

# Regeneration of woody plants along topographic gradient in subtropical evergreen broadleaved forests in Taiwan

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ABSTRACT: We developed a seedling index (SI), which measures the number of seedlings in proportion to total regeneration individuals (seedlings and sprouts), to test whether the regeneration patterns of woody plants in evergreen broadleaved forests varied across topographic gradient. Our hypothesis was that sprouting in woody plants would be higher in highly-disturbed areas such as ridges and valleys, whereas seedlings would prevail on the less-disturbed slopes. A total of 131 sample plots in evergreen broadleaved forests were sampled from 400 to 2,600 m above sea level in Hsueshan mountain, northern Taiwan. Results show that seedling is the more dominant regeneration type, with the mean number of seedlings across all sample plots three times that of sprouts. The mean values of seedling index (SI) were all higher than 0.5 in valley-, slope-, and ridge-sites, suggesting that the regeneration of woody species is more dependent on seedlings regardless of topographic location. Of the 70 woody species analyzed, 59 species were more dependent on seedlings (SIs higher than 0.5). We classified the 70 species by their SI values into three groups: seedling dependent (37 species), intermediate (22 species), and sprout dependent (11 species). The majority of species were consistent in their reproductive modes across sites, with only 17% of the species changing their seedling-sprout-dependence across the topographic gradient. This suggests that the regeneration methods of woody plants should be mostly intrinsically determined, with only a few species relying on different major reproductive methods across topographies.

KEY WORDS: Regeneration characteristic, Seeding, Sprouting, Taiwan, Topographic gradient.

### INTRODUCTION

Forest plants largely depend on two regeneration strategies: sprouting and seeding (Bellingham and Sparrow, 2000; Bond and Midgley, 2001; Hilbert, 1987; Keeley and Zedler, 1978). Woody species are usually categorized as either sprouters or seeders according to their regeneration strategies (Bell, 2001; Bellingham et al., 1994; Clarke et al., 2010; Ojeda, 1998; Zimmerman et al., 1994). Seeders have higher seed production, higher seed viability and faster height growth of seedlings (Enright and Goldblum, 1999; Hansen et al., 1991; Keeley and Keeley, 1977; Keeley, 1992; Kelly and Parker, 1990). Seeders may allocate more energy to produce larger seeds because survival and recruitment of seedlings had been documented to have relationship with both seed size and seed mass (Baraloto and Goldberg, 2004; Poorter and Rose, 2005). On the other hand, sprouting after loss of biomass maintains the persistence of the current generation (Bond and Midgley, 2001). Sprouters tend to have lower seedling recruitment rates (Bond and Midgley, 2003) and allocate more resources to root carbohydrate storage (Schwilk and Ackerly, 2005; Shibata et al., 2016).

Seeding and sprouting had been widely investigated in vegetation of arid environments under fire disturbances (Calvo *et al.*, 2003; Franklin *et al.*, 2010; Hodgkinson, 1998; Kauffman, 1991; Keeley and Zedler,

1978; Ladd et al., 2005), Mediterranean ecosystems (Hilbert, 1987; Ladd et al., 2005; Lloret et al., 1999), or forests recovered after disturbances of strong winds (Kauffman, 1991; Kruger et al., 1997; Peterson and Pickett, 1991). Previous studies had shown that regeneration strategies of woody plants were strongly influenced by disturbance regimes (Clarke and Dorji, 2008; Vesk and Westoby, 2004). In the vegetation characterized by intense disturbances, woody plants had been separated into obligate seeders or obligate sprouters (Bond and Midgley, 2003; Calvo et al., 2003; Keeley and Zedler, 1978; Ladd et al., 2005). In forests under smaller scale disturbances, there was a gradual continuum of regeneration strategies from seeders to sprouters (Bond and Midgley, 2001, 2003; Vesk and Westoby, 2004). Further studies had proposed that sprouters are favored in habitats with frequent and severe disturbances (Bellingham and Sparrow, 2000; Bond and Midgley, 2001, 2003), while seeders are dominant members of forests where canopy is high and canopy gaps are the major disturbance types (Kruger et al., 1997; Midgley, 1996). Regeneration strategies of woody plants have attracted many attentions in different ecosystems, whereas that have received little attention in evergreen broadleaved forests in East Asia (Miura and Yamatoto, 2003; Nanami et al., 2004; Tran et al., 2005).

In East Asia, evergreen broadleaved forests are major vegetation types widely distributed throughout



tropical and subtropical regions (Ohsawa, 1990, 1991, 1993; Olson et al., 2001; Qian et al., 2003; Qian et al., 2016). Since many studies explored seedling regeneration in canopy gaps (Lin et al., 2003; Yamamoto, 1992; Yao et al., 2015), seeding is supposed to be predominant in evergreen broadleaved forests. In spite of this fact, it still remains questionable that seeding is constantly predominant in evergreen broadleaved forests because forest structures, canopy heights, or woody species compositions are evidently changed along regional or local environmental gradients, such as latitude, altitude, or topography (Chen et al., 1997; Enoki, 2003; Hsieh et al., 1998; Ohsawa, 1991, 1993; Su, 1984; Wang et al., 2004). In particular, topographic gradient is one of the most important local factors related to changes of forest structures and species compositions (Chen et al., 1997; Enoki, 2003; Li et al., 2013; Liao et al., 2013; Lin et al., 2012; Wang et al., 2004). Whether or not woody plants change regeneration characteristic between seeding and sprouting along topographic gradient is unknown because few studies have emphasized on regeneration of woody plants along topographic gradient in this region (Miura and Yamatoto, 2003; Nanami et al., 2004; Wei et al., 2015).

Topographic gradient provides a complex set of environmental heterogeneity shaping soil nutrients (Chen et al., 1997) as well as forest structures and tree species compositions (Chang et al., 2004; Chao et al., 2007; Chen et al., 1997; Enoki, 2003; Kubota et al., 2004; Robert, 2003; Wang et al., 2004). Normally, mountain ridges receive constant wind blow and shallow soil layers and large rocks are constantly observed at mountain ridge (Chao et al., 2010). Meanwhile, soil erosion and rock expose caused by periodic flooding are commonly observed at valley. Although habitat types and causal factors are different between mountain ridge and valley, it is believed that there are higher degrees of stresses in ridge and valley than that in mountain slope. Higher degrees of stresses at mountain ridge and valley are hypothesized to favor sprouting, because sprouts obtain essential resources from parent tree stems (Bell and Ojeda, 1999; Busby et al., 2010) and might have higher survival chances than seedlings under stresses (Bond and Midgley, 2001, 2003).

In Taiwan, changes of forest structures and species compositions along environmental gradients have been widely investigated (Hsieh *et al.*, 1997; Li *et al.*, 2013; Liao *et al.*, 2013; Lin *et al.*, 2012; Su, 1984). Several studies had investigated regenerations of woody plants in Taiwan and had proposed that regenerations of woody plants are majorly driven by canopy gaps or landslides (Chao *et al.*, 2010; Lin *et al.*, 2003; Mabry *et al.*, 1998; Yao *et al.*, 2015). Most of these studies dedicated to seedling recruitments under canopy gaps (Chao *et al.*, 2010; Lin *et al.*, 2003; Yao *et al.*, 2015). However, there is no study addressed on sprouting of woody plants.

Seedling dependence vs. sprout dependence is evaluated at both forest stand level and species level along topographic gradient in this study. At forest stand level, regenerations of woody species in forests at slope are assumed to be more dependent on seedlings and that at ridge and valley more on sprouts. At species level, regeneration of woody species may depend either on seedlings or on sprouts and may have changed from seedling dependence to sprout dependence along topographical gradient.

The major objective of this study attempts to understand the characters of seeding and sprouting in regeneration of evergreen broadleaved forests along topographic gradient. There are three questions in this study. (1) Whether or not seeding behavior is predominant in evergreen broadleaved forests. (2) At forest stand level, regeneration of woody plants in evergreen broadleaved forests are supposed to be more dependent on seedlings at mountain slope, whereas that are more dependent on sprouts at ridge and valley. (3) At species level, regeneration of a woody species is hypothesized to be dependent more on seedlings at slope and more on sprouts at ridge and valley.

# MATERIALS AND METHODS

#### Study site

Taiwan locates at the eastern edge of Eurasian continent (Fig. 1). The island is characterized by high mountains and Hsueshan mountain system (24°25′~25°10′N; 121°14′~121°52′E) locates at northern Taiwan with the elevation ranges from 0 to 3,400 m asl (above sea level). Temperature varies with elevation and the mean annual temperature is 22.7°C at 33 m asl and 13.7°C at 1500 m asl (Chen, 1996). Annual precipitation is 2,226 mm in coastal areas and more than 2,500 mm inland. The climate is characterized by a short winter dry season, with more than 60% of its rainfall distributed in summer. Typhoons which bring strong winds and heavy rainfall frequently strike the island from July to November. Monsoon winds generally blow from the south-west in summer and from the north-east in winter. Monsoon and typhoon associated with topographic heterogeneity results in a prevalent gradient of wind disturbance (Lin et al., 2003; Mabry et al., 1998). Mountain ridges receive constant wind blow and have shallow, stony or rocky soils. Forests on mountain ridge have relatively higher density of stems and lower canopy height (Lin et al., 2012). Mountain slopes possess tall and giant trees with complex canopy layers because mountain slopes allow the development of soil and growth of giant trees (Lin et al., 2012). Mountain valley is filled with patches of rock rubble due to deposit of rock fragments and is characterized by relative poorer species richness and fewer individuals per unit area (Hsieh et al., 1998).





Fig. 1. Map shows location of Taiwan and the five major mountain systems of the island. They are (1) Hsueshan, (2) Central, (3) Yushan, (4) Alishan, and (5) Coastal mountain systems. Sample plots ( $\star$ ) in this study were established at the northwest slope of the Hsueshan mountain system.

The major forest types of Hsueshan mountain systems are evergreen broadleaved forests that are classified into three forest zones from low to high elevations (Hsieh *et al.*, 1998; Liao *et al.*, 2013; Lin *et al.*, 2005; Su, 1984). They are *Machilus-Castanopsis* zone (0 to 1,050 m asl), the lower *Quercus* zone (1,050 to 1,600 m asl), and the upper *Quercus* zone (1,600 to 2,160 m asl). Within the *Quercus* zone are some coniferous forests dominated by *Chamaecyparis* (1,000 to 2,500 m asl). Mountain tops in the 1,500 to 1,900 m asl range are often covered by deciduous forests dominated by *Fagus hayatae* (Hsieh *et al.*, 1998).

#### Plant data collection

A total of 131 plots were sampled across the Hsueshan mountain system, elevation range of the sample plots is from 400 to 2,600 m asl. Vegetation were sampled in primary and old-growth forests to minimize the impacts of natural and anthropogenic disturbances. The canopy heights of primary and old-growth forests are usually higher than 20 meters, thus, forest with canopy height lower than 15 meters was probably recovered from canopy gaps and was not sampled in this research. In addition, only a few remnant forests could be sampled in the foothills because most of the lowland forests had been cleared for agriculture and industry. Each plot was  $20 \times 20$  m<sup>2</sup> and divided into four  $10 \times 10$ m<sup>2</sup> quadrants. In each quadrant, woody plants with a diameter at breast height (DBH) larger than 1 cm were recorded and measured. Individuals lower than 1.5 m were recorded as seedlings. Nomenclature of the woody plants in this research followed the Flora of Taiwan II (Huang, 1993–2003).

Seedlings and sprouts were recorded by species. Sprouts were defined following Miura and Yamamoto (2003): for each plant individual with multiple stems, the stem with the largest diameter was considered as the main stem, and all other stems were considered as sprouts. In field observation, some small drought or dead sprouts were observed in the forests, especially small sprouts (personal observation). Small sprouts might have little contributions to the persistence of individuals

![](_page_3_Picture_2.jpeg)

because of high mortality. Therefore, only stems of an individual with diameter at breast height larger than 1 cm and with branching from below 30 cm above ground were recorded as a sprout. Only the sprouts from adults were recorded in this study because the sprouting ability of seedlings is not considered recruitment for a persistent niche (Bond and Midgley, 2001). Seedlings taller than 20 cm were recorded because those shorter than 20 cm experienced high mortality and contributed little to forest regeneration (personal observations). Angiosperm woody species were categorized into shrubs and trees according to life form descriptions in Flora of Taiwan II or plant height observed in the field, with those consistently lower than 8 m classified as a shrub.

Field observations suggested that most woody plants that sprouted also produced seedlings. Therefore, instead of classifying the species into obligate sprouters or seeders, the sprouting versus seeding of each species was expressed using measures of relative importance. The importance of seedlings versus sprouts in the regeneration pool was measured by the seedling index (SI) (Kruger *et al.*, 1997):

SI = the number of seedlings / NRS, where

NRS (new regeneration stems) = the number of seedlings + the number of sprouts.

At the species level, the SI was used to indicate the relative degree to which a species is reliant on seedlings (SI > 0.5) or on sprouts (SI < 0.5) for regeneration. The SIs were also calculated at the forest stand level to measure the relative degree to which the forest stand relies on seedlings versus sprouts for regeneration.

The level of sprouting activity was calculated using two indicators developed by Nanami *et al.* (2004), the ratio of sprouting individuals to all individual (SPIAI) and the mean number of sprouts per sprouting individual (SPSPI):

- SPIAI = the number of sprouting individuals / the number of all individuals;
- SPSPI = the number of all sprouts / the number of sprouting individuals.

The sprouts, sprouting individuals and all individuals in the calculation of SPIAI and SPSPI are the woody individuals with DBH larger than 1 cm.

To ensure that the data reflected the true regeneration characteristic of a species, only the species with more than 30 established individuals and 30 regeneration individuals tallied in the survey were included in the calculation of the indices. All tree ferns and conifers were therefore excluded because of the scarcity of seedlings and sprouts. Only 35 dicot trees and 35 shrubs were used in the analyses.

The survival and recruitment of seedlings were proposed to be related to both seed size and seed mass (Poorter and Rose, 2005). However, in addition to seeds, the fruits of woody species may also function as a dispersal unit. Therefore, for each species, we identified their diaspores (dispersal units), be it the seed or fruit, found their dried samples in the herbarium, measured their diameter, length, and width, and accordingly calculated their volume to indicate each species' diaspore size (mm<sup>3</sup>).

#### Environmental factors and statistical analysis

The effects of 5 environmental and 8 biological factors on regeneration of woody plants were evaluated in this study. The environmental and biological factors were recorded in the field study or derived from plant data of sample plots. Topographic position (TOPO) recorded in the field was recognized as ridge, slope, or valley. Exposed soil surface (SOILEXP) was the estimation of percentage of sample plot area free from herb coverage. Soil rockiness (SOILRK) was recorded as the proportion of gravel content in the soil (Li et al., 2013). Rock expose (ROCKEXP) was estimation of the percentage of sample plot area occupied by rock. The last environmental factor is the altitude (ALT) of sample plot. Among the 8 biological factors, 3 of them were recorded in the field and 5 were estimated from the plant data. Herb coverage (HERBCOV), canopy height (CNPHT) and canopy coverage (CNPCOV) were recorded in the field. Species number (SPESNO), sprout number (SPRTNO), seedling number (SELNNO), number of all individual (IND) and total stem (TLSTEM) of sample plots were calculated from the plant data.

Multi-variable generalized linear models were performed by Statistica 7.1 (StatSoft, 2005) to interpret relationships between environmental variables of sample plots and floristic composition as well as between environmental variables and densities of seedlings and sprouts. The numbers of seedlings and sprouts are likely correlated with number of individuals and stems. In order to control the effects of individual/stem in the seedling/sprout model, the residuals between numbers of seedling/sprout and total individual/stem, from simple linear model, are correlated with environmental variables. Variations in sprouting versus seeding abilities of woody plants among habitats and life forms were detected by using Chi-square tests. All statistics were tested at the P = 0.05 level of significance.

### RESULTS

# Relative abundance of seeding versus sprouting in subtropical montane forests

A total of 19,730 established woody individuals belonging to 292 angiosperm species were recorded in the field survey, with 8,970 seedlings and 2,984 sprouts (Appendix I). Mean number of seedlings per sample plot is significantly higher than that of sprouts, this is directly relevant to the high mean number of SI index (Table 1). It is true that seeding is predominant in subtropical evergreen broadleaved forests. Among all the 292

![](_page_4_Picture_1.jpeg)

angiosperm woody species in our study, 72.7% possess seedling and 54.6% possess sprouts. The SI and SPIAI were calculated to test whether trees and shrubs depend on seedlings or sprouts for regeneration (Table 2). Regeneration of trees and shrubs more depend on seedlings, because the SI is higher than 0.5 and is 0.80 and 0.66 for trees and shrubs, respectively. Lower SI value of shrubs demonstrates higher sprouting abilities than trees. Additionally, the SPIAI is only 6.56% and 13.00% for trees and shrubs, respectively (Table 2). It is surprising, because low proportion of woody individuals are able to produce sprouts.

Of the 70 woody species analyzed, the proportions of individual that can produce sprouts are less than 35%, that is, more than 65% of total woody individuals do not produce sprouts. Of the 35 dicot tree species and 35 shrub species analyzed, 30 tree species and 29 shrub species have SI values higher than 0.5 (Fig. 2). Therefore, regardless of trees or shrubs, regenerations of woody plants largely depend on seedlings in evergreen broadleaved forests.

To test seeding vs. sprouting behavior of woody species are intrinsically determined, we analyzed the relationship between diaspore size and the proportion of sprouting individuals. Results suggest a negative correlation between the log value of diaspore size and the proportion of sprouting individuals (SPIAI, Fig. 3). The relationship is significant (P < 0.0001), though not strong ( $R^2 = 0.4738$ ). In general, tree species also have larger diaspore sizes and lower sprouting abilities than shrubs. Diaspore size, however, shows no relationship with SPSPI ( $F_{1,76} = 0.6233$ ,  $R^2 = 0.0081$ , P = 0.4323).

The average number of sprouts per sprouting individual (SPSPI) is mostly between 1 and 2.5 regardless of its SPIAI (Fig. 4), indicating that the difference in sprouting intensity among species is more a result of the numbers of individuals that sprouted instead of the number of sprouts each sprouting individual produced. The SPIAI are higher for shrubs than for trees, indicating that shrubs have higher sprouting ability than trees (Fig. 4).

#### Seeding and sprouting versus environmental factors

Relationships between 8 environmental factors and forest structures and number of seedlings/sprouts were analyzed by multi-variable generalized linear model in this study. Relationships between elevation and forest structures, represented by total individual (IND) and total stem (TLSTEM), and regeneration individuals, represented by number of seedling (SDLNNO) and number of sprout (SPRTNO), are not significant (Table 3). In contrast, topography is significantly related to IND, TLSTEM, SDLNNO, and SPRTNO (Table 3). In addition to topography, three other environmental factors are related to SDLNNO, whereas are not related to IND, TLSTEM, and SPRTNO (Table 3). Accordingly, topography is an important environmental factor related to forest structure and regeneration of woody plants.

Residuals of SDLNO/SPRTNO and IND/TLSTEM, from simple linear model, is correlated with environmental variables. Residuals of SDLNO and IND and TLSTEM have negative correlation with ALT (P =0.057 and 0.039) but positive correlation with canopy height (CNPHT) (P = 0.011 and 0.008). Meanwhile, residuals of SPRTNO and IND and TLSTEM have positive correlation with ALT (P = 0.040 and 0.045) and ROCKEXP (P = 0.011 and 0.008).

In the further analysis, topography was chosen as the factor examining relationships with forest structures and regeneration individuals. Mean values of IND, TLSTEM, SDLNNO, and SPRTNO are significantly different among ridge, slope and valley (Fig. 5). Notably, numbers of the four plant parameters all significantly increase from valley to ridge sites, demonstrating that woody plants regenerate vigorously at ridge. Higher numbers of sprout at ridge seemingly supports the hypothesis that sprouting is predominant at ridge sites. However, calculations of SI values reject the hypothesis. The mean values of SI are 0.70, 0.72 and 0.58 in ridge, slope and valley sites, respectively. The mean values of SI are not significantly different among topographic positions, even though the numbers of seedling and sprout are largely different along topographic gradient (Fig. 5). Consistent SI values of different topographic positions demonstrate that seedlings and sprouts of woody plants have similar trends along topographic gradient and have similar responses to environmental factors in evergreen broadleaved forests.

# Shifts between seedling dependence and sprout dependence

Species' SI is used as the index to indicate that regeneration of a woody species depends more on seedlings (SI > 0.5) or on sprouts (SI < 0.5) and whether or not it shifts between seedling dependence and sprout dependence along topographic gradient. Species' SI responses to topography can be categorized into four groups (Table 4). Most of the species constantly depend on either seedlings or sprouts along topographic gradient, especially the woody species with SI values at the two ends in Fig 1. Only 8 species (4 species of Group III and 4 species of Group IV in Table 2) shift between seedling dependence and sprout dependence along topographic gradient. Among these species, the SI index of Prunus campanulata is 0.84 and that of the other 7 species are between 0.45 and 0.74. From the results of SI index (Appendix II) and Table 4, most of the species do not change between seedling dependence and sprout dependence along topographic gradient, especially the species sit on the two ends of the Fig. 2. The species produce similar numbers of seedlings and sprouts tend to change their regeneration characteristics along

![](_page_5_Picture_2.jpeg)

 Table 1 Mean values of 8 parameters representing characteristics of sample plots.

Parameters	Mean ± SE
Number of individual	153.1 ± 6.1
Number of seedling	$68.3 \pm 4.6$
Number of sprout	22.5 ± 1.9
SI index	0.70 ± 0.01
Number of tree seedling	28.7 ± 2.6
Number of tree sprout	$7.5 \pm 0.6$
Number of shrub seedling	38.8 ± 3.2
Number of shrub sprout	13.7 ± 1.6

Table 2 Seedling and sprout banks analyzed by life forms.

Parameters	Tree	Shrub
Number of species	116	176
All individuals (AI)	7964	8806
Number of seedling (SDLNO)	3606	5396
Number of sprout (SPRTNO)	975	1993
Sprouting individuals (SPI)	610	1221
SI* = SDLNO/(SDLNO+SPRTNO)	0.80	0.66
SPIAI* (%) = ŠPI/AI	6.56	13.00
SPSPI* = SPRTNO/SPI	1.62	1.62

Note: \* for the calculation of SI, SPIAI, and SPSPI, only the species with more than 30 individuals or 30 regeneration individuals were included. As a result, all tree ferns and conifers were excluded.

![](_page_5_Figure_8.jpeg)

**Fig. 2:** The SI value (ratio of seedling versus seedlings + sprouts) of 35 dicot tree species (left panel) and 35 dicot shrub species (right panel). The grey bars are the SI value of each species and the texts in the grey bars are scientific names of each species. SI values of tree and shrub species indicate that regeneration of a woody species depends more on seedlings or sprouts. Only 5 tree species and 5 shrub species have the SI values lower than 0.5. The SI value lower than 0.25 indicates that a woody species is strongly reliant on sprouts and 3 species fit this criterion.

![](_page_6_Picture_0.jpeg)

**Table 3** Summary of multi-variable generalized linear models for the effects of 8 environmental factors on forest structures and regeneration characteristic. The two numbers in each cell are regression coefficient (upper) and *p*-value (lower) of each environmental factors. The *p*-values less than 0.05 are marked in bold. Variables of forest structure are total individual (IND) and total stem (TLSTEM) and that of regeneration dependence number of seedling (SDLNNO) and number of sprout (SPRTNO).

Dopondont variable	Regression coefficient (upper) and significance ( <i>p</i> -value, lower)								<b>D</b> 2	
Dependent variable	ALT	TOPO	SOILEXP	SOILRK	ROCKEXP	HRBCOV	CNPHT	CNPCOV	Г	R
IND	0.001	16.122	0.511	-0.373	-0.440	-0.037	0.450	0.522	6.982	0.311
	0.933	<0.001	0.054	0.353	0.223	0.802	0.604	0.292		
TLSTEM	0.007	18.643	0.536	-0.404	-0.375	-0.072	0.248	0.545	7.43	0.324
	0.676	<0.001	0.068	0.363	0.347	0.665	0.796	0.320		
SDLNO	-0.019	8.827	0.442	-0.192	-0.661	0.104	1.777	-0.037	3.029	0.165
	0.118	0.029	0.048	0.589	0.035	0.410	0.016	0.930		
SPRTNO	0.005	2.521	0.025	-0.031	0.065	-0.034	-0.202	0.023	3.798	0.197
	0.075	0.013	0.653	0.713	0.394	0.282	0.271	0.827		

ALT: altitude; TOPO: topographical position was recorded as valley, slope and ridge; SOILEXP: exposed soil surface was estimation of percentage of sample plot area free from herb coverage; SOILRK: Soil rockiness was recorded as the proportion of gravel content in the soil; ROCKEXP: Rock expose was the estimation of the percentage of sample plot area occupied by rock; HRBCOV: herb coverage; CNPHT: canopy height; CNPCOV: canopy coverage.

Table 4 The ratio of seedlings versus sprouts of woody plants across topography as indicated by the SI index. A high SI index indicates a higher presence of seedlings, whereas a low SI index indicates a higher presence of sprouts. Significance of differences between topographic sites were tested by 2×2 table Chi-square test using the number of seedlings and sprouts. A blank space indicates the absence of sprout and seedling in the habitat. The remaining species of Group I are listed in Appendix II.

	life	diaspore size		SI index	(	Ridge vs	Slope vs	Valley vs
sp-name	form	(mm <sup>3</sup> )	Ridge	Slope	Valley	Slope	Valley	Ridge
Group I (51 species) <sup>(1)</sup> : Seedling	depende	ence						
Machilus thunbergii	Т	523.6	0.73	0.80	0.73	***(2)	ns	ns
Pasania harlandii	Т	3591.3	0.93	0.59	0.88	***	ns	ns
Blastus cochinchinensis	S	< 0.001	0.96	0.87	0.87	*	ns	ns
Michelia compressa	Т	2806.1	0.92	0.99		**		
Myrsine seguinii	Т	47.7	0.94	0.50		*		
Cinnamomum subavenium	Т	181.0	0.84	0.70		*		
Viburnum integrifolium	S	79.5	0.62	0.90		*		
Cleyera japonica var. taipinensis	S	0.7	0.91	0.64		*		
Symplocos glauca	Т	179.6	1.00					
Barthea barthei	S	0.01	1.00					
Schefflera taiwaniana	S	343	0.98					
Symplocos caudata	S	22.4	0.74					
Viburnum urceolatum	S	96	0.97					
Rhododendron rubropilosum	S	1.3	0.54					
Group II (7 species): Sprout dep	endence	•						
Rhododendron leptosanthum	S	0.3	0.19	0.45	0.06	***	***	ns
Oreocnide pedunculata	S	0.3	0.33	0.17	0.14	ns	ns	ns
Fatsia polycarpa	S	22.4	0.48	0.49	0.21	ns	*	ns
Eurya glaberrima	S	22.4	0.35	0.50		ns		
Trochodendron aralioides	Т	22.4	0.35	0.09		ns		
Lyonia ovalifolia	S	1.2	0.12					
Photinia niitakayamensis	Т	113.1	0.30					
Group III (8 species): Seedling d	epender	nce at slopes, but s	prout	depende	ence at	ridges or valle	eys	
Castanopsis cuspidata var. carlesi	iΤ	1176.2	0.80	0.54	0.14	***	*	***
Beilschmiedia erythrophloia	Т	2854.5	0.91	0.86	0.33	ns	***	**
Helicia formosana	Т	14136.8	0.91	0.80	0.06	ns	***	***
Turpinia formosana	Т	268.1	0.33	0.80	0.40	***	***	ns
Itea parviflora	Т	2.1	0.30	0.52	0.67	ns	ns	ns
Engelhardia roxburghiana	Т	1.8	0.42	0.56	0.71	ns	ns	ns
Cyclobalanopsis stenophylloides	Т	1949.8	0.31	0.60		ns		
Neolitsea konishii	Т	904.8	0.36	0.80		ns		
Group IV (4 species): seedling d	epender	nce at ridge, but sp	rout d	ependen	ce at s	lopes		
Ligustrum liukiuense	S	117.8	0.56	0.13		*		
Hydrangea angustipetala	S	0.0	0.64	0.29		**		
Prunus campanulata	S	1767.1	0.90	0.40		**		
llex formosana	S	113.1	0.93	0.47		**		

(1) Remaining species in group I are listed in the Appendix II. (2)\*\*\*: p<0.001; \*: p<0.01; \*: p<0.05; ns: p>0.05

![](_page_7_Picture_2.jpeg)

![](_page_7_Figure_3.jpeg)

**Fig. 3:** Relationship between diaspore size (log value) and sprouting ability (sprouting individual / all individual) ( $F_{1,76} = 21.714$ ,  $R^2 = 0.4738$ , P < 0.0001). Negative correlation between these two parameters indicates that woody species with a higher proportion of sprouting individuals have less volumes of diaspores. Seeding/sprouting dependence is likely intrinsically determined, though it is not strong. Trees (solid circles) have higher diaspore sizes and smaller SPIAI ratios than shrubs (open circles).

![](_page_7_Figure_5.jpeg)

**Fig. 4:** The relationship between the mean number of sprouts per sprouting individual (SPSPI) and the sprouting ability as estimated by the ratio of sprouting individual to all individual (SPIAI) ( $F_{1,76}$  = 12.61,  $R^2$  = 0.377, P < 0.0001). The range of SPSPI is between 1.0 and 2.5, indicating that number of sprouts each woody individual produced is similar among species. High range of SPIAI indicates that woody species with higher values on x axis possess more sprouting individuals than that with lower values on x axis. Shrubs (open circle) have relatively higher sprouting abilities than trees (solid circle).

![](_page_7_Figure_7.jpeg)

**Fig. 5:** Differences in forest structure and regeneration characteristic among topographic positions. Forest structure represents by total individual and total stem, while regeneration characteristic numbers of seedlings and sprouts. Analysis of variances (ANOVA) were performed for (a) the number of total individuals (*F*-test, F value = 16.94, P < 0.0001), (b) the number of total stem (F-test, F value = 18.2, P < 0.05), (c) the number of seedlings (*F*-test, F value = 5.36, P < 0.01), and (d) the number of sprouts (*F*-test, F value = 5.644, P < 0.05). The dark circle indicates the mean value, and the whiskers indicate one SE. The letters by the dark circle indicate homogeneous groups, with a same letter in different categories indicating that the two categories were not significantly different.

![](_page_8_Picture_2.jpeg)

topographic gradient.

Regenerations characteristics of Group I and Group II are mainly dependent on seedlings and sprouts, respectively. Significant tests attempt to detect whether woody plants produce either more seedlings (Group I) or more sprouts (Group II) at different topographic positions (Appendix II). Group III and Group IV present changes between seedling dependence and sprout dependence along topographic gradient. However, not all the plants of Group III and Group IV have significant differences of SI index between topographic positions.

Group I: 51 of the 70 species analyzed (73%) show SI indices larger than 0.5 across all habitat types. Regeneration of these species are seedling dependent, and their dependence on seedlings do not change across topography. Significant differences of SI between slop and ridge indicates that these species produce more seedlings either at ridge sites or slope sites.

Group II: 7 species of plants (10%) have SI indices lower than 0.5 in all habitats. Regeneration of these species are sprout dependence. Most of these species are shrubs, and they all predominantly sprout across topography. Significant differences of SI between slop and ridge or slope and valley indicates that whether or not the species produce more sprouts at slope sites.

Group III: SI indices of 8 plant species (11%) are always larger than 0.5 at slope, but smaller than 0.5 at either ridge or valley. All of the plants in this group are trees. These plants tend to depend mainly on seedlings for their regeneration at slope, but depend more on sprouts at valley or ridge. The differences of SI index are significant for only 4 species, indicating that changes of these species are not fully supported by the statistical test.

Group IV: 4 species of plants (6%) have SI indices lower than 0.5 at slope but higher than 0.5 at ridge, and these plants are absent from valley sites. All of the plants in this group are shrubs. These plants produce more sprouts than seedlings at slopes but more seedlings than sprouts at ridges. The four plants have significant differences of SI index between ridge and slope; therefore, shifts of these plants are supported by our study.

### DISCUSSION

# Seeding or sprouting in subtropical evergreen broadleaved forests

Typhoon and heavy rainfall had frequent the study area and cause several different types of disturbances and stresses. Canopy gaps and landslides are commonly observed in the study area after typhoon and heavy rainfall. Canopy gaps caused by branch fall, tree fall or uprooted, are major disturbance types in evergreen broadleaved forests. The space and time of canopy gaps formation are unpredictable in evergreen broadleaved forests. Seed behavior is thought to evolve in response to unpredictability in space and time of canopy gaps (Lehouck *et al.*, 2009; Zammit and Westoby, 1987). Seeding is more efficient in colonizing canopy gaps.

The presence of landslides, a type of severe disturbance frequently caused by typhoon in the study area, is another possible explanation for the seeding dependence of woody plant regeneration in evergreen broadleaved forests. Landslide is one of the important factors driving regenerations of woody plants. Severe disturbances, such as fire, were frequently proposed to enhance sprouting in other ecosystems (Calvo et al., 2003; Franklin et al., 2010; Hodgkinson, 1998; Kauffman, 1991; Keeley and Zedler, 1978; Ladd et al., 2005; Lloret et al., 1999). As opposed to fires and wind throws that perturb the aboveground vegetation but leave underground parts relatively intact, landslides remove all vegetation above- and below-ground and leaving nothing from which to sprout. Seeds, on the other hand, could disperse from nearby areas to colonize these newly opened sites. Therefore, the hypothesis that sprouts play a more important role than seedlings in the recovery of forests after severe disturbances should be modified to: sprouts play a more important role than seedlings in the recovery of forests after severe disturbances that remove only above-ground vegetation. For forest recovery after severe disturbances that remove both above and belowground vegetation, such as landslides, the ecosystem will have higher dependence on seeding. Common severe disturbances, landslides, in the study site removed above- and below-ground vegetation is distinct from fire disturbances or serious damages by hurricanes.

In summary, canopy gaps and landslides all favor seedling establishment because these two disturbances are all unpredictable for woody plants. The results demonstrate that selection pressures in evergreen broadleaved forests favor establishment of seedlings than reproduction of sprouts irrespective of disturbance types. Low sprouting abilities of woody plants are probably resulted by that the selective pressure of disturbance types favor woody plants of seedling dependence in evergreen broadleaved forests.

In spite of, a deficit of our study on analyzing regeneration strategies of woody plants has to be mentioned. The sprouting ability of woody plants were accounted for the number of branches from the main stem. However, some woody plants, such as some species of Fagaceae, possess a feature that they extent their roots underground more than meters and produce latent buds. These latent buds are actually sprouts but are usually identified as seedlings. This feature is commonly observed in field samplings. However, the feature lacks quantitative estimation. To what extent the feature bias our results is uncertain. Estimation of this feature is difficult in this study because it is not possible to identify each individual of woody seedling derived from seeds or latent bud. Further studies are necessary to quantify whether small woody individuals are seedlings from

![](_page_9_Picture_2.jpeg)

germination of seeds or sprouts from latent buds of extending roots.

# Seedling dependence and sprout dependence along topographic gradient

Sprouting has been previously proposed to be advantageous for survival of woody plants under wind stress, harsh or unstable environments that would prevent the establishment and survival of seedlings (Boose et al., 2004; Kubo et al., 2010; Nanami et al., 2004; Nzunda et al., 2007). Accordingly, regenerations of woody plants are hypothesized to depend on seedlings at slopes and on sprouts at ridge or valley because of higher degree of stresses at ridge and valley. The hypothesis postulated an increase of sprouts and a decrease of seedlings form slope to ridge. However, the hypothesis is rejected by our results. Our results show that number of sprouts and seedlings consistently increase from slope to ridge. The results evidently conclude that seeding is always predominant in subtropical evergreen broadleaved forests irrespective of topographic positions.

In contrast to slope, mountain ridges receive constant wind blow results in a prevalent gradient of wind disturbance (Lin et al., 2003; Mabry et al., 1998). Constant wind blow was previously presumed as an important selective pressure to suppress woody plant growth but to accelerate reproduction of sprouts. The presumption is supported by our results because our study concludes an increase of sprout number from slope to ridge (Fig. 5). Additionally, we assume that woody plants invest more resources in reproduction of sprouts in order to compensate limits of height growth at mountain ridge. Nevertheless, woody plants tend to produce more seedlings as well as sprouts at mountain ridge and this is an unexpected result. The explanation of this unexpected result is probably relevant to the lower canopy height at mountain ridge. Forest canopy at mountain ridge is not well developed and sunlight can easily reach the forest floor (Chao et al., 2010). Light intensity is expected to increase from the forest floor at slope to that at ridge. Thus, an increase of seedling number from slope to ridge is reasonable because of higher light intensity at mountain ridge, though further studies are necessary.

On the other hand, environmental factors at valley are markedly different from that at slope and ridge. Soil rockiness and rock expose are usually observed at mountain valley and that are resulted by periodic flooding and water flow due to heavy rainfall in summer. Periodic flooding and water flow removed soil from forest floor that limited seedling establishment and consequent low woody plant densities at valley. Under stress of periodic flooding and water flow, woody plants are assumed to invest resources to root growth in order to anchor on the ground. Sprouting, on the contrary, is not necessary for survival of woody plants under stress of water flow and flooding at valley. Habitat characteristics at valley have diminished both seedling establishment and sprout reproduction of woody plants. In summary, our results determined that increasing strengths of disturbances or stresses from slope to ridge or from slope to valley do not ensure acceleration of woody plants' regenerations in evergreen broadleaved forests. Distinct disturbance types, such as constant wind blow at ridge and periodic flooding at valley, have different selective effects on woody plant regenerations.

Moreover, altitude and canopy height have slightly effects on the number of seedlings, the effects is likely to be interpreted by changes of species richness along elevation. Species richness had been proposed to decrease from evergreen broadleaved forests at lower elevation to mixed conifer-broadleaved forests at higher elevation (Hsieh et al., 1997; Li et al., 2013; Liao et al., 2013). Evergreen broadleaved forests at lower elevation possess higher species richness and is probably related to higher number of seedlings. On the other hand, number of sprouts is slightly affected by altitude and rock expose. Topographic gradient seems a more appropriate interpretation of the effects between sprouts and altitude and rock expose, since constant wind stress causes shallow soil layer and rock expose at mountain ridge.

# Shifts between seedling dependence and sprouting dependence

Whether sprouting is an intrinsic regeneration ability or triggered by environmental factors is uncertain. Regeneration characteristics, estimated by sprouting ratio and relative seedling density, had been proposed to change across ranges of plant distributions (García et al., 2003; Wei et al., 2015). Previous studies implied that regeneration characteristic is triggered by environmental factors, and, therefore, intrinsic sprouting ability have less influence compared to disturbances (Vesk and Westoby, 2004). In this study, seeding and sprouting of woody plants had been compared across small-scale environmental gradients. The results demonstrated that most of the woody species did not change their regeneration dependence. Since most of the woody species do not change their regeneration dependence, ecological effects serve as an external factor and are independent of intrinsic regeneration abilities. Disturbances, thus, presumably play as an evolutionary force selecting genotypes suited to the disturbance regimes in Taiwan.

Hypothesis of intrinsic determining regeneration characteristic is further supported by results that the proportion of individuals of a species that sprouted is negatively related to its diaspore size (Fig. 3). Species with higher proportion of sprouting individuals, such as *Lyonia ovalifolia*, *Rhododendron rubropilosum*,

![](_page_10_Picture_1.jpeg)

Oreocnide pedunculata, and Hydrangea angustipetala all have relatively small diaspores; whereas species with lower proportion of sprouting individuals, including Symplocos glauca, Prunus phaeosticta, Microtropis fokienensis and Symplocos wikstroemiifolia all have larger diaspores. It can be assumed that these species with lower proportion of sprouting individuals allocated more resources to seeds than to sprouts.

For the remaining 11% of the species, the prevalence of seeding versus sprouting at a site was not determined intrinsically, but triggered by ecological factors. Two such groups can be observed in these forests: 4 species in Group III and 4 species in Group IV. Regeneration of these two groups of woody plants were clearly separated by life forms. Tree species in Group III maintain a predominantly seedling dependence when located in the less stressful slope environments. This may be because woody plants of sprout dependence generally have to allocate resources to sprouts at the expense of height growth (Midgley, 1996; Vesk, 2006), whereas in favorable environments, regeneration by seeds did not always reduce growth (Chang et al., 2004; Reekie and Bazzaz, 1987). Therefore, at slopes, where trees are more sheltered from disturbance but have a good chance to reach the canopy, they relinquish the opportunity for sprouting in favor of reaching for the canopy, but in more stressed or disturbed ridge environments, trees shift towards the more resilient mode of sprouting. Shrubs in similar environments (Group IV), however, assume a different mode because they cannot reach the canopy. At the slopes where trees grew tall in competition for light, shrubs persisted in the understory by producing more sprouts. In contrast, at ridgetops where trees are shorter due to wind stress (Chao et al., 2007), shrubs have a higher chance of competing for light with their shorter tree neighbors. In such environments, shrubs redirect their resources to growing upwards, reducing their ability to sprout with height growth (Hodgkinson 1998), and as a result, rely more on the seedling establishment. These findings echo the importance of plant height (Barot et al. 2005) and light availability (Brock et al. 2005) in influencing shift of regeneration of woody plants.

### CONCLUSIONS

In summary, our results demonstrate that seeding is predominant in regeneration of evergreen broadleaved forests in Taiwan. Seedling establishment is adapted to the unpredictable canopy gaps and landslides in this area and is abundant in the forest floor at ridge probably because of higher light intensity, while sprouts are assumed to compensate height growth under wind stress at ridge. The advantageous of woody plants that changes regeneration behavior along topographic gradient is unknown. Since most of the woody plants in the study area are seedling dependence, seedling establishment may result in a fitness advantage for woody species in evergreen broadleaved forests. However, the effects of distinct stresses on sprouting of woody plants at mountain ridge are unknown and dynamic of sprouts is lack in this area. Long-term ecological experiments to record birth, growth, and mortality of sprouts in different forests along topographic gradient are necessary in evergreen broadleaved forests because it is useful to provide direct evidence to understand the persistence of woody plants under distinct stresses and disturbances.

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![](_page_13_Picture_2.jpeg)

**Appendix I.** Alphabetical order of 318 woody plant species sampled in this study. Five plant variables of each species were calculated from the data recorded in sample plots. A blank space indicates the value is 0. The plant list only include angiosperm woody species. Thus, the sum of each variable in this table are different from the values described in the Results.

Species name	All individual (IND)	Total stem (TLSTEM)	Sprouting individual (SPI)	Number of seedling (SDLNO)	Number of sprout (SPRTNO)
Acer albopurpurascens	2	2			
Acer kawakamii	48	53	2	21	5
Acer morrisonense	55	57	1	15	2
Acer palmatum var. pubescens	4	6	1	2	2
Acer serrulatum	26	26	07	1	40
Adinandra formosana	218	258	27	56	40
Adinandra lasiosiyla Alaiabullum atereanormum	142	151	0	84	9
Almphylium pleiospermum	2 52	2 52			
Amnelonsis cantoniensis	1	1			
Antidesma japonicum var densiflorum	8	10	1	4	2
Aphananthe aspera	2	2	•	•	-
Archidendron lucidum	12	12		3	
Ardisia cornudentata subsp. morrisonensis	18	22	3	16	4
Ardisia quinquegona	28	32	2	17	4
Ardisia sieboldii	39	51	8	8	12
Ardisia virens	33	36	2	104	3
Barthea barthei	42	42		70	
Beilschmiedia erythrophloia	87	100	8	39	13
Bischofia javanica	2	2			10
Blastus cochinchinensis	112	128	9	225	16
Calamus quiquesetinervius	1	1			
Callicarpa dichotoma	12	1	2	2	2
Callicarpa formosana	10	15	Z	3	Z
Callicarpa Rocillana Callicarpa randajensis	33	35	2	27	2
Camellia tenuifolia	246	285	28	62	39
Carninus kawakamii	5	5	20	02	00
Castanopsis cuspidata var. carlesii	368	449	44	156	81
Castanopsis fargesii	15	19	2	3	4
Celtis sinensis	8	8		1	
Cinnamomum austrosinense	2	2		1	
Cinnamomum camphora	1	1			
Cinnamomum insularimontanum	6	7	1	2	1
Cinnamomum macrostemon	6	6		9	
Cinnamomum micranthum	10	10		8	
Cinnamomum osmophloeum	8	8	07	2	47
Cinnamomum subavenium	240	287	27	182	47
Clerodendrum cyrtopnyllum	1	1	4	4	4
Clevere inpenies	4	5 204	1	52	27
Clevera japonica Clevera japonica var. morij	22	204	20	JZ 12	2
Clevera japonica var. taininensis	85	93	8	42	8
Cryptocarva chinensis	26	33	2	13	7
Cvclobalanopsis gilva	47	50	3	8	3
Cyclobalanopsis glauca	76	99	8	5	23
Cyclobalanopsis longinux	308	346	23	60	38
Cyclobalanopsis morii	60	62	2	5	2
Cyclobalanopsis salicina	10	22	2	8	12
Cyclobalanopsis sessilifolia	533	573	31	126	40
Cyclobalanopsis stenophylloides	126	154	13	31	28
Daphniphyllum glaucescens subsp. oldhamii var. oldhamii	79	81	2	62	2
Daphniphyllum himalaense subsp. macropodum	140	149	6	86	9
Debregeasia orientalis	6	6	10	105	40
Dendropanax dentiger	228	241	10	105	13
Deutzia puichra	19	23	3		4
Diculzia laiwaliciisis Dicenvros priantha	10	े। २	5	3	10
Diospyros enantria Diospyros ianonica	2	2			
Diospyros japonica Diospyros morrisiana	 118	124	4	19	6
Ecdysanthera rosea	1	1	7	10	0
Elaeaanus alabra	3	4	1	2	1
Elaeagnus grandifolia	1	1		-	
Elaeagnus thunbergii	3	3		4	

![](_page_14_Picture_0.jpeg)

Species name	All individual (IND)	Total stem (TLSTEM)	Sprouting individual (SPI)	Number of seedling (SDLNO)	Number of sprout (SPRTNO)
Elaeocarpus japonicus	442	468	19	158	26
Elaeocarpus sylvestris	68 1	73	3	14	5
Engelhardia roxburghiana	61	86	10	24	25
Eriobotrya deflexa	47	52	3	9	5
Erycibe henryi	1	1			
Euonymus carnosus	2	2		1	
Euonymus spraguei	8	9	1	0	1
Eurya chinensis	6	8	2		2
Eurya crenatifolia	64	82	11	34	18
Eurya glaberrima Eurya gnaphalocarpa	190	228	27	19 7	38
Eurya ghaphaiocarpa Furya leptophylla	119	142	17	88	23
Eurya loquaiana	611	727	85	206	116
Eurya strigillosa	51	59	5	7	8
Eustigma oblongifolium	13	13		5	
Fagus nayalae Fatsia polycarpa	298	423	65	111	125
Ficus erecta var. beecheyana	36	37	1	14	1
Ficus fistulosa	11	11		1	
Ficus formosana	15	15	4	18	0
FISSISTIGMA GIAUCESCENS Eissistiama oldhamii	9	12	1	14	3
Gardenia iasminoides	1	1			
Glochidion acuminatum	23	23		10	
Glochidion rubrum	4	5	1		1
Glycosmis citrifolia Cordonia avillaris	2	2	5	73	7
Helicia cochinchinensis	90 13	15	2	1	2
Helicia formosana	102	123	11	29	21
Helwingia japonica subsp. taiwaniana	21	23	1	22	2
Hiptage benghalensis	2	2	20	<u></u>	<b>F</b> 4
Hydrangea angustipetala Hydrangea aspera	134	188	30	03	54 3
Hydrangea chinensis	29	37	3	38	8
Hydrangea integrifolia	4	4			
Idesia polycarpa	1	1	0	4	0
llex hioritsensis	0	0 1	2	4	Z
llex ficoidea	24	33	4	3	9
llex formosana	93	104	11	20	11
llex goshiensis	367	390	19	111	23
llex hayatalaha Ilex lonicerifolia	3 24	3 25	1	3	1
llex lonicerifolia var. matsudai	21	23	1	5	2
llex maximowicziana	1	1			
llex pedunculosa	2	2	4	44	4
llex sugerokii var. brevipedunculata	17	18	1	11 14	1
llex uraiensis	8	8	-	1	0
llex yunnanensis var. parvifolia	1	1		5	
Illicium anisatum	1	1	10		
Illicium arborescens Itea oldhamii	303	326	18	144	23
Itea parviflora	177	216	21	29	39
Juglans cathayensis	19	20	1		1
Kadsura japonica	26	26			•
Lagerstroemia subcostata	13	22	2	11	9
Lasianthus appressihirtus var. maximus	2	2		2	
Lasianthus fordii	56	56		188	
Lasianthus formosensis	1	1		1	•
Lasianthus japonicas	8	10	1	12	2
Lasianthus japonicus var. satsumensis	4	1 4		2 5	
Lasianthus wallichii	11	12	1	14	1

![](_page_15_Picture_2.jpeg)

Species name	All individual (IND)	Total stem (TLSTEM)	Sprouting individual (SPI)	Number of seedling (SDLNO)	Number of sprout (SPRTNO)
Ligustrum liukiuense	74	92	11	16	18
Ligustrum pricei	1	1			
Ligustrum sinense	15	15		16	
Limlia uraiana	19	21	1	13	2
Lindera communis	20	22	2	1	2
Lindera erythiocarpa	3	3 2			
Linuera megapinyila Liquidambar formosana	2	2	2		4
Litsea acuminate	1026	1088	49	548	62
Litsea cubeba	20	21	1	010	1
Litsea elongata var. mushaensis	192	203	9	56	11
Litsea hypophaea	2	2			
Lonicera acuminate	1	1			
Lyonia ovalifolia	129	228	45	14	99
Machilus japonica	126	135	8	58	9
Machilus japonica var. kusanoi	41	45	4	4	4
Machilus thunbergii	565	637	41	235	72
Machilus zuinoensis Maabilus zuibaanais var. muabaanais	28	28	2	20	2
Machinus zumoensis var. mushaensis Maesa japonica	13	10 71	3	2	3
Maesa perlaria var formosana	18	22	2	37	4
Mahonia iaponica	4	4	2	12	7
Mahonia oiwakensis	6	6		2	
Mallotus japonicas	11	11		2	
Mallotus paniculatus	6	6			
Malus doumeri	24	25	1	11	1
Melastoma candidum	3	3			
Meliosma rhoifolia	5	5		_	
Meliosma rigida	7	7		5	
Meliosma squamulata	44	48	4	22	4
Michella compressa Microtropio fokiononoio	528 77	538	5	237	10
Morus australis	1	04	2	03	I
Mucuna macrocarna	13	13			
Mvrica rubra	9	9		1	
Myrsine africana	2	2		20	
Myrsine seguinii	72	77	4	67	5
Neolitsea aciculate	26	28	2	9	2
Neolitsea aciculata var. variabillima	119	136	14	42	17
Neolitsea acuminatissima	889	1076	120	525	187
Neolitsea konisnii Orogonida podunaulata	96	113	11	13	17
Osmanthus beteronbyllus	66	90 76	7	0	20
Osmanthus marginatus	54	59	3	27	5
Osmanthus matsumuranus	31	33	2	13	2
Pasania cornea	5	6	1	5	1
Pasania hancei var. ternaticupula	77	92	8	33	15
Pasania harlandii	145	166	13	68	21
Pasania kawakamii	108	113	4	89	5
Pentapanax castanopsisicola	1	1	•		
Perrottetia arisanensis	11	15	3		4
Phoebe formosana Bhatinia niitakayamanaia	3	3	11	10	00
Photinia milakayamensis Photinia serratifolia yar Jasionetala	42	00	14	10	23
Phyllanthus oligospermus	4	4	2	2	2
Pieris taiwanensis	6	8	2	15	2
Pilea angulate	1	1	-	4	-
Pittosporum daphniphylloides	3	3			
Pittosporum illicioides	74	75	1	18	1
Platycarya strobilacea	42	44	2		2
Pourthiaea beauverdiana var. notabilis	12	15	2	3	3
Pourthiaea lucida	26	29	2	12	3
Pourthiaea villosa var. parvifolia	12	19	3	1	7
Premna micropnylla	1	1		1	
Ficilila scilalii0ila Prinsenia scandens	ა 1	ა 1			
Prunus campanulata	60	66	4	31	6

![](_page_16_Picture_0.jpeg)

Species name	All individual (IND)	Total stem (TLSTEM)	Sprouting individual (SPI)	Number of seedling (SDLNO)	Number of sprout (SPRTNO)
Prunus obtusata	1	1			
Prunus phaeosticta	1073	1126	37	530	53
Prunus takasagomontana Prunus transprisanensis	5	5		1	
Prunus transansanensis Psychotria rubra	32	33	1	1 27	1
Pyrenaria shinkoensis	27	28	1	14	1
Quercus tatakaensis	1	1	•		•
Quercus variabilis	20	20			
Radermachia sinica	2	2			
Randia cochinchinensis	24	27	1	7	3
Rhamnus kanagusuki	1	1		1	
Rhamnus pilushanensis	38	42	2	11	4
Rhaphiolepis Indica var. tashiroi Rhadadandran bravinarulatum	- - - -	1	o	26	24
Rhododendron formosanum	21	1/18	0 /3	30 Q/	24 63
Rhododendron lentosanthum	1294	1680	222	109	386
Rhododendron mariesii	1	1		100	000
Rhododendron oldhamii	28	49	8	12	21
Rhododendron ovatum	6	9	3	10	3
Rhododendron pseudochrysanthum	44	50	5	11	6
Rhododendron rubropilosum	52	82	17	35	30
Rhododendron simsii	1	1			
Rhus javanica var. roxburghiana	1	1	0	0	~
Rhus succedanea Pubus kawakamii	34 7	39	3	2	Э
Sabia transarisanensis	3	3			
Sarcandra dlabra	9	9		36	
Sassafras randaiense	1	1			
Saurauia tristyla var. oldhamii	36	40	4	10	4
Schefflera octophylla	199	211	9	46	12
Schefflera taiwaniana	53	54	1	44	1
Schima superba	173	181	6	63	8
Schizophragma integrifolium var. fauriei	1	1		4	
Scolopia oldnamii Sinononov formosono	2	2		1	
Shiopanax Tornosana Skimmia arisanensis	17	17		56	
Skimmia reevesiana	72	82	7	60	10
Sloanea formosana	22	22	·	6	
Stachyurus himalaicus	8	12	3	2	4
Stauntonia obovatifoliola	17	17		1	
Stellaria arisanensis	1	1		1	
Stephanandra incisa	7	7		4	
Stropliantnes cusia	1	1	4	1	10
Styrax suberifolia	24	21	4	2	10
Swida controversa	4	5	1	0	1
Swida macrophvlla	8	14	1		6
Sycopsis sinensis	275	343	37	120	68
Symplocos arisanensis	164	176	11	225	12
Symplocos caudate	113	126	9	37	13
Symplocos congesta	6	6		8	_
Symplocos formosana	24	32	4	9	8
Symplocos glauca	102	102	2	51	2
Symplocos konishii	30 10	40	2	6	2
Symplocos migoi	179	186	7	87	7
Symplocos morrisonicola	466	503	31	245	37
Symplocos sasakii	18	23	3	2	5
Symplocos sonoharae	1	1		1	
Symplocos stellaris	64	73	5	43	9
Symplocos theophrastifolia	40	40	-	28	
Symplocos wikstroemiifolia	31	33	2	37	2
Syzygium buxitolium	40	45 15	4	0	5
Syzygiuiii ioiiiiosaiiuiii Ternstroemia aymnanthera	155	10	1	4 103	2 5
Tetradium alabrifolium	9	9	7	100	5
Tetradium ruticarpum	4	4		3	

![](_page_17_Picture_2.jpeg)

Species name	All individual (IND)	Total stem (TLSTEM)	Sprouting individual (SPI)	Number of seedling (SDLNO)	Number of sprout (SPRTNO)
Tetrapanax papyriferus	2	2			
Toddalia asiatica	5	5			
Trachelospermum gracilipes	2	2		1	
Tricalysia dubia	58	61	2	12	3
Trochodendron aralioides	346	416	32	34	70
Turpinia formosana	317	379	45	74	62
Ulmus uyematsui	3	3			
Vaccinium bracteatum	7	9	2	1	2
Vaccinium dunalianum var. caudatifolium	1	1			
Vaccinium japonicum var. lasiostemon	2	2		1	
Vaccinium randaiense	25	38	6	2	13
Vaccinium wrightii	49	58	8	9	9
Ventilago leiocarpa	1	1		1	
Viburnum aboricolum	32	49	11	12	17
Viburnum erosum	3	3		16	
Viburnum foetidum var. rectangulatum	175	231	26	110	56
Viburnum formosanum	5	8	3		3
Viburnum integrifolium	78	102	11	54	24
Viburnum Iuzonicum	32	41	6	12	9
Viburnum propinquum	1	1		2	
Viburnum sympodiale	17	41	7	2	24
Viburnum taitoense	28	30	2	81	2
Viburnum urceolatum	43	46	1	89	3
Vitex quinata	2	2			
Wendlandia formosana	24	24		1	
Zanthoxylum scandens	6	6			
Zelkova serrata	14	18	3	1	4
	19730	22714	1829	8970	2984

**Appendix II.** Full table 4. The ratio of seedlings versus sprouts of woody plants across topography as indicated by the SI index. A high SI index indicates a higher presence of seedlings, whereas a low SI index indicates a higher presence of sprouts. Significance of differences between topographic sites were tested by 2 × 2 table Chi-square test using the number of seedlings and sprouts. A blank space indicates the absence of sprouts and seedlings in the habitat.

	life	dispersal unit	Ş	SI inde	Х	Ridge vs	Slope vs	Valley vs
Species name	form	(mm <sup>3</sup> )	Ridge	Slope	Valley	Slope	Valley	Ridge
Group I (51 species)					-	•		
Machilus thunbergii	Т	523.6	0.73	0.80	0.73	***	ns	ns
Pasania harlandii	Т	3591.3	0.93	0.59	0.88	***	ns	ns
Blastus cochinchinensis	S	< 0.001	0.96	0.87	0.87	*	ns	ns
Michelia compressa	Т	2806.1	0.92	0.99		**		
Myrsine seguinii	Т	47.7	0.94	0.50		*		
Cinnamomum subavenium	Т	181.0	0.84	0.70		*		
Viburnum integrifolium	S	79.5	0.62	0.90		*		
Cleyera japonica var. taipinensis	S	0.7	0.91	0.64		*		
Symplocos glauca	Т	179.6	1.00					
Barthea barthei	S	0.01	1.00					
Schefflera taiwaniana	S	343	0.98					
Symplocos caudate	S	22.4	0.74					
Viburnum urceolatum	S	96	0.97					
Rhododendron rubropilosum	S	1.3	0.54					
Dendropanax dentiger	S	131.9	0.91	0.77	0.80	ns	ns	ns
Neolitsea acuminatissima	Т	179.6	0.72	0.77	0.50	ns	ns	ns
Litsea acuminate	Т	1767.1	0.87	0.91	0.98	ns	ns	*
Neolitsea aciculata var. variabillima	Т	523.6	0.71	0.83	0.50	ns	ns	ns
Eurya leptophylla	S	6.0	0.77	0.79	0.90	ns	ns	ns
Illicium arborescens	S	220.9	0.87	0.87	0.71	ns	ns	ns
Schefflera octophylla	S	65.4	0.80	0.81	0.71	ns	ns	ns
Eurya loguaiana	S	22.4	0.62	0.63	0.85	ns	ns	*
Prunus phaeosticta	Т	220.9	0.89	0.93	0.90	ns	ns	ns
Pasania hancei var. ternaticupula	Т	1767.1	0.92	0.60		*		

100	
S.	
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Taiwania

1.21								
Successis sinensis	т	65.4	0.77	0.50		*		
Sycopsis sinensis Clevera janonica	۱ د	05.4	0.77	0.59		ne		
Camellia tenuifolia	6	150.8	0.59	0.33		115		
Phododendron formosonum	S	0.8	0.59	0.70		ne		
Cyclobalanansis sessilifalia	т	1058.0	0.57	0.01		nc		
Litsee elongata var. mushaensis	ŝ	1150.3	0.72	0.04		ne		
Machilus janonica	т	Q0/L8	0.35	0.70		ne		
Symplocos stellaris	Ś	142 A	0.33	0.02		ne		
Eurva crenatifolia	S	10.0	0.70	0.00		ne		
Viburnum foetidum var rectangulatum	S	113.1	0.00	0.02		ns		
Symplocos morrisonicola	S	254.4	0.00	0.00		ne		
Adinandra lasiostvla	S	65.4	0.00	0.88		ns		
llex aoshiensis	s	22.4	0.80	0.00		ne		
Gordonia axillaris	ŝ	219.9	0.00	0.83		ns		
Symplocos arisanensis	s	127.2	0.02	0.00		ns		
Cyclobalanonsis longinux	т	606.1	0.63	0.56		ns		
Ternstroemia gymnanthera	Ť	1022.6	0.00	0.00		ns		
Adinandra formosana	s	0.6	0.50	0.54		ns		
Schima superba	т	94.5	0.00	0.86		ns		
Elaeocarnus ianonicus	Ť	104.7	0.86	0.84		ns		
Daphniphyllum himalaense subsp. macropodum	Ť	33.5	0.00	0.04		ns		
Pasania kawakamii	Ť	5963.9	0.00	0.01		ns		
Osmanthus marginatus	Ś	942.5	0.74	1 00		ns		
Symplocos wikstroemiifolia	s	890.1	1 00	0.87		ns		
Sympleces minoria	s	207.3	0.85	1 00		ne		
Daphniphotos migor Daphniphyllum glaucescens subsp. oldhamii var. oldhamii	т	188 5	0.00	1.00		ns		
Microtronis fokienensis	•	884.9	0.00	1.00		ns		
Group II (7 species)		004.0	0.00	1.00		110		
Rhododendron lentosanthum	S	0.3	0 19	0 45	0.06	***	***	ns
Oreocnide pedunculata	ŝ	0.3	0.33	0.17	0.00	ns	ns	ns
Fatsia polycarpa	s	22.4	0.48	0.49	0.21	ns	*	ns
Furva glaberrima	ŝ	22.4	0.35	0.50	0.21	ns		110
Trochodendron aralioides	т	22.4	0.35	0.09		ns		
l vonia ovalifolia	s	12	0.00	0.00		no		
Photinia niitakavamensis	T	113 1	0.30					
Group III (8 species)			0.00					
Turpinia formosana	т	268.1	0.33	0.80	0.40	***	***	ns
Castanopsis cuspidata var. carlesii	Ť	1176.2	0.80	0.54	0.14	***	*	***
Beilschmiedia ervthrophloia	Т	2854.5	0.91	0.86	0.33	ns	***	**
Helicia formosana	т	14136.8	0.91	0.80	0.06	ns	***	***
Itea parviflora	Ť	2.1	0.30	0.52	0.67	ns	ns	ns
Engelhardia roxburghiana	Ť	1.8	0.42	0.56	0.71	ns	ns	ns
Cvclobalanopsis stenophylloides	Ť	1949.8	0.31	0.60		ns		
Neolitsea konishii	Ť	904.8	0.36	0.80		ns		
Group IV (4 species)								
Ligustrum liukiuense	S	117.8	0.56	0.13		*		
Hydrangea angustipetala	Ŝ	0.0	0.64	0.29		**		
Prunus campanulata	S	1767.1	0.90	0.40		**		
llex formosana	S	113.1	0.93	0.47		**		

\*\*\*: <0.001; \*\*: <0.01; \*: < 0.05; ns: > 0.05