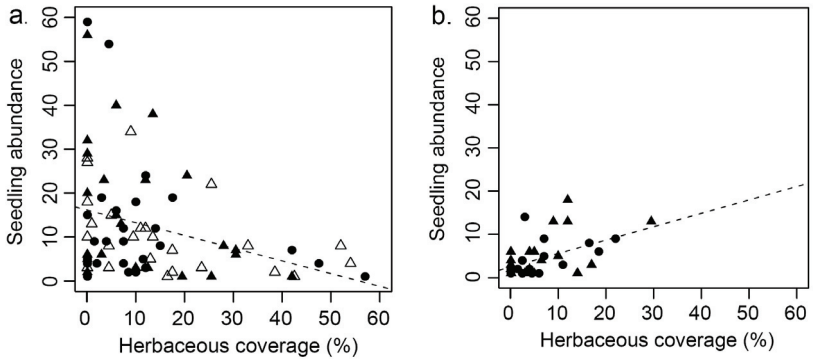


Fig. 3. Relationship between herbaceous coverage and seedling abundance for each of the following herb-seedling pairs with relatively high abundance: (a) *Diplazium donianum* and *Illicium arborescens* (y = 16.14-0.29x, r^2 = 0.10, *p* = 0.0041), and (b) *Diplazium dilatatum* and *Helicia formosana* (y = 2.45 + 0.31x, r^2 = 0.24, *p* = 0.0008). Different symbols indicate different groups of re-selected quadrats at distance intervals of (a) three or (b) two quadrats.

showed variable transpiration rates under wind stress (Chang, 2008). Seedlings of windward species showed good resistance to wind-blow and had a higher photosynthetic rate than those found in sheltered area, while seedlings of leeward species showed high mortality when exposure to wind (Fan, 2005). In Figure 2, the scattering of quadrats classified by seedling composition along a gradient of monsoon exposure might imply that tree individuals < 1 cm in diameter had been selected by wind stress, showing a consistent pattern with the overstory trees. In addition, the close relationship between overstory and seedling compositions might result from poor seed dispersal of most dominant tree species. However, further studies are needed to quantify the importance of dispersal limitation for the restricted distribution of seedlings near their parents.

Seasonal fluctuations in seedling abundance as well as definition of tree seedling used in our census might have influenced the estimates of seedling density under the forest canopy. The seedling density calculated in our study (3.76 seedlings m^{-2}) was relatively low compared to the densities found in previous studies (11 stems m^{-2} in Li (1995) and 9 stems m^{-2} in Lai (1996)) performed in the same area. Li (1995) and Lai (1996) studied seedling dynamics and found that seedling density varied among both seasons and years as well as the level of seed production. The relatively low density of seedlings in our study might be attributed to climatic variation. Li (1995) reported that the high monsoon precipitation caused a peak in seedling density in February and that the mei-yu (plum rains) brought another peak in July (Wang et al., 2005). In addition, Lai (1996) also observed a peak in seedling densityin July. The four months during which we conducted our study was a major growth season for seedlings. We suggest that our omission of tiny seedlings with only cotyledons might account for our lower seedling numbers, which only reached about half that of reported in the previous studies by Li (1995) and Lai (1996). Because the definition of a seedlings varies widely among studies, we could not fairly compare our seedling abundance data with that of other studies, and no general trend in seedling density could be observed. However, the seedling densities of forests with high degrees of climatic seasonality were extremely high (12-20 stems m^{-2}) during the growth season (Lieberman and Li, 1992; Dech et al., 2008; Li et al., 2009; Viani and Rodrigues, 2009). For example, there were 12 seedlings m^{-2} in a semi-deciduous lowland forest of Panama (Metz et al., 2008) and more than 20 seedlings m^{-2} in a temperate hemlock forest of North America (Maguire and Forman, 1983).

The species composition and density of seedlings in the Lanjenchi plot was influenced more by the monsoon exposure than canopy openness (Fig. 2 and Appendix). Light is usually the most limiting resource affecting understory tree growth and survival (Chen et al., 1996; Chen, 1997) and may cause differentiation in the understory composition (Aiba and Nakashizuka, 2007). However, Vargas-Rodriguez et al. (2005) studied the seedling composition in a tropical dry forest and found that soil resources were of great importance for seedling habitat specialization while heterogeneity in light conditions instead determined differences in growth. In Nanjenshan, the branch-breaks and defoliation caused by typhoons or monsoons (Liu, 1994) might elevate both light availability in the understory and organic matter on the soil surface. Due to the canopy damage observed in both the herbaceous and overstory layers, a high degree of light intensity in the understory was unlikely to be a limiting factor for the understory plants (Lin, 2007). Therefore, the seedlings species composition was less related to canopy openness, which

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is considered to be a good indicator of understory light transmission. In addition, seedling densities varied between windward and leeward slopes. Li (1995) found that the windward slopes had more seedlings than the leeward slopes (> 20 and < 10 stems m^{-2} respectively). The elevated light availability and low tree growth rates (Yeh, 2006) may allow more seedlings accumulation on the windward slopes of the Lanjenchi plot.

Compared to the strong wind effect, competition between tree seedlings and the herbaceous layer under monsoon stress was undetectable by our methods. In terms of species-species interactions, except for the abundant species, *Diplazium donianum* and *Illicium arborescens*, all other species showing significant correlations were rare species (herb coverage <1% or seedling density < 5 stems m^{-2}). Significant correlations in small data-sets are doubtful and might not indicate real biological interspecific interaction. The existence of competition between two sparse species for light or nutrients might not be possible within a large sampling area (25 m^2), as in our investigation. Two species that show inverse responses to the same environmental gradient might coexist in reverse abundance patterns. With regard to the effects of the herbaceous structure, coverage by tall herbs did not correlate with the seedling abundance, indicating that wind sheltering or light shading from the herbaceous canopy probably dose not have significant effect on seedlings in our study plot.

Most of the 2,160 species-species pairs were positively rather than negatively correlated. Positive plant-plant interactions under monsoon stress support with the concept of facilitation under stressful conditions (Bertness and Callaway, 1994; Callaway and Walker, 1997; Brooker and Callaghan, 1998). However, we doubt that facilitative effects are truely present in most of the positive correlations between rare species. The positive correlation exhibited by two relatively abundant species, *Diplazium dilatatum* and *Helicia formosana,* might present facilitation with reciprocal action of wind sheltering or merely the result of two species possessing similar response to the same environmental factors. The mechanism of positive correlation between these two species should be clarified in future studies.

In conclusion, in the Lanjenchi plot, herbaceous species did not have significant inhibitory or facilitative effects on seedlings. Opportunities for seedling establishment might arise from the release of resources due to a high frequency of strong wind stress. In addition, the habitat differentiation that results from the interaction of topography and monsoon exposure generally prevents species from competing with each other and promotes species coexistence. The linkage between seedling composition and herbaceous composition was mainly caused by similar responses of seedling and herbaceous plants to monsoon effects. Seedlings with < 1 cm in diameter might suffer more from the strong influence of wind stress than the effects of the herbaceous layer in the Nanjenshan forests.

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Appendix I. Cluster analysis-based comparison of species composition data between two seedling communities of the Lanjenchi plot in Nanjenshan, southernmost Taiwan. Seedlings were defined as the plant individuals <1 cm diameter at breast height. N was the total number of individual per species counted during the census. The density (ha^{-1}) of each species was calculated as the total number of individual per species divided by the total census area within a group. Frequency (%) indicates the percentage of quadrats that a given species occupied. 'a' and 'b' represent Bonferroni's test for multiple comparison.

		Density (ha^{-1})		Frequency (%)	
Scientific name	**N**	**Windward, n=124**	**Leeward, n=56**	**Windward**	**Leeward**
Illicium arborescens Hayata	2,167	6,623 ^{a}	814 ^{b}	96	57
Osmanthus marginatus (Champ. ex Benth.) Hemsl.	1,317	3,994 ^{a}	564 ^{b}	93	55
Daphniphyllum glaucescens Bl. ssp. *oldhamii* (Hemsl.) Huang	802	2,400 ^{a}	414 ^{b}	91	54
Ardisia cornudentata Mez	482	1,519 ^{a}	79 ^{b}	80	13
Melastoma candidum D. Don	476	1,519 ^{a}	36 ^{b}	62	9
Microtropis japonica (Fr. & Sav.) Hall. f.	497	1,471 ^{a}	293 ^{b}	88	48
Antidesma hiiranense Hayata	455	1,300 ^{a}	371 ^{b}	73	45
Castanopsis carlesii (Hemsl.) Hayata	445	1,281 ^{a}	343 ^{b}	73	34
Myrsine seguinii Lev.	234	755 ^{a}	0 ^{b}	35	0
Syzygium buxifolium Hook. & Arn.	216	697 ^{a}	0 ^{b}	44	0
Neolitsea buisanensis Yamamoto & Kamikoti	189	597 ^{a}	29 ^{b}	45	7
Tarenna gracilipes (Hayata) Ohwi	187	584 ^{a}	43 ^{b}	52	9
Garcinia multiflora Champ.	183	552 ^{a}	86 ^{b}	53	21
Lasianthus wallichii Wight	563	535 ^{b}	2,836 ^{a}	44	95
Ilex cochinchinensis (Lour.) Loes.	672	1,281 ^{b}	1,964 ^{a}	65	71
Beilschmiedia tsangii Merr.	675	1,310 ^{b}	1,921 ^{a}	76	96
Helicia formosana Hemsl.	205	168 ^{b}	1,093 ^{a}	16	57
Archidendron lucidum Benth.	149	19 ^{b}	1,021 ^{a}	4	46
Lasianthus fordii Hance	182	213 ^{b}	829 ^{a}	31	71
Callicarpa remotiflora Lin & Wang	195	371 ^{b}	571 ^{a}	42	63
Neolitsea hiiranensis Liu & Liao	202	526 ^{a}	279 ^{b}	62	43
Rhaphiolepis indica (L.) Lindl. var. *hiiranensis* (Kanehira) Li	162	519 ^{a}	7 ^{b}	23	2
Eurya nitida Korthals var. *nanjenshanensis* Hsieh, Ling & Yang	156	494 ^{a}	21 ^{b}	45	5
Ilex maximowicziana Loes.	152	481 ^{a}	21 ^{b}	42	5
Ilex lonicerifolia Hayata var. *matsudai* Yamamoto	145	439 ^{a}	64 ^{b}	47	7
Wikstroemia taiwanensis Chang	126	406 ^{a}	0 ^{b}	38	0
Symplocos theophrastaefolia Sieb. & Zucc.	126	345 ^{a}	136 ^{b}	44	23
Symplocos congesta Benth.	105	326 ^{a}	29 ^{b}	47	7
Cyclobalanopsis longinux (Hayata) Schott.	114	316 ^{a}	114 ^{b}	35	23
Lithocarpus amygdalifolius (Skan ex Forbes & Hemsl.) Hayata	106	303 ^{a}	86 ^{b}	44	16
Podocarpus macrophyllus (Thunb.) Sweet	93	287 ^{a}	29 ^{b}	34	5

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Appendix. Continued.

Scientific name	N	Density (ha^{-1}) Windward, n=124	Density (ha^{-1}) Leeward, n=56	Frequency (%) Windward	Frequency (%) Leeward
Gordonia axillaris (Roxb.) Dietr.	84	265 [a]	14 [b]	37	4
Mallotus paniculatus (Lam.) Muell. -Arg.	82	255 [a]	21 [b]	31	5
Cinnamomum rigidissimum H. T. Chang	80	248 [a]	21 [b]	31	5
Nageia nagi (Thunb.) O. Ktze.	75	242 [a]	0 [b]	29	0
Tricalysia dubia (Lindl.) Ohwi	85	239 [a]	79 [b]	35	14
Cyclobalanopsis pachyloma (O. Seem.) Schott.	79	232 [a]	50 [b]	26	13
Elaeocarpus sylvestris (Lour.) Poir.	80	226 [a]	71 [b]	37	18
Machilus obovatifolia (Hayata) Kanehira & Sasaki	75	223 [a]	43 [b]	31	7
Glochidion rubrum Blume	66	206 [a]	14 [b]	34	4
Schima superba Gardn. & Champ. var. *kankoensis* (Hayata) Keng	54	155 [a]	43 [b]	26	5
Symplocos shilanensis Liu & Lu	48	155 [a]	0 [b]	23	0
Clerodendrum cyrtophyllum Turcz.	55	152 [a]	57 [b]	25	13
Sapium discolor Muell.-Arg.	48	142 [a]	29 [b]	23	5
Decaspermum gracilentum (Hance) Merr. & Perry	51	139 [a]	57 [b]	26	11
Cyclobalanopsis championii (Benth.) Oerst. ex Schott.	33	106 [a]	0 [b]	19	0
Lasianthus bunzanensis Simizu	73	100 [b]	300 [a]	17	29
Callicarpa remotiserrulata Hayata	69	106 [b]	257 [a]	10	30
Ardisia sieboldii Miq.	41	52 [b]	179 [a]	10	29
Sloanea formosana Li	34	39 [b]	157 [a]	6	30
Ficus fistulosa Reinw. ex Blume	30	35 [b]	136 [a]	6	25
Adinandra formosana Hayata	30	90 [a]	14 [b]	16	4
Pasania formosana (Skan ex Forbes & Hemsl.) Schottky	29	90 [a]	7 [b]	15	2
Tetradium meliaefolia (Hance) Benth	21	68 [a]	0 [b]	9	0
Engelhardtia roxburghiana Wall.	22	65 [a]	14 [b]	15	4
Magnolia kachirachirai (Kanehira & Yamamoto) Dandy	21	61 [a]	14 [b]	13	4
Wendlandia formosana Cowan	14	16 [b]	64 [a]	4	13
Saurauja tristyla DC. var. *oldhamii* (Hemsl.) Finet & Gagncp.	8	3 [b]	50 [a]	1	11
Glycosmis citrifolia (Willd.) Lindl.	7	0 [b]	50 [a]	0	5
Cryptocarya chinensis (Hance) Hemsl.	9	6 [b]	50 [a]	2	5
Bridelia balansae Tutch.	5	0 [b]	36 [a]	0	9
Lasianthus obliquinervis Merr. var. *taitoensis* (Simizu) Liu & Chao	51	152 [a]	29 [a]	7	7
Syzygium kusukusense (Hayata) Mori	51	142 [a]	50 [a]	6	2
Syzygium euphlebium (Hayata) Mori	79	139 [a]	257 [a]	19	25
Lasianthus obliquinervis Merr.	54	132 [a]	93 [a]	15	21
Machilus zuihoensis Hayata	58	129 [a]	129 [a]	23	18
Melicope semecarpifolia	46	123 [a]	57 [a]	12	13
Pasania harlandii (Hance) Oersted	44	106 [a]	79 [a]	19	16
Lasianthus hiiranensis Hayata	33	94 [a]	29 [a]	12	5
Rhododendron simsii Planch.	23	74 [a]	0 [a]	6	0
Psychotria rubra (Lour.) Poir.	1,185	2,755 [a]	2,364 [a]	94	98
Litsea acutivena Hayata	431	1,061 [a]	729 [a]	59	64
Schefflera octophylla (Lour.) Harms	182	439 [a]	329 [a]	52	34
Ardisia quinquegona Blume	255	632 [a]	421 [a]	45	45
Lasianthus cyanocarpus Jack	190	432 [a]	400 [a]	55	52
Euonymus pallidifolia Hayata	173	423 [a]	300 [a]	46	39
Ilex uraiensis Mori & Yamamoto	120	303 [a]	186 [a]	48	32
Beilschmiedia erythrophloia Hayata	130	297 [a]	271 [a]	38	50
Machilus thunbergii Sieb. & Zucc.	141	284 [a]	379 [a]	44	41
Prunus phaeosticta (Hance) Maxim.	131	281 [a]	314 [a]	31	46
Ficus formosana Maxim.	90	229 [a]	136 [a]	35	27
Sarcandra glabra (Thunb.) Nakai	73	187 [a]	107 [a]	26	14
Diospyros eriantha Champ. ex Benth.	69	181 [a]	93 [a]	27	21
Ternstroemia gymnanthera (Wight & Arn.) Sprague	17	55 [a]	0 [a]	10	0
Castanopsis stellato-spina Hayata	24	48 [a]	64 [a]	11	14
Camellia hengchunensis Chang	13	42 [a]	0 [a]	6	0
Cleyera japonica Thunb.	12	39 [a]	0 [a]	4	0
Lasianthus curtisii King & Gamble	17	35 [a]	43 [a]	7	5
Glochidion zeylanicum (Gaertn.) A. Juss. var. *lanceolatum* (Hayata) M. J. Deng & J. C. Wang	10	29 [a]	7 [a]	6	2
Michelia compressa (Maxim.) Sargent	13	26 [a]	36 [a]	6	5
Astronia formosana Kanehira	7	10 [a]	29 [a]	2	5
Ilex rotunda Thunb.	3	6 [a]	7 [a]	2	2

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Appendix. Continued.

Scientific name	N	Density (ha^{-1})		Frequency (%)	
		Windward, n=124	Leeward, n=56	Windward	Leeward
Eurya chinensis R. Br.	4	3 [a]	21 [a]	1	5
Champereia manillana (Blume) Merr.	2	3 [a]	7 [a]	1	2
Ehretia longiflora Champ. ex Benth.	1	3 [a]	0 [a]	1	0
Drypetes karapinensis (Hayata) Pax	1	3 [a]	0 [a]	1	0
Syzygium densinervium Merr. var. *insulare* Chang	1	3 [a]	0 [a]	1	0
Bischofia javanica Blume	1	0 [a]	7 [a]	0	2
Machilus japonica Sieb. & Zucc. var. *kusanoi* (Hayata) Liao	1	0 [a]	7 [a]	0	2
Maesa perlarius (Lour.) Merr. var. *formosana* (Mez) Yuen P. Yang	1	0 [a]	7 [a]	0	2
Itea parviflora Hemsl.	1	0 [a]	7 [a]	0	2
Reevesia formosana Sprague	1	0 [a]	7 [a]	0	2
Total	16,925	44,245	22,921		
No. of species		95	88		
Shannon index		8.47	8.02		

臺灣南部南仁山受季風影響森林中小苗的組成及草本層的促進作用

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摘要：木本小苗對於森林的更新扮演著重要的角色。為了瞭解影響木本小苗建立的主要因子，我們於臺灣南部南仁山一處受風影響的森林中進行調查，(1) 比較其林下木本小苗與上層成樹的組成分布，(2) 檢視影響木本小苗組成的環境因子以及 (3) 評估木本小苗與草本層間是否有競爭或促進的關係。我們於試驗地中建立了三條樣帶共計 180 個 5 × 5 公尺的樣方；並進行樣帶中所有冠層、次冠層及灌木種類的小苗 (具有真葉且胸徑小於 1 公分) 數量及草本層 (表含草本植物、爬藤及小於 1 米的樹蕨) 覆蓋度的調查。支序分析及序列分析被使用來顯示林下小苗組成的分群情況及小苗組成與環境因子的相關。各物種和類別組合的草本覆蓋度及小苗數量可以計算其相關係數，以用來評估草本層及木本小苗間的相互作用。木本小苗組成的空間分布與過去研究中所呈現的上層成樹組成分布十分吻合。木本小苗組成與草本層組成及地形特徵有強烈關聯，尤其是對季風暴露程度。由於缺乏木本小苗及草本層結構/物種的競爭與促進關係。我們認為小苗組成與草本層組成的關聯，來自於彼此對季風平行的反應。總而言之，研究推論小於 1 公分胸徑的木本小苗已受到強烈的季風影響，呈現與上層相似的組成格局，而草本層各物種及結構對木本小苗直接的影響較弱。

關鍵詞：森林更新、種間交互作用、序列分析、林下植群、植群分層。

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