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Research paper

Survival and Height Growth Dynamics of Seedlings Growing in the Windward Slopes of Nanjenshan Forest Over a 9-Year Period

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ABSTRACT

The recruitment and growth of seedlings influence the subsequent composition and structure of forests. This study set up 44 1-m² seedling plots in the windward slopes of Nanjenshan Forest, Kenting National Park, and conducted monthly censuses over a 9-year period from 2002 to 2011. The objectives of this study were to explore the species richness, abundance, survival time, and height growth of newly recruited seedlings under long-term chronic stress due to the northeast monsoon, as well as differences in the seedling dynamics of other subtropical forests in Taiwan. In the study sites, 71 species of adult trees were recorded. In the seedling plots, 75 species of advanced seedlings and newly recruited seedlings were found, among them 59 species of seedlings and adult trees were the same composition. The density of seedlings increased from 25 stems m^{-2} to 35 stems m^{-2} between the initial census and the subsequent years. During the investigation, 64 species and 1,688 individuals of newly recruited seedlings were recorded, with *Microtropis japonica* and *Rhaphiolepis indica* var. *hiiranensis* being the most abundant. There were 30 seedling species in abundance ≥ 10 individuals, and the average survival proportions of these 30 species at the age classes of 13–24, 25–36, and 37–48 months were 70%, 53%, and 42%, respectively. Survival analysis indicated that 12 seedling species had a median survival time (MST) ≥ 36 months, and the MST value of overall new recruits was 34 months, which was much higher than the MST values of six months for Fushan Forest, Kenting Karst Forest, and Nanjenshan Leeward Forest in Taiwan. Seedlings of shade-intolerant species in the study sites had an MST value of 12 months, and new recruits could grow as high as 20 cm in 1.5 years; seedlings of shade-tolerant species had an MST value of 39 months and needed 2.7 to 21 years to grow as high as 20 cm. Sporadic typhoon disturbance damage to forest canopies thus increased understory light availability, while gusty monsoon winds inhibited understory herbaceous plants from light competition. Both factors enhanced the recruitment and growth of understory woody seedlings. Under this environment, the species richness, density, and survival time of seedling communities

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in the windward slopes of Nanjenshan were all higher than those of seedling communities in the other three subtropical forests of Taiwan.

Keywords: long-term chronic stress, median survival time, northeast monsoon, seedling species richness, typhoon disturbance

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INTRODUCTION

Seedling recruitment is a key ecological process in forest ecosystems. As it enables both natural regeneration and post-disturbance recovery, it plays a critical role in both maintaining forest composition and structure and promoting species diversity (Ribbens et al. 1994, Green et al. 2014). Previous studies on seedling dynamics in tropical and subtropical forests have identified several ecological patterns: (1) Most seedlings have short survival times during early life-history stages, with high mortality occurring within the first year after germination (Chang-Yang et al. 2013, Lin et al. 2017). (2) Seedlings grow slowly in the understory (Chang-Yang et al. 2021, Wright et al. 2024). (3) Seedling recruitment, growth, and survival all rise with increasing light availability in the understory (Montgomery and Chazdon 2002, Kuo et al. 2007, Rüger et al. 2009, Chao et al. 2022). (4) Shade-tolerant seedlings have longer survival times than shade-intolerant seedlings (Lin et al. 2017, Lin et al. 2024), with the former capable of persisting for decades in low-light understory environments (Delissio et al. 2002, Condit et al. 2025).

Studies on seedling dynamics in subtropical forests of Taiwan have shown that most newly recruited seedlings have very short survival times after germination (Lai 1996, Leu 2004, Chang-Yang et al. 2013, Lin et al. 2017, Lin et al. 2024). For seedling communities in the Fushan Forest Dynamics Plot, Kenting Karst Forest Dynamics Plot, and Nanjenshan Plot I, the median survival time (MST) estimated using the Kaplan-Meier survival method was six months at all three plots (Chang-Yang et al. 2013, Lin et al. 2017, Lin et al. 2024). This indicates that most newly recruited seedlings in these three forests die within the first year after germination. However, some studies have reported that the survival proportion of 1-year-old newly recruited seedlings reaches ≥ 60% (Li 1995, Liao 2019). Moreover, studies of seedling dynamics over a 5–8 year period in Fushan Forest, Kenting Karst Forest, and Nanjenshan Plot I have shown that the number of newly recruited seedling species is consistently less than half that of overstory tree species (Chang-Yang et al. 2013, Lin et al. 2017, Lin et al. 2024), indicating strong recruitment limitation in these forest communities.

The survival of woody seedlings in the forest understory is determined by the interaction between heritable species traits and surrounding biotic and abiotic factors (Kobe and Vriesendorp 2011, Lu et al. 2015). Under conditions of limited light availability in the understory, seedlings of shade-intolerant species are expected to die shortly

after germination because they cannot obtain sufficient light to support photosynthetic carbon gain. By contrast, seedlings of shade-tolerant species are genetically characterized by extremely low dark respiration rates, which reduce carbon expenditure, and low light compensation points (Kuo et al. 2021), as well as a greater capacity to utilize the CO_2 released from soil respiration (Chen and Kuo 2025), thereby enabling them to maintain a positive carbon balance and prolong survival under low-light understory conditions. Among the biotic factors influencing seedling survival, negative conspecific density dependence (NCDD) is widely considered an important driver (Comita and Hubbell 2009, Johnson et al. 2012, Lu et al. 2015). Seedlings surrounded by a high density of conspecific seedlings are more likely to die due to herbivory, pathogen attack, or intraspecific competition (Metz et al. 2010, Paine et al. 2012, Comita et al. 2014). Strong negative effects of high conspecific seedling density on seedling survival have been reported for Fushan Forest (Chang-Yang et al. 2013), Kenting Karst Forest (Lin et al. 2017), Lienhuachih Forest Dynamics Plot (Huang et al. 2022), and Nanjenshan Plot I (Lin et al. 2024). In Fushan Forest, only two seedlings per 1 m^2 have survived (Chang-Yang et al. 2013). Additionally, higher heterospecific seedling density has been reported to affect seedling survival positively (Fan et al. 2010, Huang et al. 2022).

The Nanjenshan area experiences long-term chronic wind stress associated with the northeast monsoon during autumn and winter, as well as episodic typhoon disturbances in summer and autumn. At windward sites directly exposed to the northeast monsoon, forest physiognomy is characterized by a low canopy, thin stems but high stem density, and a composition dominated by warm-temperate and subtropical species. By contrast, leeward sites with milder monsoon influence support forests of taller stature, lower stem density, and a tree community dominated by tropical species (Hsieh et al. 2000, Fan et al. 2005, Chao et al. 2010, Ku et al. 2021). Species occurring on windward slopes typically have tougher leaves and higher leaf mass per area, which confer greater resistance to mechanical damage from strong winds (Wu and Kuo 2011, Fan and Kuo 2013). Physiologically, these species exhibit greater tolerance to dehydration stress (Kuo and Lee 2003, Wu and Kuo 2011), show less stomatal closure under wind exposure (Kuo et al. 2011), and maintain relatively higher net photosynthetic rates under low-temperature conditions (Chen and Kuo 2008).

A study of seedling dynamics at leeward sites in the Nanjenshan area reported survival proportions of 51% and 20% for seedlings aged ≥ 0.5 and ≥ 1.25 years, respectively, and an overall MST of only six months for understory seedlings (Lin et al. 2024), indicating low survival proportions and short survival times. Sun et al. (1996) proposed that, under long-term wind stress, plants at windward sites in the Nanjenshan area exhibit slow growth and low survival proportions. This raises the question of whether seedlings at windward sites have lower survival proportions than those at leeward sites. To date, no studies on seedling dynamics have addressed this comparison. To address this gap, we conducted a 9-year seedling dynamics study in a windward forest in the Nanjenshan area to examine the following questions: (1) What is the species richness of seedlings in the windward forest, and is it less than half that of the overstory adult tree community? (2) How many seedlings can be supported per 1 m^2 in the windward forest? (3) How does the survival proportion of newly

recruited seedlings change with increasing seedling age? (4) What are the MST values of the overall seedling community, shade-tolerant and shade-intolerant groups, and individual species as estimated by survival analysis, and how do these compare with those in other subtropical forests in Taiwan? (5) What are the height growth dynamics of different seedling species in the study plot?

MATERIALS AND METHODS

Study sites

The study sites are in the Nanjenshan Ecological Reserve (120°51′37″E, 22°02′51″N) within Kenting National Park (Figure 1a). Two study sites were established on the windward slopes to the south and north of the 3.5-km mark of the Nanjen Trail, which leads to Nanjen Lake (Figure 1b, Sites A and B). The southern site, surrounded by a narrow pond on three sides, covers approximately 0.15 ha, is at an elevation of about 330 m, and has a relatively gentle slope. The northern site is located approximately 250 m from the southern site, at an elevation of about 345 m, near a ridgeline, and has a steeper slope. The two sites exhibit similar forest physiognomy: the canopy is low (3–5 m) and discontinuous, and most trees have a diameter at breast height (DBH) < 10 cm, yet the stand stem density is high, and the understory of herbaceous plants is sparse. According to data from the Binlang station (code: COR280) of the Central Weather Administration, located near the ecological reserve, the area had a mean annual temperature of 22.6℃ from 2001 to 2011, with the lowest monthly mean in January (17.9℃) and the highest in July (26.2℃). Mean annual precipitation was 3,219 mm, with 66% occurring from June to September and relatively low rainfall from November to the following April. At the study sites, the northeast monsoon prevails annually from October to the following March. According to data from weather stations established by the Nanjenshan Long-Term Ecological Research network, one at a windward site near Nanjen Lake and another at a leeward site 0.5 km south of the Nanjen Trail, during the six-month period of prevailing northeast monsoon from 1996 to 2004, the mean monthly wind speed at the windward site was 5.2 m s^{-1}, with maximum wind speeds of 9–13 m s^{-1}, whereas the mean monthly wind speed at the leeward site was consistently below 2.0 m s^{-1} (Chen and Kuo 2008). Typhoons frequently strike the Nanjenshan area between July and September, and typhoon disturbances often damage the canopy and create canopy gaps, thereby increasing understory light availability (Pen et al. 2007).

Adult tree and seedling census

In July 2002, an adult tree census plot was established at the southern study site (Figure 1b, Site A) to characterize the composition and parameters of the adult tree community. For the census, a theodolite (TOPCON DT30, Japan) was used to lay out aluminum stakes at 10 m intervals along the north–south and east–west directions. Each set of four stakes defined a 10 m × 10 m plot, which was further divided into four 5 m × 5 m quadrats for a complete tree census. A total of 14 10 m × 10 m plots were established, and one additional plot near the water contained only two 5 m × 5 m quadrats due to limited space, yielding 58 quadrats in total. Within each quadrat, all tree and shrub individuals with a DBH ≥ 1 cm were tagged with numbered aluminum tags, and for each tagged individual, the species name, DBH, and tree height were recorded. Species shade

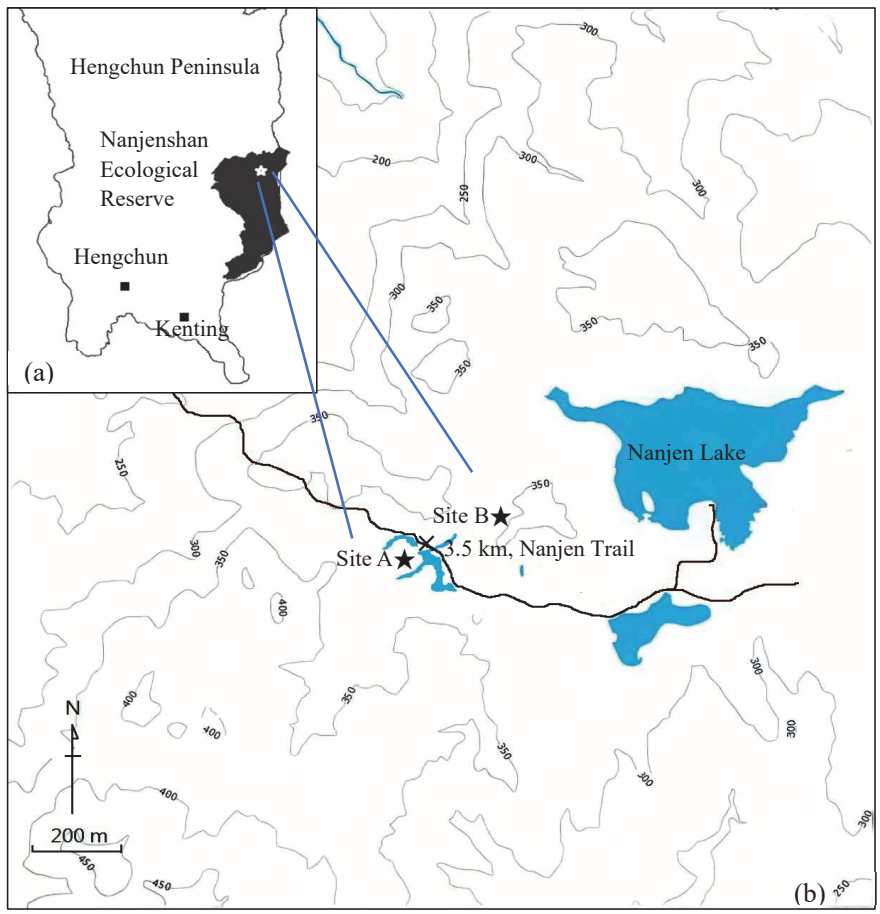

Figure 1. The study sites were located in the Nanjenshan Ecological Reserve (南仁山生態保護區), Kenting National Park (墾丁國家公園) of southern Taiwan (a). Site A and B indicate the seedling dynamics plots south and north of the 3.5-km mark of the Nanjen Trail, respectively (b).

tolerance classes followed Kuo et al. (2021) but were simplified into three groups: species in classes I and II were assigned to the shade-intolerant group, those in classes VI and V to the shade-tolerant group, and those in class III remained in the moderately shade-tolerant group.

Within the adult tree census plot at the southern site, microhabitats with relatively high seedling species richness (≥ 8 species) and a relatively high number of seedling individuals (≥ 15, while avoiding dominance by a few species) were subjectively selected, and 20 seedling plots were established there. Each seedling plot measured 2.0 m × 0.5 m (area = 1 m²). This subjective, non-random, and non-systematic sampling approach did not provide an unbiased representation of seedling community composition and abundance but allowed for the collection of detailed information on recruitment, mortality, and height-growth dynamics across a relatively large number of species. All woody seedlings < 100 cm in height (excluding woody lianas) within each seedling plot were tagged with numbered plastic tags (46

mm × 12 mm), and species identity, height, and leaf number were recorded for each individual. Individuals present at the initial census were classified as advanced seedlings, whereas those that were recruited thereafter were classified as newly recruited seedlings. Seedling plots were resurveyed monthly. When newly recruited seedlings were encountered, they were tagged, their species were identified, and they were recorded for height and leaf number. During each census, if a seedling was found dead (with the tag still present), the tag was collected. If both the seedling and its tag were missing and did not reappear in the subsequent two censuses, the individual was recorded as dead. On 3 September 2003, Typhoon Dujuan struck southern Taiwan, causing partial canopy damage and creating several canopy gaps at the study site, which substantially increased understory light intensity. Expecting that these gaps would promote the recruitment of shade-intolerant seedlings, we established four additional seedling plots beneath different canopy gaps in October 2003 to monitor post-typhoon regeneration dynamics. In addition, to increase the sample size of seedling plots, 10 additional plots were established in February 2004 at the northern windward slope forest (Site B, Figure 1b) at the 3.5-km mark of the Nanjen Trail, using the same approach. Eleven more plots were added in August of the same year, giving a total of 21 seedling plots at the northern site. Although no forest composition census was conducted at this site, field observations indicated that the forest physiognomy and species composition were highly similar to those at the southern site. Initially, the boundaries of each seedling plot at both sites were delineated by yellow nylon ropes placed on the ground surface, but these boundaries were frequently obscured by litterfall and became difficult to discern. Therefore, in August 2004, all plot boundaries were replaced with three-dimensional rectangular frames constructed from PVC pipes (outer diameter: 28 mm), while the original length and width of the plots were maintained. Four supporting stakes were added along the 2-m sides of each frame and inserted into the understory, and the entire frame was elevated 5 cm above the ground, thereby providing clearly visible plot boundaries. One plot (#24) located beneath a canopy gap at the southern site was abandoned in 2006 due to severe invasion by bamboo *Schizostachyum diffusum* (Blanco) Merr. Therefore, the analysis of seedling dynamics in this study was based on data from 44 plots. Scientific names of plant species follow the Catalogue of Life in Taiwan (TaiCOL 2025). The compositional similarity between the seedling community and the overstory adult tree community was calculated using the Dice-Sørensen coefficient (DSC) (Dice 1945):

$$DSC = \frac{2C}{A+B} \times 100\% \quad \cdots\cdots (1)$$

where A and B are the number of species in the seedling community and the adult tree community, respectively, and C is the number of species shared by both communities.

Light environment measurements

To quantify light availability in the seedling plots, measurements were conducted semiannually from 2005 to 2011, with additional measurements following typhoon disturbances. A total of 16 measurements were conducted during the study period. On each measurement occasion, photosynthetic photon flux density (PPFD) was measured between 10:30 and 13:00 using a quantum sensor (LI-190SA, LI-COR, Lincoln, NE, USA) connected to a light meter (LI-250, LI-COR).

Measurements were taken at five positions within each seedling plot at a height of 60 cm above the ground, and the mean PPFD was calculated for each plot. Simultaneously, full-light PPFD was measured on a platform located 4 m above the ground within the study area, and relative light intensity for each seedling plot was calculated as the ratio of mean plot-level PPFD to full-light PPFD.

Age-specific survival proportions and MST of newly recruited seedlings

The survival time (lifespan) of a newly recruited seedling was defined as the interval between its first and last recorded occurrences. For advanced seedlings, germination time was unknown, so their survival time and age-specific survival proportions could not be calculated. In this study, newly recruited seedlings were classified into two categories: (1) individuals that died during the study period, for which the exact survival time (in months) was known; and (2) individuals that were still alive at the final census in July 2011, for which the observed survival time was known but the ultimate lifespan had not yet ended. Six age classes (1, 2, 3, 4, 5, and 6 years) were defined, corresponding to survival time ranges of 13–24, 25–36, 37–48, 49–60, 61–72, and 73–84 months, respectively. The lower bound of each range was defined as the threshold month for that age class. For example, the threshold months for the 1-year and 2-year age classes were the 13th and 25th months, respectively. For a given species and age class *i*, the survival proportion was calculated as the number of seedlings whose survival time ≥ the threshold month (including individuals from both newly recruited seedlings categories), designated as N_i, divided by an adjusted denominator. Specifically, the denominator was the total number of newly recruited seedlings of that species (N_T) minus the number of second-category seedlings whose survival time was still below the threshold month at the final census (AL_i). For instance, if a newly recruited seedling was still alive at the final census with a known survival time of 48 months, which is below the 49-month threshold for the four-year age class, this individual was excluded from the denominator when calculating the survival proportion for that age class. The formula for age-specific seedling survival proportion (SP, %) is as follows:

$$SP_i = \frac{N_i}{N_T - AL_i} \times 100\% \quad \cdots\cdots (2)$$

where SP_i is the survival proportion for age class *i*; N_i is the number of seedlings with survival time ≥ the threshold month for that age class; N_T is the total number of newly recruited seedlings of the species; and AL_i is the number of second-category seedlings that were still alive but had not yet reached the threshold month at the final census.

In this study, we also estimated the MST (in months) of newly recruited seedlings using the Kaplan-Meier method (Lee and Wang 2003), implemented with the R package *survival* (R Core Team 2025), for the following groups: (1) the overall community of newly recruited seedlings; (2) seedlings of different shade-tolerance groups, namely shade-intolerant, moderately shade-tolerant, and shade-tolerant species; and (3) each of the 30 species with the highest numbers of newly recruited seedlings. After obtaining species-level MST values, regression analysis was used to examine, for each species, whether the age-specific survival proportions were significantly associated with its MST.

RESULTS

Adult tree composition at the study site

A total of 71 adult tree species (DBH ≥ 1 cm) comprising 2,330 individuals were recorded within the 1,450 m² plot located in the southern forest of the study site (Table 1), corresponding to a density of 16,100 stems ha^{-1}. At the family level, the most species-rich families were Lauraceae (8 species), Fagaceae (6 species), and Aquifoliaceae (5 species). At the species level, the most abundant species in descending order were *Illicium arborescens* Hayata (386 individuals), *Microtropis japonica* (Franch. & Sav.) Hallier f. (121 individuals), *Psychotria rubra* Poir. (108 individuals), *Ilex cochinchinensis* Loes. (102 individuals), and *Castanopsis cuspidata* var. *carlesii* (Hemsl.) T.Yamaz. (101 individuals). Conversely, 15 species were represented by only 1–3 individuals (Table 1). Among the recorded species, *Quercus championii* Benth. contained large individuals exceeding 60 cm DBH, while *Polyspora axillaris* (Roxb. ex Ker Gawl.) Sweet and *Engelhardia roxburghiana* Wall. reached DBH values of 30–40 cm. Individuals of *C. cuspidata* and *Quercus longinux* var. *kuoi* (J.C.Liao) C.F.Shen attained DBH values of 20–29 cm. Individuals of *Q. championii*, *C. cuspidata*, *Quercus pachyloma* Seemen, and *E. roxburghiana* exceeded 8 m in height (unpublished data).

Seedling composition, abundance, and density

At the initial census, 495 advanced seedlings representing 51 species were recorded across 20 seedling plots located in the southern study site (Table 1). After the addition of 24 seedling plots established later in the study, a total of 964 advanced seedlings representing 65 species were recorded, among which 55 species subsequently exhibited seedling recruitment during the study period. During the 9-year study period, a total of 1,688 seedlings representing 64 species were recruited (Table 1, TNR). At the final census in 2011, a total of 65 species were recorded among all seedlings (advanced and newly recruited seedlings combined), including 530 advanced seedlings and 1,019 newly recruited seedlings, for a total of 1,549 individuals. Seedling density was 24.8 stems m^{-2} at the initial census and increased progressively throughout the study period, reaching 35.2 stems m^{-2} at the final census (Figure 2). At the family level, the most species-rich seedling families were Lauraceae (8 species), Rubiaceae (7 species), and Fagaceae (5 species). One gymnosperm species, *Nageia nagi* (Thunb.) Kuntze, was also recorded (Table 1). Twelve species present in the adult tree community were not observed in the seedling layer, including *Ilex lonicerifolia* var. *matsudae* (Yamam.) Yamam., *Lithocarpus amygdalifolius* (Skan) Hayata, and *Camellia hengchunensis* C.E.Chang (Table 1). The adult tree and total seedling communities comprised 71 and 75 species, respectively. Of these, 59 species were shared between the two communities, whereas 16 species were exclusive to the seedling community. The Dice-Sørensen coefficient between the two communities was 80.8%, indicating high compositional similarity.

Temporal dynamics of newly recruited seedling abundance

The five species with the highest abundance of newly recruited seedlings were *M. japonica* (tree, 268 individuals), *Rhaphiolepis indica* var. *hiiranensis* (Kaneh.) H.L.Li (shrub, 179 individuals), *P. rubra* (shrub, 125 individuals), *I. arborescens* (tree, 102 individuals), and *P. axillaris* (tree, 95

Table 1. Abundance (stems) and shade-tolerance classes (STC) of trees with DBH ≥ 1 cm within 58 plots (25-m²) surveyed in July 2002 at the southern site of the windward slope of Nanjenshan Forest. Abundance of advanced seedlings at 20 seedling plots of 1-m² as of the initial census in July 2002 and the re-censuses of all seedlings in 44 seedling plots in August 2005, July 2007, 2009, and 2011. TNR: total newly recruited seedlings. INT: intolerant, MT: moderately tolerant, T: tolerant species

Species	Trees	Seedlings					
	Stems (STC)	2002	2005	2007	2009	2011	TNR
Podocarpaceae							
*Nageia nagi*竹柏EN[2,*5]	25 (T)	4	4	15	10	8	15
Aquifoliaceae							
*Ilex cochinchinensis*革葉冬青[6]	102 (T)	1	4	4	5	5	1
Ilex loniceri folia var. *matsudae*松田氏冬青#[1*]	94 (T)	0	0	0	0	0	0
*Ilex maximowicziana*倒卵葉冬青[*]	3 (T)	2	34	34	53	60	85
*Ilex rotunda*鐵冬青	1 (MT)	1	1	1	2	2	2
*Ilex uraiensis*烏來冬青	55 (T)	1	2	3	4	4	4
Araliaceae							
*Heptapleurum heptaphyllum*江某	6 (MT)	7	10	17	16	18	26
Celastraceae							
*Microtropis fokienensis*福建賽衛矛	0 (T)	1	10	6	6	5	0
*Microtropis japonica*日本賽衛矛[*]	121 (T)	116	172	188	220	258	268
Chloranthaceae							
*Sarcandra glabra*紅果金粟蘭	0 (T)	5	9	16	17	27	37
Clusiaceae							
*Garcinia multiflora*恆春福木	28 (T)	4	12	12	12	13	3
Daphniphyllaceae							
Daphniphyllum glaucescens subsp. *oldhamii* 奧氏虎皮楠	30 (T)	6	30	29	37	25	21
Ebenaceae							
*Diospyros eriantha*軟毛柿	10 (T)	2	4	4	4	3	2
*Diospyros morrisiana*山紅柿	14 (T)	0	1	1	1	1	0
Elaeocarpaceae							
*Elaeocarpus sylvestris*杜英	16 (MT)	2	8	8	9	12	7
Ericaceae							
*Rhododendron simsii*唐杜鵑[*]	28 (MT)	3	3	3	2	2	0
Euphorbiaceae							
*Macaranga tanarius*血桐	0 (INT)	0	1	0	0	0	1
*Mallotus paniculatus*白匏子	0 (INT)	0	40	44	39	19	85
*Melanolepis multiglandulosa*蟲屎	0 (INT)	0	10	13	4	0	31
*Triadica cochinchinensis*白桕	0 (INT)	0	40	32	23	14	35
Fabaceae							
*Archidendron lucidum*頷垂豆	54 (MT)	16	27	28	29	40	15
*Ormosia hengchuniana*恆春紅豆樹# NT[4]	11 (T)	1	1	1	1	0	0
Fagaceae							
Castanopsis cuspidata var. *carlesii*長尾尖葉櫧	101 (T)	18	37	40	37	33	20
*Lithocarpus amygdalifolius*杏葉石櫟	26 (T)	0	0	0	0	0	0
*Lithocarpus harlandii*短尾葉石櫟	6 (T)	0	0	0	0	0	1
*Quercus championii*嶺南青剛櫟[*]	27 (MT)	1	3	3	2	2	1
Quercus longinux var. *kuoi* 郭氏錐果櫟#	68 (T)	1	4	3	4	4	5
*Quercus pachyloma*捲斗櫟[*]	41 (MT)	5	5	5	6	7	4

Table 1. (continue)

Species	Trees	Seedlings				
	Stems (STC)	2002	2005	2007	2009	2011	TNR
Garryaceae							
*Aucuba chinensis*桃葉珊瑚	1 (T)	0	1	1	2	2	1
Hydrangeaceae							
*Hydrangea chinensis*華八仙	0 (T)	0	0	0	0	0	2
Juglandaceae							
*Engelhardia roxburghiana*黃杞	32 (T)	6	4	4	4	3	1
Lamiaceae							
*Callicarpa remotiflora*疏花紫珠# NT	0 (MT)	0	1	1	2	2	1
Lauraceae							
*Beilschmiedia erythrophloia*瓊楠	0 (T)	0	2	1	0	0	0
*Beilschmiedia tsangii*華河瓊楠	79 (MT)	4	18	12	14	16	2
*Cinnamomum brevipedunculatum*小葉樟#VU	13 (T)	6	11	8	8	7	1
*Cryptocarya chinensis*厚殼桂	5 (T)	0	0	0	0	0	0
*Litsea acutivena*銳脈木薑子	28 (T)	4	4	4	4	6	2
*Machilus thunbergii*紅楠	23 (T)	2	14	11	10	5	6
*Machilus obovatifolia*恆春楨楠#	1 (T)	0	0	0	1	1	1
*Machilus zuihoensis*香楠#	0 (MT)	12	10	8	9	11	15
*Neolitsea buisanensis*武威山新木薑子*	35 (T)	13	26	33	44	27	19
*Neolitsea hiiranensis*南仁山新木薑子# VU[3]	1 (T)	0	0	0	0	0	0
Magnoliaceae							
*Magnolia kachirachirai*烏心石舅# VU	33 (MT)	0	2	2	2	1	0
Michelia compressa var. *formosana*臺灣烏心石#	4 (MT)	0	1	1	1	1	0
Melastomataceae							
*Melastoma candidum*野牡丹	60 (INT)	0	1	12	44	33	54
Moraceae							
*Ficus formosana*天仙果	0 (MT)	1	6	7	6	8	3
Ficus superba var. *japonica*雀榕	1 (INT)	0	0	0	0	0	0
Myricaceae							
*Myrica adenophora*青楊梅EN	1 (MT)	0	0	0	0	0	1
Myrtaceae							
*Decaspermum gracilentum*十子木	2 (MT)	0	0	0	0	0	0
*Syzygium elliptifolum*橢圓葉赤楠#*	29 (T)	17	53	59	58	62	34
*Syzygium euphlebium*細脈赤楠	10 (T)	8	10	53	41	22	62
Oleaceae							
*Osmanthus marginatus*小葉木犀	26 (T)	7	17	38	37	35	50
Opiliaceae							
*Champereia manillana*山柚	3 (T)	0	0	0	0	0	0
Pentaphylacaceae							
*Adinandra formosana*臺灣楊桐#	6 (T)	0	0	0	0	0	0
Anneslea fragrans var. *lanceolata*細葉茶梨* #VU	29 (T)	1	0	0	1	1	1
*Cleyera japonica*紅淡比*	6 (T)	0	0	0	0	0	0
*Eurya nanjenshanensis*南仁山柃木# NT*	56 (T)	4	13	14	16	11	10
*Ternstroemia gymnanthera*厚皮香*	11 (T)	0	0	0	0	0	0

Table 1. (continue)

Species	Trees	Seedlings				
	Stems (STC)	2002	2005	2007	2009	2011	TNR
Phyllanthaceae							
*Antidesma hiiranense*南仁五月茶# NT	51 (T)	2	9	4	6	7	3
*Glochidion philippicum*菲律賓饅頭果	6 (INT)	0	5	5	2	2	0
*Glochidion rubrum*細葉饅頭果	5 (INT)	2	2	2	5	5	3
*Glochidion zeylanicum*錫蘭饅頭果	0 (INT)	0	0	0	3	3	3
Primulaceae							
*Ardisia quinquegona*小葉樹杞	26 (T)	0	2	2	2	1	1
*Ardisia sieboldii*樹杞	0 (T)	1	3	2	10	8	16
*Ardisia cornudentata*雨傘仔	25 (T)	43	73	74	69	80	43
*Myrsine seguinii*大明橘*	53 (T)	16	23	39	53	57	37
Proteaceae							
*Helicia rengetiensis*蓮華池山龍眼	4 (T)	0	0	0	0	0	0
Rosaceae							
*Prunus phaeosticta*墨點櫻桃	1 (MT)	0	1	1	1	1	0
Rhaphiolepis indica var. *hiiranensis*恆春石斑木#*	21 (MT)	48	137	139	110	103	179
Rubiaceae							
*Gardenia jasminoides*山黃梔	1 (MT)	5	9	17	39	37	47
*Lasianthus cyanocarpus*毛雞屎樹	0 (T)	2	14	15	16	28	21
*Lasianthus obliquinervis*雞屎樹	3 (T)	4	9	7	12	23	21
*Litosanthes biflora*壺冠木	0 (T)	0	2	2	1	3	2
*Psychotria rubra*九節木	108 (T)	33	85	94	108	113	125
*Tarenna gracilipes*薄葉玉心花#	8 (T)	0	2	2	3	0	3
*Tricalysia dubia*狗骨仔	40 (T)	1	6	10	8	7	5
Rutaceae							
*Melicope semecarpifolia*山刈葉	1 (MT)	0	1	3	2	3	6
*Tetradium glabrifolium*賊仔樹	0 (INT)	0	1	2	1	0	1
Sabiaceae							
*Meliosma squamulata*綠樟*	47 (T)	0	5	3	2	2	4
Schisandracea							
*Illicium arborescens*臺灣八角#	386 (T)	36	142	174	138	135	102
Symplocaceae							
*Symplocos congesta*楊桐葉灰木*	57 (T)	3	7	6	7	7	1
*Symplocos shilanensis*希蘭灰木# VU*	18 (T)	1	1	1	0	0	0
*Symplocos theophrastifolia*山豬肝	21 (T)	4	17	14	14	10	10
Theaceae							
*Camellia hengchunensis*恆春山茶# VU	3 (T)	0	0	0	0	0	0
*Polyspora axillaris*大頭茶*	58 (MT)	6	19	44	66	69	95
Schima superba var. *kankaoensis*港口木荷#	24 (MT)	2	2	2	2	2	0
Thymelaceae							
*Wikstroemia taiwanensis*臺灣蕘花#*	1 (T)	2	18	22	20	27	25
Total individuals	2,330	495	1,261	1,465	1,547	1,549	1,688
Total species	71	51	68	68	69	65	64

[1] #: Endemic to Taiwan, [2] EN: Endangered, [3] VU: Vulnerable, [4] NT: Near-threatened, [5] *: characteristic species of ridge-type community (Fan et al. 2005), [6] The underlined species are expected to persist in future forest composition.

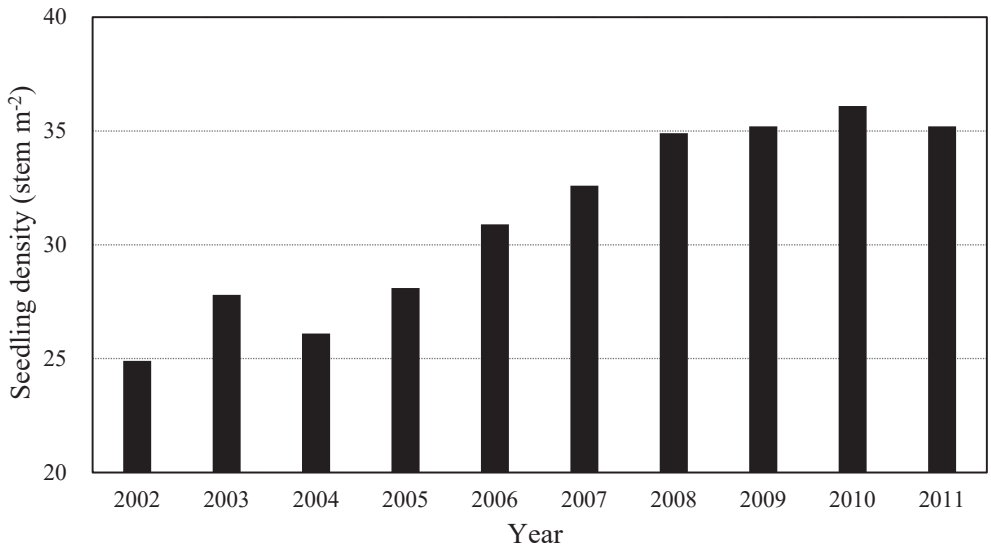

Figure 2. Density of advanced seedlings at the initial census (July 2002) and of all seedlings during subsequent re-censuses (July 2003–2011; August 2005) on the windward slopes of Nanjenshan Forest.

individuals). Thirty species each had ≥ 10 newly recruited seedlings, accounting for a total of 1,603 individuals (Table 2), whereas the remaining 34 species had < 10 newly recruited seedlings (85 individuals in total), including 14 species represented by only a single individual (Table 1). Among the 30 most abundant species, 28 occurred in both the southern and northern study sites, whereas *Syzygium euphlebium* (Hayata) Mori and *Archidendron lucidum* (Benth.) I.C.Nielsen were restricted to the southern study site.

Temporal patterns in newly recruited seedling abundance could be classified into four types (Figure 3). Type I was characterized by a progressively increasing abundance of newly recruited seedlings that remained consistently high thereafter. Representative species included *M. japonica*, *Ilex maximowicziana* Loes., *Ardisia cornudentata* Mez, *Syzygium elliptifolium* (Merr.) Merr., *Heptapleurum heptaphyllum* (L.) Y.F.Deng, and *Lasianthus cyanocarpus* Jack (Figure 3a, d, j, m, n, s). Type II showed a similar increasing trend, with newly recruited seedling abundance remaining high for several years before gradually declining. Species belonging to this group included *R. indica*, *I. arborescens*, *P. rubra*, *P. axillaris*, *Myrsine seguinii* H.Lév., *Gardenia jasminoides* J.Ellis, and *Osmanthus marginatus* (Champ. ex Benth.) Hemsl. (Figure 3b, c, e, f, g, h, i). Type III was characterized by a relatively stable abundance of newly recruited seedlings across all seven census years. This pattern was observed in *Daphniphyllum glaucescens* subsp. *oldhamii* (Hemsl.) T.C.Huang, *Neolitsea buisanensis* Yamam. & Kamik., and *C. cuspidata* (Figure 3p, q, r). Type IV was characterized by a marked recruitment pulse during a specific census year, followed by a sharp decline in newly recruited seedling abundance. Species showing this pattern included *Mallotus paniculatus* (Lam.) Müll.Arg., *S. euphlebium*, *Melastoma candidum* D.Don, *Triadica cochinchinensis* Lour., and *Melanolepis multiglandulosa* (Reinw. *ex* Blume) Rchb. & Zoll. (Figure 3k, l, o, t, u).

Table 2. Survival proportion (%) of newly recruited seedlings within various age ranges for 30 woody species growing in the windward slopes of Nanjenshan Forest. *n*, sample size, numbers in brackets are surviving individuals at the final census. MST, median survival time (months). A_{max}, the maximum photosynthetic rate (μmol CO_2 m^{-2} s^{-1}, reported by Kuo et al. 2021). Growth form T: tree, S: shrub. Species are listed in descending order of A_{max} values

Species and growth form	*n*	Seedling age (months)						MST	A_{max}
		13~24	25~36	37~48	49~60	61~72	73~84		
Melanolepis multiglandulosa (蟲屎) T	31 (0)	10	7	3	0	0	0	6	31.0
Mallotus paniculatus (白匏仔) T	85 (15)	45	28	22	18	15	0	11	29.4
Triadica cochinchinensis (白桕) T	35 (4)	63	41	38	18	13	3	19	26.0
Melastoma candidum (野牡丹) S	54 (24)	53	27	23	15	7	3	17	24.6
Machilus zuihoensis (香楠) T	15 (7)	71	62	45	45	22	11	53	19.7
Polyspora axillaris (大頭茶) T	95 (51)	75	61	49	31	26	20	64	19.4
Rhaphiolepis indica [1] (恆春石斑木) S	179(58)	64	42	29	22	15	12	19	18.1
Heptapleurum heptaphyllum (江某) T	26 (14)	80	62	55	39	31	0	48	17.4
Gardenia jasminoides (山黃梔) T	47 (31)	91	64	50	44	11	11	59	16.5
Archidendron lucidum (頷垂豆) T	15 (8)	69	36	30	22	13	13	22	16.1
Ardisia cornudentata [2] (雨傘仔) S	43 (32)	90	81	76	68	57	40	80	15.2
Ardisia sieboldii (樹杞) T	16 (6)	64	43	25	9	9	9	20	15.0
Daphniphyllum glaucescens [3] (奧氏虎皮楠) T	21 (9)	75	65	47	42	37	33	47	14.5
Castanopsis cuspidata [4] (長尾尖葉櫧) T	20 (9)	85	63	58	50	41	31	57	14.1
Psychotria rubra (九節木) S	125 (67)	79	65	44	38	30	5	48	13.8
Wikstroemia taiwanensis (臺灣蕘花) S	25 (14)	76	63	50	29	21	15	44	13.7
Ilex maximowicziana (倒卵葉冬青) T	85 (38)	64	37	19	8	2	0	26	13.5
Syzygium elliptifolum (橢圓葉赤楠) T	34 (16)	64	50	38	36	25	5	33	13.3
Myrsine seguinii (大明橘) T	37 (22)	83	66	62	50	21	6	59	12.9
Symplocos theophrastifolia (山豬肝) T	10 (3)	60	44	33	22	22	22	26	12.8
Osmanthus marginatus (小葉木犀) T	50 (24)	82	61	55	41	19	4	49	12.6
Neolitsea buisanensis (武威山新木薑子) T	19 (11)	82	71	71	63	44	38	71	11.6
Syzygium euphlebium (細脈赤楠) T	62 (14)	85	69	47	25	20	4	33	10.9
Illicium arborescens (臺灣八角) T	102 (48)	74	58	53	46	32	22	49	10.3
Microtropis japonica (日本賽衛矛) T	268(150)	74	54	39	26	16	11	37	8.7
Nageia nagi (竹柏) T	15 (4)	80	73	67	50	18	9	54	8.3
Sarcandra glabra (紅果金粟蘭) S	37 (19)	69	54	50	35	18	10	37	-
Lasianthus cyanocarpus (毛雞屎樹) S	21 (13)	60	46	33	27	20	20	30	-
Lasianthus obliquinervis (雞屎樹) S	21 (10)	62	31	15	8	8	8	22	-
Eurya nanjenshanensis (南仁山柃木) T	10 (4)	80	60	50	29	14	0	40	-
Mean		70.3	52.8	42.5	31.9	20.9	12.2		

[1] var. *hiiranensis*, [2] subsp. *cornudentata*, [3] subsp. *oldhamii*, [4] var. *carlesii*.

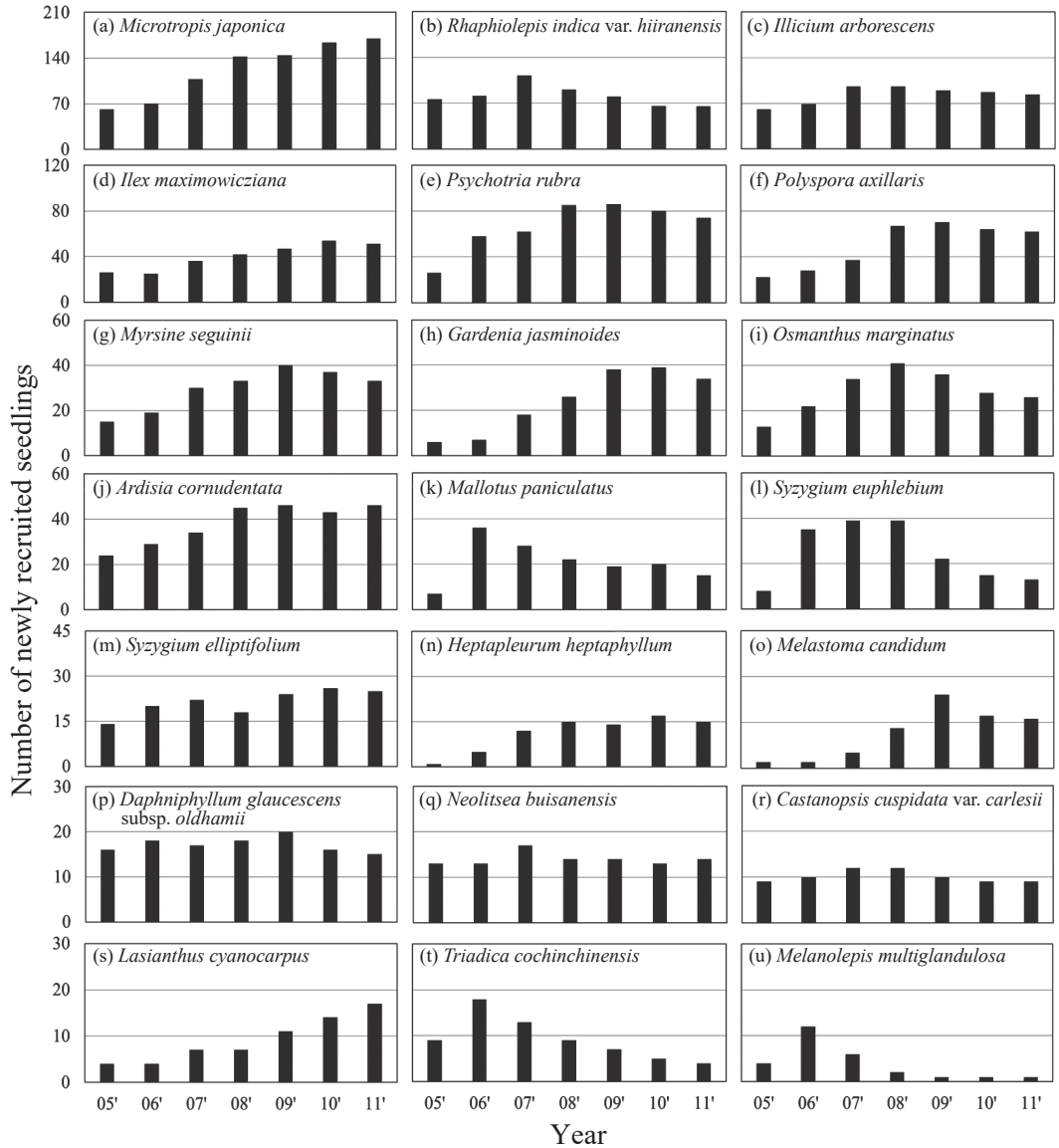

Figure 3. Annual abundance of newly recruited seedlings of 21 tree species during the July or August census (2005–2011) on the windward slopes of Nanjenshan Forest.

Survival proportions and MST across age classes of newly recruited seedlings

During the 9-year study period, a total of 1,688 newly recruited seedlings were recorded, of which 1,019 individuals remained alive at the final census. Seedling age ranged from 1 to 107 months. Nineteen individuals representing 12 species survived for ≥ 8 years (96 months), among which *I. arborescens* (5 individuals) and *C. cuspidata* (3 individuals) accounted for the greatest numbers. For the 30 species with ≥ 10 newly recruited seedlings, mean survival proportions

(mean ± 1 SD) across the six age classes of 13–24, 25–36, 37–48, 49–60, 61–72, and 73–84 months were 70.3 ± 17.2%, 52.8 ± 17.3%, 42.3 ± 17.2%, 31.9 ± 17.3%, 20.9 ± 13.6%, and 12.2 ± 12.4%, respectively (Table 2). In the 13–24-month age class, only *M. multiglandulosa* and *M. paniculatus* exhibited survival proportions below 50%. In the 25–36-, 37–48-, and 49–60-month age classes, the numbers of species with survival proportions ≥ 50% were 19, 11, and 5, respectively. In the 73–84-month age class, the survival proportions for *A. cornudentata* and *N. buisanensis* were as high as 40% and 38%, respectively (Table 2).

Across all 64 species (1,688 newly recruited seedlings), the MST, estimated using the Kaplan-Meier method, was 34 months (Figure 4). Among shade-tolerance groups, the MST of shade-intolerant species (8 species) was 12 months, whereas the MST values of moderately shade-tolerant (18 species) and shade-tolerant species (38 species) were 40 and 39 months, respectively. Among the 30 species with ≥ 10 newly recruited seedlings, MST values ranged from 6 to 80 months. The highest MST was observed in *A. cornudentata* (80 months), followed by *N. buisanensis* (71 months) and *P. axillaris* (64 months). MST values of 53–59 months were observed in five species: *Machilus zuihoensis* Hayata, *G. jasminoides*, *C. cuspidata*, *M. seguinii*, and *N. nagi*. MST values of 40–49 months were observed in seven species: *H. heptaphyllum*, *D. glaucescens*, *P. rubra*, *Wikstroemia taiwanensis* C.E.Chang, *O. marginatus*, *I. arborescens*, and *Eurya nanjenshanensis* (C.F.Hsieh, L.K.Ling & Sheng Z.Yang) Sheng Z.Yang & S.Y.Lu. By contrast, two species with relatively high abundance of newly recruited seedlings, *M. japonica* and *R. indica*, had MST values of 37 and 19 months, respectively (Table 2). Four shade-intolerant species, including *M. multiglandulosa*, *M. paniculatus*, *T. cochinchinensis*, and *M. candidum*, had relatively low MST values of 6, 11, 19, and 17 months, respectively (Table 2). Across the 30 species, MST was significantly positively correlated with

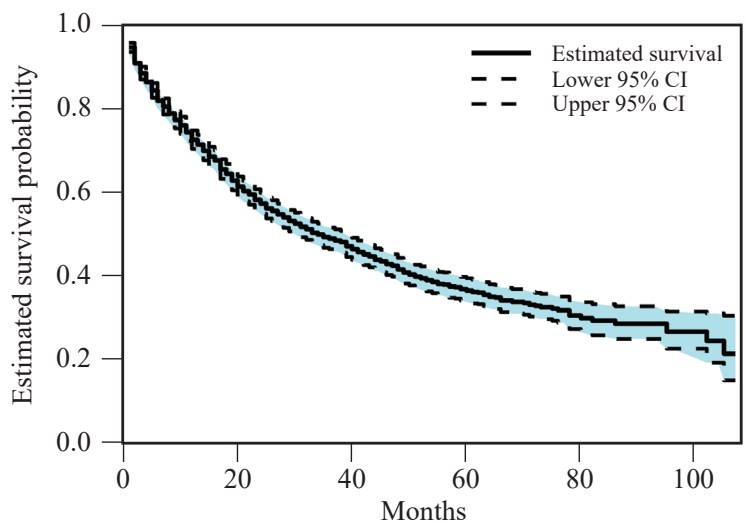

Figure 4. Estimated survival function of all new recruits combined on the windward slopes of Nanjenshan Forest based on monthly seedling censuses (July 2002–July 2011). Estimated survival average probability (solid line) and 95% confidence interval (CI) (dotted lines) are shown.

survival proportions in the 25–36-, 37–48-, and 49–60-month age classes ($r^2 \geq 0.80$), with the strongest relationship observed for the 49–60-month age class ($r^2 = 0.83$). Among these 30 species, 22 were tree species, and eight were shrub species (Table 2). Mean MST values (± 1 SD) were 40.1 ± 18.1 months for tree species and 37.1 ± 10.4 months for shrub species, with no significant difference between the two groups.

Height growth of newly recruited and advanced seedlings

Among the 30 species with ≥ 10 newly recruited seedlings, initial seedling height ranged from 4.0 to 7.4 cm, with *C. cuspidata* exhibiting the greatest initial height. By contrast, *H. heptaphyllum*, *Ardisia sieboldii* Miq., *P. rubra*, and *E. nanjenshanensis* had relatively low initial heights, all ≤ 4.5 cm (Table 3). Shade-intolerant species, including *M. paniculatus*, *T. cochinchinensis*, and *M. candidum*, exhibited rapid height growth. Collectively, these three species had mean heights (± 1 SD) of 27.5 ± 6.3 cm and 58.9 ± 21.3 cm at seedling ages of 24 and 48 months, respectively. Although photosynthetic capacity has not yet been measured for *Sarcandra glabra* (Thunb.) Nakai, *L. cyanocarpus*, *Lasianthus obliquinervis* Merr., and *E. nanjenshanensis* (Table 2), observations of their microhabitat light environments suggest that these species are shade-tolerant. Including these four species, the 26 shade-tolerant species in the study site exhibited slow height growth overall, with mean heights (± 1 SD) of 8.6 ± 1.5 cm and 13.6 ± 5.1 cm at 24 and 48 months, respectively. However, substantial interspecific variation was observed. Species exhibiting relatively rapid height growth included *M. zuihoensis*, *D. glaucescens*, *C. cuspidata*, and *W. taiwanensis*. At a seedling age of 48 months, the mean height of these four species exceeded 20 cm, and by 72 months, their mean heights were 33–53 cm. By contrast, such species as *A. sieboldii*, *P. rubra*, *O. marginatus*, *M. japonica*, and *S. glabra* exhibited extremely slow height growth. Mean seedling height remained < 10 cm at 48 months in each of these species (Table 3). At the final census, 1,019 newly recruited seedlings remained alive, among which 40 individuals representing 14 species had reached heights of ≥ 50 cm.

At the initial census, 495 advanced seedlings were recorded in 20 plots, of which 215 survived to the final census. At the initial census, individuals < 10 cm in height accounted for 40% of all advanced seedlings, whereas only 6% were ≥ 60 cm in height. After nine years, the height distribution of these advanced seedlings shifted markedly upward, with the 20–29 cm height class becoming the most abundant, while the proportion of individuals ≥ 60 cm increased to 26% (Figure 5). Across all 44 plots, 530 advanced seedlings survived to the final census, of which 108, 13, and three individuals reached heights of ≥ 100, 200, and 300 cm, respectively. At the final census, a total of 1,549 seedlings, including both advanced and newly recruited seedlings, remained alive. Among these, 122, 19, and three individuals reached heights of ≥ 100, 200, and 300 cm, respectively. The six tallest seedlings were *M. candidum* (360 cm, advanced seedling), *D. glaucescens* (363, 312, and 288 cm, advanced seedlings), *T. cochinchinensis* (297 cm, newly recruited seedling), and *C. cuspidata* (290 cm, advanced seedling).

Based on regression relationships between seedling age and height for newly recruited seedlings (Figure 6), the time required for the seedlings of each species to

Table 3. Mean height (cm) of newly recruited seedlings within various age ranges for 30 woody species growing in the windward slopes of Nanjenshan Forest. Numbers in brackets are sample size. Age_{20}, the age (years) when seedlings grow to 20 cm in height

Species and diaspore type	Initial	12 mo	24 mo	48 mo	72 mo	Age_{20}
Melanolepis multiglandulosa (capsule)	6.0 (31)	9.3 (9)	9.7 (3)	-	-	5.4 [3]
Mallotus paniculatus (capsule)	6.2 (85)	12.6 (41)	20.2 (20)	35.0 (12)	82.5 (9) [2]	1.3
Triadica cochinchinensis (capsule)	6.5 (35)	17.0 (24)	30.7 (15)	65.6 (8)	297 (1)	1.4
Melastoma candidum (capsule)	5.8 (54)	12.0 (25)	31.6 (12)	76.0 (5)	95 (1)	1.5
Machilus zuihoensis (drupe)	6.9 (15)	8.9 (11)	9.7 (9)	22.8 (6)	53.0 (1)	4.2
Polyspora axillaris (capsule)	5.1 (95)	5.6 (71)	8.1 (53)	11.7 (19)	14.3 (11)	6.2
Rhaphiolepis indica var. *hiiranensis* (pome)	5.7 (179)	6.7 (109)	8.1 (72)	13.4 (32)	26.4 (16)	4.9
Heptapleurum heptaphyllum (drupe)	4.3 (26)	6.3 (21)	10.3 (13)	17.1 (9)	20.6 (5) [2]	5.5
Gardenia jasminoides (berry)	4.8 (47)	6.6 (42)	7.3 (27)	10.1 (11)	21.5 (2)	6.4
Archidendron lucidum (legume)	6.1 (15)	8.5 (11)	9.5 (4)	12.5 (2)	16.1 (1)	10.4 [3]
Ardisia cornudentata (drupe)	5.8 (43)	7.7 (36)	9.5 (31)	12.3 (17)	20.8 (6)	6.5
Ardisia sieboldii (drupe)	4.0 (16)	4.8 (9)	6.3 (6)	7.3 (4)	9.0 (1)	12.8 [3]
Daphniphyllum glaucescens [1] (drupe)	6.2 (21)	8.8 (15)	11.6 (13)	22.3 (8)	53.1 (6)	3.4
Castanopsis cuspidata var. *carlesii* (nut)	7.4 (20)	7.9 (18)	9.4 (12)	22.4 (9)	32.8 (6)	4.7
Psychotria rubra (drupe)	4.5 (125)	5.3 (96)	6.3 (73)	8.6 (35)	11.2 (10)	16.4 [3]
Wikstroemia taiwanensis (drupe)	6.6 (25)	9.6 (20)	10.2 (12)	26.6 (4)	48.0 (2)	2.7
Ilex maximowicziana (drupe)	5.4 (85)	6.9 (49)	7.7 (27)	10.7 (7)	19.7 (1) [2]	5.6
Syzygium elliptifolum (berry)	5.6 (34)	7.4 (23)	9.2 (16)	12.0 (10)	15.9 (4)	7.8
Myrsine seguinii (drupe)	5.8 (37)	7.1 (29)	8.3 (21)	10.3 (13)	19.0 (1)	6.8
Symplocos theophrastifolia (drupe)	6.8 (10)	8.5 (6)	9.4 (5)	13.0 (2)	17.0 (2)	10.3
Osmanthus marginatus (drupe)	5.8 (50)	5.9 (40)	6.6 (30)	9.3 (16)	12.7 (3)	7.6
Neolitsea buisanensis (drupe)	6.4 (19)	6.6 (14)	7.8 (12)	12.9 (10)	14.0 (6)	8.0
Syzygium euphlebium (berry)	6.8 (62)	8.8 (53)	10.8 (41)	15.6 (17)	18.5 (2)	5.6
Illicium arborescens (follioles)	4.9 (102)	7.4 (73)	9.0 (59)	16.4 (40)	26.0 (13)	4.8
Microtropis japonica (capsule)	5.4 (268)	6.7 (180)	7.7 (108)	9.8 (43)	11.8 (15)	8.7
Nageia nagi (seed)	6.9 (15)	10.3 (11)	10.6 (11)	13.0 (8)	15.0 (1)	10.5 [3]
Sarcandra glabra (drupe)	4.9 (37)	5.7 (21)	6.5 (15)	8.1 (9)	8.0 (2)	21.0 [3]
Lasianthus cyanocarpus (drupe)	5.1 (21)	6.6 (10)	7.5 (6)	10.7 (3)	12.5 (2)	ns [4]
Lasianthus obliquinervis (drupe)	5.0 (21)	5.9 (8)	7.7 (4)	10.2 (1)	27.0 (1)	5.5
Eurya nanjenshanensis (berry)	4.2 (10)	6.7 (9)	9.7 (6)	18.7 (3)	33.0 (1) [2]	4.4

[1] subsp. *oldhamii*, [2] height of the 60-month-old seedlings, [3] values obtained by linear extrapolation, [4] not significant relationship.

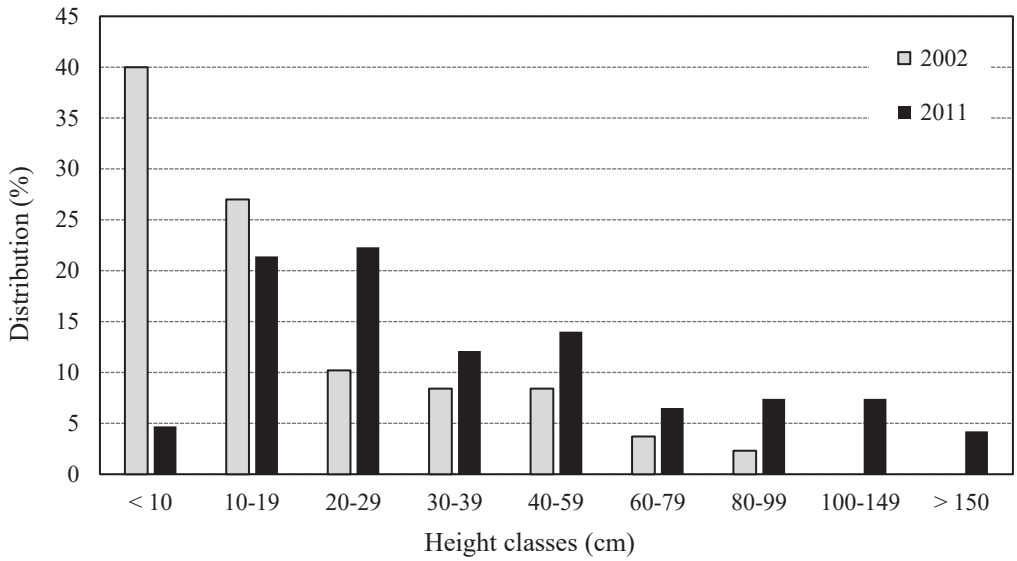

Figure 5. Height-class distributions for 215 advanced seedlings in 20 plots at the southern study site of Nanjenshan Forest (2002–2011).

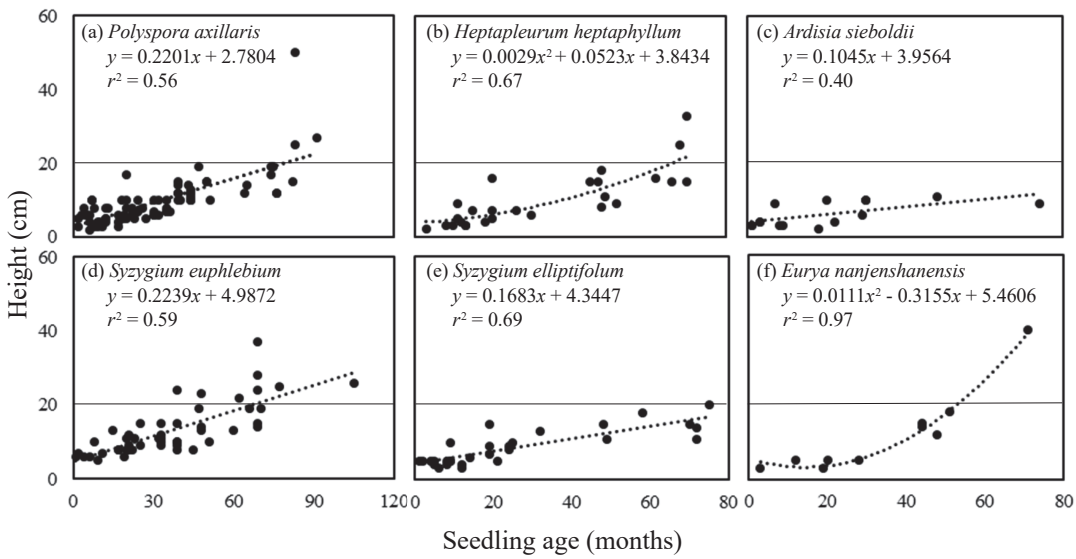

Figure 6. Seedling heights as a function of seedling ages for six representative species on the windward slopes of Nanjenshan Forest.

reach 20 cm in height (Age_{20}) was estimated. *M. paniculatus*, *T. cochinchinensis*, and *M. candidum* required only 1.3–1.5 years to reach 20 cm in height (Table 3). Among shade-tolerant species, 20 species required 2.7–10.3 years to reach 20 cm. Among these shade-tolerant species, *W. taiwanensis*, *D. glaucescens*, and *M. zuihoensis* exhibited relatively rapid height growth, with Age_{20} values of 2.7, 3.4, and 4.2 years, respectively

(Table 3). For five species, newly recruited seedlings did not reach 20 cm in height during the study period, and linear extrapolation was applied to estimate their Age_{20}, yielding values ranging from 10.4 to 21.0 years. Notably, *P. rubra* and *S. glabra* exhibited extremely slow height growth, requiring 16.4 and 21.0 years, respectively, to reach 20 cm. No significant relationship between seedling age and height was detected for *L. cyanocarpus*, and therefore, Age_{20} could not be estimated for this species (Table 3).

Effects of typhoon disturbance on seedling recruitment and mortality

During the 9-year survey period, the study site experienced four major typhoon disturbances that substantially affected seedling recruitment and mortality: Typhoon Dujuan (September 2003), Typhoon Haitang (July 2005), Typhoon Kaemi (July 2006), and Typhoon Morakot (August 2009). According to data from the Binlang station near the Nanjenshan Ecological Reserve, monthly precipitation during the four typhoon months was 425, 976, 847, and 1,315 mm, respectively. Typhoon Kaemi brought intense rainfall that caused severe erosion within the forest stand, whereas Typhoon Morakot brought both strong winds and heavy rainfall, severely affecting both the canopy and understory vegetation. Within six months following Typhoon Kaemi and Typhoon Morakot, seedling mortality exceeded recruitment, resulting in net declines in seedling density of 2.6 and 4.5 stems m^{-2}, respectively. By contrast, following Typhoon Dujuan and Typhoon Haitang, seedling recruitment exceeded mortality because large numbers of seedlings of the shade-intolerant species, including *M. multiglandulosa*, *T. cochinchinensis*, and *M. paniculatus*, were recruited after the disturbances. Consequently, overall seedling density increased by 6.5 and 3.2 stems m^{-2}, respectively, within six months after the two typhoons. Eight months after Typhoon Haitang, the numbers of newly recruited seedlings of *M. multiglandulosa*, *M. paniculatus*, and *T. cochinchinensis* increased by 22, 45, and 12 individuals, respectively, whereas recruitment of *M. candidum* showed no clear response to typhoon disturbance. In the three months preceding Typhoon Morakot, 105 seedlings from 26 species died. In the three months following this disturbance, mortality increased to 205 individuals across 41 species. Notably, 62% of the recorded seedling mortality involved individuals that could no longer be located after being covered by fallen canopy debris. From 2005 to 2011, seedling recruitment was similar between summer and autumn, whereas seedling mortality was markedly higher in summer than in autumn (Figure 7).

Mean relative light intensity across all seedling plots was 5.8% two weeks before Typhoon Haitang and increased to 16.7% and 11.3% at four and eight months after disturbance, respectively, indicating increased understory light availability following typhoon disturbance. Before Typhoon Morakot, the mean relative light intensity across all seedling plots was 7.5%, increasing to 12.2% one month after the disturbance, before declining to 7.6% four months later. During the 9-year study period, relative light intensity was measured 16 times across all seedling plots. Relative light intensity was < 4.5% on three sampling occasions, 5.8–9.8% on eight occasions, and 11.3–16.7% on five occasions. The mean relative light intensity across the 16 measurements was 8.4 $\pm$ 3.9% ($\pm$ 1 SD).

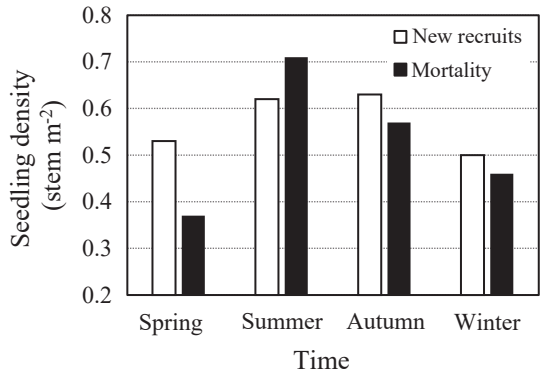

Figure 7. Seasonal variations in the seedling density of new recruits and mortality on the windward slopes of Nanjenshan Forest (2005–2011).

DISCUSSION

The windward habitat of Nanjenshan is ecologically distinctive

The northeast monsoon brings cold air masses that lower local temperatures. In addition, wind-chilling effects further reduce temperatures in the microhabitats exposed to monsoonal influence relative to sheltered habitats. Consequently, many species in the Aquifoliaceae and Fagaceae, which are typically distributed in the warm-temperate zone of mid-elevation forests in Taiwan, occur on the windward slopes of Nanjenshan despite the latter's relatively low elevation of only 330 m (Table 1). Chronic exposure to the northeast monsoon has created the distinctive ecological conditions of Nanjenshan's windward habitat. Only species capable of tolerating harsh winter winds, low temperatures, and nutrient-poor soils (Chen et al. 1997) can persist under these conditions, allowing many regionally rare species to establish in this habitat (Ku et al. 2021). Among the 71 adult tree species recorded in the study plot, 20 are endemic to Taiwan, including two classified as endangered, six as vulnerable, and five as near threatened (Editorial Committee of the Red List of Taiwan Plants 2017). Notably, newly recruited seedlings of 11 of these 13 rare species were recorded in the study plot (Table 1). In the Nanjen Lake Plot of Nanjenshan, 20 tree species have been identified as characteristic species of the windward ridge-type plant community (Fan et al. 2005), and all 20 species were also recorded in the adult tree layer of the present study plot (Table 1). Fan and Hsieh (2010) reported that the spatial distribution of understory seedlings in the Lanjenchi Forest Dynamics Plot closely corresponded to that of the overstory adult trees. Similarly, in the present study, seedlings of most adult tree species were recorded in the seedling plots (59 of 71 species, 83%), in contrast to the pattern observed in Fushan Forest, where most adult tree species lack regenerating seedlings (Chang-Yang et al. 2013).

The windward forest of Nanjenshan supports relatively high seedling species richness and density

At the time of plot establishment, micro-sites with relatively high species richness and abundance of advanced seedlings were intentionally selected for seedling plot

installation, whereas previous studies on seedling dynamics (Chang-Yang et al. 2013, Lin et al. 2017, Lin et al. 2024) employed systematic sampling designs. Although the sampling design used in this study does not fully represent the overall dynamics of seedling community composition and abundance in this habitat, it is sufficient to demonstrate the potential of this environment to support seedling species richness and density per unit area. In terms of seedling species richness, the initial census recorded 51 species of advanced seedlings (< 100 cm in height) across 20 1-m² seedling plots and a total of 65 species across all 44 seedling plots. Over the 9-year study period, newly recruited seedlings of 75 species were recorded. By the final census, living seedlings representing 65 species were still present, with species richness per plot ranging from seven to 21 species (mean = 13.1). By comparison, in Fushan Forest, where the total seedling plot area was approximately six times larger than that in this study (261 m²), only 36 species of advanced seedlings (DBH < 1 cm) were recorded in the initial census, and newly recruited seedlings of only 28 species were recorded over an 8-year period (Chang-Yang et al. 2013). In Kenting Karst Forest, where the seedling plot area was approximately five times larger than that of this study (216 m²), only 36 species of newly recruited seedlings were recorded over five years (Lin et al. 2017). In Nanjenshan Plot I, where the sampling area exceeded that of this study by 70% (75 m²), only 43 species of newly recruited seedlings were recorded over 8.3 years (Lin et al. 2024). Compared with these three forest sites, the seedling community in the present study exhibited substantially higher species richness. In terms of seedling density, the initial census recorded a mean density of 24.8 stems m^{-2} for seedlings < 100 cm in height. Over the 9-year period, total seedling density, including both advanced seedlings and newly recruited seedlings, continued to increase, reaching 35.2 stems m^{-2} by the final census. Seedling density per plot ranged from 15 to 65 stems m^{-2}. By contrast, Tsai (2002), based on a census of 1,284 quadrats (1 m² each) in Nanjenshan Plot I, recorded 70 seedling species (DBH < 1 cm) and 6,287 individuals, corresponding to a mean density of 4.9 stems m^{-2}. In Fushan Forest, the mean seedling density at the final census was only 2 stems m^{-2} (Chang-Yang et al. 2013). These comparisons suggest that the study site can sustain exceptionally high seedling density.

Relationship between adult tree and seedling communities in the study plot

The adult tree and seedling communities in the study plot exhibited high compositional similarity. Of the 71 species recorded in the adult tree layer, 59 produced regenerating seedlings, and the seedlings of 54 species were still present at the final census. A comparison of species-specific abundances between adult trees and seedlings (Table 1) revealed contrasting regeneration patterns. Within Aquifoliaceae, *I. cochinchinensis*, *I. lonicerifolia*, and *Ilex uraiensis* Mori & Yamamoto had abundant adult individuals but very few seedlings, suggesting that they may be unable to maintain their current dominance in the future. By contrast, *I. maximowicziana* was represented by a few adult individuals but abundant seedlings, suggesting that its dominance may increase in the future. Among the Fagaceae species, *L. amygdalifolius*, *Q. championii*, *Q. longinux*, and *Q. pachyloma* similarly exhibited high adult abundance but very few regenerating seedlings. Only *C. cuspidata* showed both high adult and seedling abundance,

suggesting that it would likely maintain its dominance in the future. *I. arborescens* and *M. japonica* were both highly abundant in both the adult tree and seedling communities and were therefore expected to remain dominant components of the community. In addition, *D. glaucescens*, *A. lucidum*, *N. buisanensis*, *M. seguinii*, *O. marginatus*, and *P. axillaris* all had dozens of adult individuals and regenerating seedlings and were therefore likely to remain important components of the adult tree community. Conversely, *E. roxburghiana*, *Magnolia kachirachirai* (Kanehira & Yamamoto) Dandy, *Tricalysia dubia* (Lindl.) Ohwi, *Meliosma squamulata* Hance, and *Symplocos congesta* Benth. each had ≥ 30 adult individuals but fewer than 10 seedlings, suggesting that they may have difficulty maintaining their current abundance in the community. To evaluate the potential long-term persistence of species in the community, two criteria were applied. A species was considered likely to remain a component of the forest community over the coming decades if it satisfied at least one of the following conditions: (1) the number of adult individuals in 2002 was ≥ 10, regardless of whether seedlings survived to the final census, because a sufficiently large number of reproductive individuals would remain capable of producing offspring over the coming decades; or (2) the number of adult individuals in 2002 was < 10, but ≥ 15 seedlings remained alive at the final census, because sufficient surviving seedlings would be available to recruit into the adult layer in the future, excluding short-lived species, such as *M. paniculatus*. Based on these criteria, 46 and seven species satisfied criteria (1) and (2), respectively, for a total of 53 species (underlined in Table 1), and were therefore likely to remain components of the windward forest community at the study site.

Comparison of tree and shrub species in the study plot

Among the 30 species with the greatest numbers of newly recruited seedlings in the study plot, tree species were more numerous than shrub species (22 vs. 8 species, Table 2), and the total number of newly recruited seedlings was also higher for tree species than for shrub species (1,133 vs. 480 individuals). By the final census, 1,549 surviving seedlings from 65 species were recorded in the seedling plots, including both advanced and newly recruited seedlings (Table 1). Of these, tree species comprised 50 species and 1,086 seedlings, whereas shrub species comprised 15 species and 463 seedlings. Tree species, therefore, accounted for 77% of total surviving seedling species richness and 70% of total seedling abundance. These results indicate that the surviving seedling community in the study plot was dominated by tree species in both species richness and abundance, which should help maintain the future composition of the forest canopy community.

Diaspore types and dispersal modes of regenerating species

Seedling recruitment in forest ecosystems is closely associated with diaspore type and dispersal mode. Among the 30 species with the greatest numbers of newly recruited seedlings in the study plot, diaspore types were dominated by drupes (15 species), followed by capsules (6 species) and berries (4 species). In addition, one species each produced a pome (*R. indica*), a legume (*A. lucidum*), a nut (*C. cuspidata*), and a follicle (*I. arborescens*), whereas the gymnosperm *N. nagi* dispersed by seeds (Table 3). The capsules of *M. candidum* were fleshy and could be consumed and dispersed by animals after dehiscence. *P.*

axillaris produced winged seeds that were dispersed by wind (anemochory) following capsule dehiscence, and wind dispersal of this species was commonly observed in the study plot during periods of northeast monsoon activity. Four species bearing berries, including *G. jasminoides*, *S. elliptifolium*, *S. euphlebium*, and *E. nanjenshanensis*, were primarily dispersed by animals (zoochory). The relatively large seeds of *N. nagi* were dispersed by gravity (barochory), and newly recruited seedlings were often found near parent trees within the study plot. Several species bearing drupes, including *M. zuihoensis*, *H. heptaphyllum*, *A. sieboldii*, *W. taiwanensis*, *I. maximowicziana*, *S. glabra*, *L. cyanocarpus*, and *L. obliquinervis*, as well as the berry-producing *G. jasminoides*, had very few reproductive adult individuals within the plot (0–6 individuals). Nevertheless, they exhibited relatively high numbers of newly recruited seedlings (15–85 individuals) distributed across more than 10 seedling plots. This pattern suggests that most seedlings of these species may originate from diaspores dispersed from outside the study plot. By contrast, such species as *M. candidum*, *P. axillaris*, *R. indica*, *A. cornudentata*, *C. cuspidata*, *P. rubra*, *M. seguinii*, *O. marginatus*, *I. arborescens*, and *M. japonica* already had numerous adult individuals within the plot (21–386 individuals, Table 3), and their newly recruited seedlings were distributed across ≥ 15 seedling plots. This suggests that most seedlings of these species were derived primarily from diaspores produced by local parent trees. Finally, shade-intolerant species, such as *M. multiglandulosa*, *M. paniculatus*, and *T. cochinchinensis*, all of which produced capsules as diaspores, lacked reproductive adult individuals within the study plot. Their seedling recruitment was associated with typhoon disturbances, and their newly recruited seedlings were likely derived from externally dispersed diaspores accumulated in the soil seed bank.

Comparative dynamics of seedling survival in the subtropical forests of Taiwan

In several subtropical forest sites in Taiwan, including the Nanjenshan Transect (Lai 1996), Fushan Forest (Leu 2004), and Nanjenshan Plot I (Lin 2018), the survival proportions of 1-year-old seedlings were 22.5%, 33.0%, and 22.3%, respectively. In Kenting Karst Forest, seedling survival proportions were 51% at age 0.5 years and 11% at age 2 years (Lin et al. 2017). These results indicate that more than half of newly recruited seedlings in these four forests die within the first year after recruitment. By contrast, the mean survival proportion of seedlings across 30 species in the present study was as high as 70.3% at ages 13–24 months (Table 2), markedly higher than the values reported for the four forests described above. Moreover, in the Lanjenchi Forest Dynamics Plot (Li 1995) and Nanjenshan Transect (Liao 2019), seedling survival proportions at age 1 year were 60% and 70%, respectively, suggesting that more than half of newly recruited seedlings at these sites survived beyond the first year after germination.

Negative conspecific density dependence (NCDD) causes seedling survival to decrease with increasing conspecific density (Johnson et al. 2012, Zhu et al. 2018, Comita et al. 2024). Accordingly, at the community level, overall seedling survival proportion or MST may also decline under strong NCDD. In the present study, the overall MST of newly recruited seedlings across 64 species was 34 months, which was substantially higher than the MST of six months reported for Fushan

Forest, Kenting Karst Forest, and Nanjenshan Plot I (Chang-Yang et al. 2013, Lin et al. 2017, Lin et al. 2024). This pattern suggests that the influence of NCDD may be relatively weak in the study plot. At the species level, strong NCDD effects have been reported in other forests. In Fushan Forest, *M. seguinii*, *H. heptaphyllum*, and *Glochidion acuminatum* Müll.Arg. accounted for 63%, 11%, and 9% of a total of 10,848 newly recruited seedlings, respectively, and had MST values of only 7, 6, and 4 months (Chang-Yang et al. 2013). Similarly, in Nanjenshan Plot I, *Bischofia javanica* Blume accounted for 49% of 1,810 seedlings, but its survival proportion at age 1 year was only 4.5% (Lin 2018). These highly abundant species may have experienced substantial early mortality due to NCDD. However, species-specific responses to NCDD can vary substantially (Comita and Hubbell 2009, Zhu et al. 2018). In the present study, *M. japonica*, *R. indica*, and *P. rubra* accounted for 16%, 11%, and 7% of the total of 1,688 newly recruited seedlings, respectively. Their MST values were 37, 19, and 48 months, and their survival proportions at ages 13–24 months were 74%, 64%, and 79%, respectively (Table 2). *R. indica* exhibited lower survival proportions and shorter MST than the other two species across all age classes (Table 2). Between 2002 and 2007, 60 seedlings of *R. indica* were newly recruited within a single seedling plot, and the dead seedlings had an MST of 21 months. By contrast, among the 33 seedlings of the same species that were recruited in nine other plots during the same period, the dead seedlings had an MST of 32 months. This comparison suggests that seedling survival time decreased under higher conspecific seedling density, indicating an NCDD effect in *R. indica*. By contrast, in several abundant species in the study sites, including *M. japonica*, *P. rubra*, *I. arborescens*, *P. axillaris*, *I. maximowicziana*, and *S. euphlebium*, seedling survival time did not decrease in plots with higher conspecific seedling density (data not shown), suggesting that NCDD effects may be weak or absent in these species.

Sun et al. (1996) proposed that persistent wind stress in the windward habitats of Nanjenshan reduces plant growth rates and lowers seedling survival. However, available evidence has not supported this hypothesis. In the Lanjenchi Forest Dynamics Plot, the survival proportion of newly recruited seedlings at age 1 year reached 60% (Li 1995), indicating relatively high seedling survival. Similarly, seedling dynamics along the Nanjenshan Transect did not support this hypothesis, as survival proportions of newly recruited seedlings at ages 1 and 2 years were 70% and 61%, respectively (Liao 2019). The present study likewise does not support this hypothesis. The overall MST of newly recruited seedlings was 34 months, indicating relatively high seedling persistence, and was substantially longer than that reported for Nanjenshan Plot I, which was less strongly influenced by the northeast monsoon (MST = 0.5 years, Lin et al. 2024), as well as Fushan Forest, which was also exposed to the northeast monsoon (MST = 0.52 years, Chang-Yang et al. 2013). At the species level, the MST values of *M. seguinii*, *H. heptaphyllum*, *M. zuihoensis*, *D. glaucescens*, *S. elliptifolium*, and *Symplocos theophrastifolia* Siebold & Zucc. in the present study were 59, 48, 48, 47, 33, and 30 months, respectively (Table 2). By contrast, seedlings of the same species in Fushan Forest exhibited markedly shorter MST values of only 7, 6, 7, 21, 15, and 7 months, respectively (Chang-Yang et al. 2013), representing increases of 17–52 months in the present study. The maximum

MST reported for any species in Fushan Forest was 38 months (*Helicia formosana* Hemsl., Chang-Yang et al. 2013), whereas the maximum MST in Kenting Karst Forest was 33 months (*Excoecaria formosana* (Hayata) Hayata, Lin et al. 2017). By contrast, 19 species in the present study exhibited MST values ≥ 33 months, and *A. cornudentata* reached as high as 80 months (Table 2). Based on these observations, we propose that, relative to leeward forests, the windward forests of Nanjenshan are characterized by higher seedling survival proportions and longer seedling survival times. The potential mechanisms underlying this pattern are discussed below.

Potential mechanisms underlying prolonged seedling survival in windward forests

Grime (1979) classified plant life-history strategies into three major categories: (1) Competitive strategists, which are able to establish in resource-rich habitats characterized by intense interspecific interactions; (2) Ruderal strategists, which are short-lived species adapted to habitats subjected to frequent disturbance; and (3) Stress-tolerant strategists, which are capable of establishing under severe environmental stress, typically characterized by slow growth, evergreen habit, and low palatability to herbivores. Differences in the relative intensities of competition, disturbance, and environmental stress generate diverse ecological conditions, thereby allowing species with different life-history strategies to occupy distinct positions along environmental gradients (Grime 1979). In the windward habitat of Nanjenshan, which is subject to chronic monsoonal stress, seedlings exhibit relatively high survival proportions and prolonged survival times during early life stages. This pattern may be explained by several non-mutually exclusive mechanisms: (1) The species composition of seedlings on the windward slope largely mirrors that of the overstory, suggesting that these species have undergone long-term ecological filtering and are thus well adapted to the stress imposed by the northeast monsoon. Their life-history characteristics are consistent with Grime's (1979) stress-tolerant strategy. To withstand harsh environmental conditions, these seedlings maintain high survival resilience at the cost of slow growth. This trade-off likely reduces the intensity of both intra- and interspecific competition, ultimately contributing to higher seedling density and prolonged survival in windward forests. (2) Seedling communities in the study plot are both species-rich and high in density, with 7–21 species co-occurring within each 1 m² plot and, on average, 13 species and 35 seedlings of varying ages and sizes coexisting within a single quadrat. Such dense seedling communities may provide mutual protection against strong monsoonal winds, thereby reducing wind-induced mechanical damage and enhancing seedling survival. (3) Understory light availability may also play a critical role. Due to persistent strong winds, the herbaceous ground layer in the study plot is relatively sparse (personal observation), resulting in limited interception of incoming light. In addition, periodic typhoon disturbances partially damage the canopy and increase understory light availability. The mean relative light intensity in the understory of the windward forest reached 8.4%, substantially higher than that in the leeward Nanjenshan Plot I (mean = 1.3%, Chao et al. 2022). By contrast, in Nanjenshan Plot I, dense herbaceous vegetation reduced light availability for woody seedlings by 24% (Chao et al. 2022). Similarly, although Fushan Forest experiences frequent typhoon

disturbances that increase understory light availability, much of the incoming light is intercepted by herbaceous vegetation, thereby limiting the light resources available to seedlings and reducing seedling survival (Chang-Yang et al. 2013). By contrast, the relatively high understory light availability in the present study plot likely facilitates seedling recruitment, growth, and survival (Kuo et al. 2007, Peng et al. 2007, Rüger et al. 2009, Chao et al. 2022).

Comparison between seedling survival proportions and MST

In forest understories, seedling populations of most species typically comprise individuals of heterogeneous ages and only rarely consist of age cohorts established within a short time. Accordingly, when estimating survival proportions of newly recruited seedlings for a given age class, the denominator was not the total number of seedlings of that species, but instead excluded individuals that were still alive at the final census but had not yet reached the age threshold of that age class. Using the total number of seedlings as the denominator would underestimate age-specific survival proportions. The MST of newly recruited seedlings for each species, estimated using Kaplan-Meier survival analysis, was generally consistent with the age range at which the survival proportion approached 50% (Table 2). For example, in *S. elliptifolium*, the age range corresponding to 50% survival was 25–36 months, and the estimated MST was 33 months, which fell within this interval. Similarly, for *S. glabra*, *E. nanjenshanensis*, and *W. taiwanensis*, the 50% survival threshold occurred at 37–48 months, with corresponding MST values of 37, 42, and 44 months, respectively, showing close agreement between the two measures. Likewise, for *C. cuspidata*, *M. seguinii*, and *N. nagi*, the 50% survival threshold was observed at 49–60 months, whereas their MST values were 57, 59, and 59 months, respectively, indicating strong concordance between MST and survival proportion estimates. For most other species, MST values fell within the age class in which survival proportion approached 50%, or within the monthly ranges of the immediately adjacent (preceding and following) age classes (Table 2). These results confirm the logical soundness of the method employed to calculate age-specific survival proportions of newly recruited seedlings.

Seedling height growth

Is the height growth of understory seedlings invariably slow? This depends strongly on species identity and light environment (Kuo and Fan 2003, Kuo et al. 2007, Rüger et al. 2009). In Fushan Forest, the net height increment of *M. seguinii*, *M. zuihoensis*, and *H. heptaphyllum* at age 1 year was 1.2, 0.8, and 0.8 cm, respectively (Leu 2004). By contrast, the same species in the present study exhibited higher net height increment, at 1.3, 2.0, and 2.0 cm, respectively (Table 3). In Fushan Forest, the mean annual net height increment of newly recruited seedlings was only 1.55 cm, and over an 8-year monitoring period, only four individuals exceeded 50 cm in height (Chang-Yang et al. 2013). By comparison, in the present study, 40 individuals from 14 species reached heights ≥ 50 cm during the 9-year study period, and 14 individuals from four species exceeded 100 cm in height. These included three individuals of the shade-tolerant species *D. glaucescens* (163, 162, and 100 cm at seedling ages of 71–76 months), indicating that some individuals of this species can exhibit relatively rapid height growth. For the shade-intolerant species

M. paniculatus, *T. cochinchinensis*, and *M. candidum*, the net height increment reached 52.8 cm by age 48 months, corresponding to an annual net height increment of 13.2 cm. By contrast, seedlings of 26 shade-tolerant species exhibited much slower height growth, with a net height increment of only 8.2 cm by age 48 months and a mean annual net height increment of 2.1 cm (Table 3). Nevertheless, the annual net height increment of shade-tolerant species in the present study (2.1 cm) still exceeded that observed in Fushan Forest (1.55 cm). In Fushan Forest, newly recruited seedlings of different species require approximately 22–200 years to reach the sapling stage (height ≥ 2 m and DBH ≥ 1 cm, Chang-Yang et al. 2021). In the present study, two individuals exceeded 2 m in height, both belonging to shade-intolerant species: *T. cochinchinensis* (297 cm at 7.7 years) and *M. paniculatus* (211 cm at 5.9 years). These individuals likely attained DBH ≥ 1 cm and remained alive at the final census, suggesting successful recruitment into the sapling stage.

Advanced seedlings as key successors of forest regeneration

Previous studies on seedling dynamics have primarily focused on the survival and mortality of newly recruited seedlings with known ages, whereas comparatively less attention has been paid to advanced seedlings, whose exact ages are often difficult to determine. However, although still in the seedling stage in terms of size, these older individuals have already passed through the most vulnerable early life stages and therefore exhibit a higher survival probability (Green et al. 2014). In addition, they tend to show faster net height growth (Pan et al. 2007) and may persist in the understory for decades (Connell and Green 2000, Condit et al. 2025). At the southern study site, 495 advanced seedlings were recorded across 20 seedling plots at establishment. After nine years, 215 individuals remained alive, corresponding to a survival proportion of 43%. By the final census, a total of 530 advanced seedlings remained alive across the two study sites, with a mean density of 12 individuals per 1 m^{-2}. These individuals had all persisted for more than seven years, and some had already attained considerable height, including 13 individuals ≥ 200 cm and three individuals ≥ 300 cm. Some of these advanced seedlings are likely to recruit into the sapling stage, thereby serving as key successors and contributing to the long-term maintenance of forest community structure and composition.

CONCLUSIONS

Among the 71 tree species recorded in the windward study plot of Nanjenshan, 59 exhibited seedling recruitment, suggesting relatively weak regeneration limitation for most species. At the final census, 1-m^2 seedling plots contained 7–21 species (mean = 13), with seedling densities ranging from 15 to 65 stems m^{-2} (mean = 35 stems m^{-2}), indicating that the forest had considerable capacity to sustain high seedling species richness and abundance. The overall MST of newly recruited seedlings was 34 months, while the MST values of moderately shade-tolerant and shade-tolerant species were 40 and 39 months, respectively, indicating that more than half of the seedlings survived beyond the first year after germination. During the 9-year study period, the forest experienced four typhoon disturbances that partially damaged the canopy but increased understory light availability, with mean relative light intensity reaching 8.4%, thereby facilitating seedling recruitment and growth. At the same time, the strong northeast

monsoon, which persisted for approximately six months each year, suppressed the development of wind-intolerant herbaceous vegetation in the understory, thereby reducing competitive effects on shade-tolerant woody seedlings adapted to these conditions. Under the combined influences of the northeast monsoon and typhoon disturbance, the seedling community of the windward forest at Nanjenshan exhibited greater species richness, density, and survival time than those reported for the Fushan Forest Dynamics Plot, Kenting Karst Forest Dynamics Plot, and Nanjenshan Plot I.

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研究報告

南仁山迎風坡森林小苗9年期間的存活及高生長動態

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摘 要

小苗的新增及成長，影響森林後續的組成結構。本研究於墾丁國家公園南仁山迎風坡森林，設置44個1-m²的小苗樣區，於2002~2011年9年期間每月複查小苗動態。研究目的在探討遭東北季風長期慢性逆境影響的森林，小苗新增種類、數量、存活時間及高生長動態，及其與他處森林小苗動態的差異。試驗地調查到成樹71種，小苗樣區則發現前生苗及後續萌發的新生苗共75種，其中59種與成樹組成相同。小苗密度由首次調查的25 stem m^{-2}提高到35 stem m^{-2}並維持數年。調查期間新生苗記錄到64種1,688株，以日本賽衛矛、恆春石斑木的數量較多。新生苗豐量≥ 10株者30種，該30種小苗於苗齡13~24、25~36、37~48個月之平均存活比例分別為70、53、42%。存活分析顯示有12種新生苗之存活中位時間(MST) ≥ 36個月，整體新生苗MST值為34個月，較福山森林、墾丁高位珊瑚礁森林、南仁山背風坡森林整體小苗之MST值均為6個月高出甚多。試驗地不耐陰物種小苗MST值12個月，新生苗1.5年可長至20 cm高；耐陰性物種小苗MST值39個月，需2.7~21.0年才達20 cm高。偶發性颱風擾動破壞森林冠層，提高林下光資源，而強勁季風抑制地被草本植物競爭光資源，此兩作用有利於林下木本小苗的新增及成長。在此環境下，南仁山迎風坡森林小苗群聚的物種豐度、密度及存活時間，都高於臺灣其他3處亞熱帶森林。

關鍵詞：長期慢性逆境、存活中位時間、東北季風、小苗物種豐度、颱風擾動

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前言

小苗新增(recruitment)，是森林生態系重要的生態過程(ecological process)，因為具有自行繁衍及由擾動後恢復的功能，因此對維持森林組成結構及促進物種多樣性都具重要性(Ribbens et al. 1994, Green et al., 2014)。過去對熱帶或亞熱帶森林小苗動態的研究可歸納出幾個生態現象：(1)大多數小苗在生命史(life-history)初期的存活時間很短，植株在萌發一年內的死亡率高(Chang-Yang et al. 2013, Lin et al. 2017)；(2)小苗在林下環境生長緩慢(Chang-Yang et al. 2021, Wright et al. 2024)；(3)小苗的新增、生長、存活隨著林下可用光資源(light availability)的提高而增多(Montgomery and Chazdon 2002, Kuo et al. 2007, Rüger et al. 2009, Chao et al. 2022)；(4)耐陰(shade-tolerant)小苗存活時間較不耐陰(shade-intolerant)小苗長(Lin et al. 2017, Lin et al. 2024)，前者可在光資源低的林下環境生存數十年(Delissio et al. 2002, Condit et al. 2025)。

臺灣亞熱帶森林小苗動態的研究，發現大多數新生苗(newly recruited seedlings)萌發後的存活時間很短(Lai 1996, Leu 2004, Chang-Yang et al. 2013, Lin et al. 2017, Lin et al. 2024)。福山森林動態樣區(Fushan Forest Dynamics Plot)、墾丁高位珊瑚礁森林動態樣區(Kenting Karst Forest Dynamics Plot)、南仁山溪谷樣區(Nanjenshan Plot I)的小苗群聚，藉Kaplan-Meier存活分析法估算的存活中位時間(median survival time, MST)都是6個月(Chang-Yang et al. 2013, Lin et al. 2017, Lin et al. 2024)，顯示此3處森林多數新生苗在萌發一年內會死亡。然而，也有研究發現苗齡1年的新生苗存活率≥ 60% (Li 1995, Liao 2019)。福山森林、墾丁高位珊瑚礁森林、南仁山溪谷樣區的小苗動態研究，5~8年期間調查到的新生苗物種數都不及上層成樹種類的一半(Chang-Yang et al. 2013, Lin et al. 2017, Lin et al. 2024)，顯示森林群聚有很高的更新限制(recruitment limitation)。

森林下層木本植物小苗能否存活，是物種遺傳性狀與周遭生物及非生物因子交互作用的結果(Kobe and Vriesendorp 2011, Lu et al. 2015)。在光資源受限的林下環境，可預期不耐陰物種小苗因無法獲得足夠的光資源合成所需光合產物，常於萌發後短期間即死亡；相對的，耐陰物種小苗遺傳上有極低的暗呼吸率(dark respiration rate)可降低碳支出，且光合作用光補償點(light compensation point)低(Kuo et al. 2021)，又有較高能力利用土壤呼吸釋出的CO_2 資源(Chen and Kuo 2025)，因而在林下低光環境也可維持正值碳平衡提高存活時間。在影響小苗存活死亡的生物因子中，負同種密度依存(negative conspecific density dependence, NCDD)效應，常被認為是重要的作用因子(Comita and Hubbell 2009, Johnson et al. 2012, Lu et al. 2015)。某小苗周遭若生長著密度較高的相同物種小苗，則該小苗遭到動物取食、病原菌危害或因競爭而死亡的機會越高(Metz et al. 2010, Paine et al. 2012, Comita et al. 2014)。福山森林(Chang-Yang et al. 2013)、墾丁高位珊瑚礁森林(Lin et al. 2017)、蓮華池森林動態樣區(Lienhuachih Forest Dynamics Plot) (Huang et al. 2022)、南仁山溪谷樣區(Lin et al. 2024)等處都發現同種小苗密度較高之處，對小苗存活具強烈負面效應，福山森林小苗樣區每1-m²僅存活2株小苗(Chang-Yang et al. 2013)。另有研究發現異種小苗密度(heterospecific seedling density)較高處，對小苗存活卻具正面效應(Fan et al. 2010, Huang et al. 2022)。

南仁山區秋、冬季節有東北季風(northeast monsoon)長期慢性的風逆境(wind stress)，夏、秋季節也會遭偶發性的颱風擾動(disturbance)。南仁山區遭東北季風直接吹襲的迎風生育地(windward sites)，森林形相(physiognomy)特徵為樹冠層低矮、樹幹細小但密度高，主要組成樹種為暖溫帶及亞熱帶樹種；相對的，季風影響較輕微的背風生育地(leeward sites)，生長著體型高大、密度較低、以熱帶樹種為主要組成的森林(Hsieh et al. 2000, Fan et al. 2005, Chao et al. 2010, Ku et al. 2021)。迎風坡樹種的葉片較堅韌、比葉重(leaf mass per area)高，可抵抗強風機械危害(Wu and Kuo 2011, Fan and Kuo 2013)。在生理方面，迎風

坡樹種葉片較耐脫水(dehydration)逆境(Kuo and Lee 2003, Wu and Kuo 2011)，在風的作用下氣孔關閉程度較輕微(Kuo et al. 2011)，且在低溫條件下可維持相對較高的淨光合作用率(Chen and Kuo 2008)。

南仁山背風生育地的小苗動態研究，發現苗齡≥ 0.5年或≥ 1.25年的小苗其存活率分別為51、20%，林下小苗整體的存活中位時間僅6個月(Lin et al. 2024)，小苗存活率不高且存活時間不長。Sun et al. (1996)提出假說，認為南仁山遭長期風吹逆境的迎風生育地，植株生長率慢且存活率低。相較於背風生育地的小苗，南仁山迎風生育地小苗的存活率會更低嗎？目前尚無小苗動態研究結果可資比較。本研究在南仁山迎風坡森林進行9年的小苗動態研究，探討下列5個問題：(1)南仁山迎風坡森林小苗物種豐度(species richness)如何？小苗物種組成數量不到上層成樹組成的一半嗎？(2)迎風坡林地每1-m²能容納多少小苗數量？(3)隨著苗齡增加，試驗地新生苗的存活比例變化如何？(4)藉由存活分析估算的整體小苗、不同耐陰性小苗、個別物種小苗的存活中位時間如何？與臺灣其他亞熱帶森林比較有何差異？(5)試驗地不同小苗物種的高生長動態如何？

材料與方法

試驗地

試驗地位於墾丁國家公園所轄的南仁山生態保護區(120° 51′ 37” E, 22° 02′ 51” N) (Figure 1 a)，於前往南仁湖(Nanjen Lake)的南仁步道(Nanjen Trail) 3.5 km標誌處之南、北兩側迎風坡森林各設置一處試驗地(Figure 1 b, Site A and B)。南側試驗地三面遭狹窄池水包圍，面積約0.15 ha，海拔高約330 m，坡度較平緩。北側試驗地距南側試驗地約250 m，海拔高約345 m，接近稜線，坡度較陡。兩處試驗地的林相類似，樹冠層低矮(3~5 m)不連續，大多數林木胸徑< 10 cm，但林分植株密度高，林下草本植物不茂盛。根據鄰近此生態保護區的中央氣象署檳榔測候站(Binlang station, code: COR280)資料，該處2001至2011年的年均溫22.6℃，月均溫於1月最低(17.9℃)，7月最高(26.2℃)；年均降水量3,219 mm，6~9月雨量為全年的66%，11月至翌年4月雨量較少。試驗地每年10月至翌年3月盛行東北季風。根據南仁山長期生態研究網設在南仁湖邊迎風處之氣象站，以及設在南仁步道0.5 km標誌處之南方背風生育地氣象站的資料，1996~2004年東北季風盛行的半年期間，迎風處月均風速 5.2 m s^{-1}，最大風速9~13 m s^{-1}，而背風處月均風速都低於2.0 m s^{-1} (Chen and Kuo 2008)。南仁山區7~9月常有颱風侵襲，颱風擾動常破壞樹冠形成林冠孔隙(canopy gaps)，提高林下光資源(Pen et al. 2007)。

成樹及小苗調查

於2002年7月在南側試驗地(Figure 1 b, Site A)設置成樹調查樣區，調查該處成樹群聚的組成及介量。成樹調查時以經緯儀(TOPCON DT-30, Japan)依循南-北、東-西方向，每隔10 m以鋁桿標記，4根鋁桿之間即為一個10 m × 10 m樣區，其內區分成4個5 m × 5 m的樣方進行每木調查。成樹調查共設置14個 10 m × 10 m樣區，另1樣區因鄰近水邊，腹地不足，只設2個5 m × 5 m的樣方，成樹調查樣區計有58個樣方。樣方內胸徑(diameter at breast height, DBH) ≥ 1 cm的喬木、灌木單株均掛上有編號的鋁牌，並記錄該植株名稱、胸徑、樹高。樹種的耐陰性等級(shade tolerance classes)是依據Kuo et al. (2021)的報導，但簡化成三類群：耐陰等級I, II的樹種合併在不耐陰類群(shade-intolerant group)，耐陰等級VI, V兩級樹種合併在耐陰類群(shade-tolerant group)，耐陰等級III的樹種則維持在中等耐陰類群(moderately shade-tolerant group)。

在南側試驗地成樹樣區內主觀的選取小苗物種數較多(≥ 8種)，以及小苗數量較多(≥ 15株，但避免集中在少數物種)之微生育地，設置20個小苗樣區。小苗樣區長2.0 m、寬0.5 m，面積1-m²。此主觀取樣方式並非逢機或系統性取樣，雖不能客觀的代表此處森林小苗群聚的組成及豐量，但可獲得到較多小苗物種的新增(recruitment)、死亡

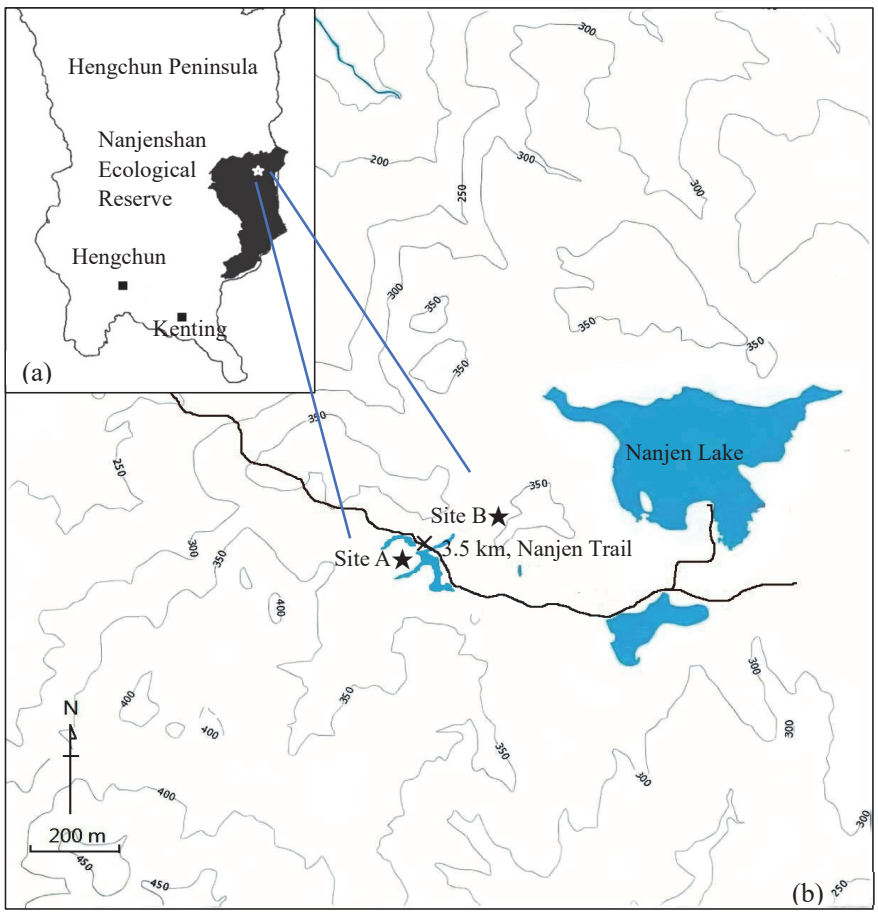

Figure 1. The study sites were located in the Nanjenshan Ecological Reserve (南仁山生態保護區**), Kenting National Park (**墾丁國家公園**) of southern Taiwan (a). Site A and B indicate the seedling dynamics plots south and north of the 3.5-km mark of the Nanjen Trail, respectively (b).**

(mortality)、高生長(height growth)動態的資訊。小苗樣區內所有高度< 100 cm的木本植物小苗(不計木質藤本)，以塑膠牌(46 mm × 12 mm)書寫編號，標記在小苗個體上，並記錄各單株的種類、高度及葉片數。首次調查標定的植株視為前生苗(advanced seedlings)，之後才萌發的小苗視為新生苗。小苗樣區每月複查一次，遇有新生苗則編號掛牌，鑑定種類並記錄苗高度及葉片數。調查時若發現小苗已死亡(標牌仍留存)則收回標牌；若小苗與標牌均失蹤，後續兩次調查都未出現即視為死亡。2003年9月3日杜鵑颱風(Typhoon Dujuan)侵襲南臺灣，試驗地部分樹冠層枝葉折損形成幾處林冠孔隙(gaps)，林下入射光量(light intensity)大幅提高，預期會有不耐陰類群的小苗萌發，因此於同年10月在不同林冠孔隙下方增設4個小苗樣區，監測颱風過後的更新動態。此外，為增加小苗樣區樣本數，2004年2月於步道3.5 km北側迎風坡森林(Figure 1 b, Site B)，依同樣方式另設10個小苗樣區，同年8月再增設11個樣區，北側試驗地共設置21個小苗樣區。北側試驗地並未設置樣區調查森林組成，但現地觀察其林相及樹種組成與南側試驗地森林極為類似。南、北兩處試驗地最初設置小苗樣區時，樣區四邊是以黃色尼龍繩置於地表界定邊界，但該邊界常遭凋落物遮蓋難

以辨認，故於2004年8月將所有小苗樣區邊界改用PVC塑膠管(外徑28 mm)組合的立體長方形框架，長度、寬度仍維持原樣，另於長2 m的邊框新增4個支柱插入林地，整體框架高出地表5 cm，如此樣區邊界清楚可辨。南側森林有1個孔隙下方的樣區(#24)於 2006年遭到莎勒竹(*Schizostachyum diffusum* (Blanco) Merr.)嚴重入侵而放棄，因此本研究以44個樣區的資料進行小苗動態分析。植物學名依據臺灣物種名錄網站(TaiCOL 2025)。本研究藉Dice-Sørensen coefficient (DSC) (Dice 1945)計算小苗群聚與上層成樹群聚之組成相似性：

$$DSC = \frac{2C}{A+B} \times 100\% \cdots\cdots (1)$$

式中A、B分別為小苗群聚、成樹群聚的物種數，C為兩者共有的物種數。

光環境測定

為瞭解小苗樣區接受到的可用光資源程度，於2005~2011年每半年測定一次小苗樣區接受到的可用光資源，遇有颱風擾動時則增加測定次數，試驗期間共測定光量16次。光量測定日於10:30~13:00在各小苗樣區上方60 cm 處以光量計(Quantum sensor, LI-190SA, LI-COR, Lincoln, NE, USA)，配合光量記錄器(LI-250, LI-COR)，測定5個位置的光合作用有效光子量(photosynthetic photon flux density, PPFD)，將其平均之，於同一時間在試驗地4 m高的平台上測定全光(full light)數值，可計算各小苗樣區PPFD平均值與全光PPFD值比例，此即為小苗樣區的相對光量(relative light intensity)數值。

新生苗於不同齡級的存活比例及存活中位時間

新生苗單株存活時間(survival time)或壽命(lifespan)，可藉植株最後出現的時間減去首次出現的時間得知。前生苗不知何時萌發，不知存活時間，無法計算不同年齡的存活比例(survival proportion)。本研究將新生苗分為兩類：第一類為新生苗植株於調查期間死亡，依前述方法可確知其存活月數；第二類為新生苗在2011年7月最終調查(final census)時仍存活，可確知已經存活的月數，但該植株壽命尚未結束。本研究計算某物種新生苗存活分別滿1、2、3、4、5、6年，6個齡級(age class)的存活比例，各齡級對應的存活月數範圍分別是13~24, 25~36, 37~48, 49~60, 61~72, 73~84個月，而各齡級起始的月數，即為其門檻月數(threshold months)，例如齡級1、2年之新生苗，其存活門檻月數分別為第13、25個月。本研究計算某物種新生苗某齡級的存活比例時，是以存活月數≥ 該齡級門檻月數的新生苗總數(包括調查期間曾出現的第一及第二類新生苗)當計算式分子(N)，但分母不是該物種新生苗總數(N_T)，而是將NT扣除第二類仍存活但萌發時間< 該齡級門檻月數的小苗數量(AL)，當作計算該齡級存活比例之計算式分母，例如某株最終調查仍存活的新生苗其存活月數為48個月，低於齡級4的門檻月數49個月，計算齡級4新生苗的存活比例時，分母要扣除該植株樣本。各齡級新生苗存活比例(SP, %)計算公式如下：

$$SP_i = \frac{N_i}{N_T - AL_i} \times 100\% \cdots\cdots (2)$$

式中SP_i為某物種新生苗於齡級i之月數範圍的存活比例；N_i為存活月數≥ 該齡級門檻月數的新生苗總數；N_T為該物種新生苗總數；AL_i為仍存活但萌發時間 < 該齡級門檻月數的新生苗數量。

本研究也藉Kaplan-Meier存活分析法(Lee and Wang 2003)，使用R的“Survival Package” (R Core Team 2025)估算下列各類物種新生苗的存活中位時間(median survival time, MST)，單位為月：(1)整體新生苗群聚的MST；(2)不同耐陰類群物種的MST，包括不耐陰、中等耐陰、耐陰三類群；(3)新生苗數量較多的30物種各別物種的MST。獲得物種階層的MST值後，藉迴歸分析探討各物種在不同齡級的存活比例，與其MST值是否具有顯著關係。

結果

試驗地成樹組成

試驗地南側森林在1450 m²樣區調查到71種成樹(DBH ≥ 1 cm)，總株數2,330株(Table 1)，密度為16,100 stem ha^{-1}。成樹物種豐度較高的科別，包括樟科(Lauraceae) 8種，殼斗科(Fagaceae) 6種、冬青科(Aquifoliaceae) 5種。在物種階層，數量較多者依序為臺灣八角(*Illicium arborescens* Hayata) 386株、日本賽衛矛(*Microtropis japonica* (Franch. & Sav.) Hallier f.) 121株、九節木(*Psychotria rubra* Poir.) 108株、革葉冬青(*Ilex cochinchinensis* Loes.) 102株、長尾尖葉櫧(*Castanopsis cuspidata* var. *carlesii* (Hemsl.) T.Yamaz.)101株，而數量1~3株者15種(Table 1)。組成樹種中嶺南青剛櫟(*Quarcus championii* Benth.)有胸徑> 60 cm的大徑木，大頭茶(*Polyspora axillaris* (Roxb. et Ker Gawl.) Sweet)、黃杞(*Engelhardia roxburghiana* Wall.)有胸徑 30~40 cm的林木，長尾尖葉櫧、郭氏錐果櫟(*Quercus longinux* var. *kuoi* (J.C.Liao) C.F.Shen)有胸徑20~29 cm的單株；嶺南青剛櫟、長尾尖葉櫧、捲斗櫟(*Quercus pachyloma* Seemen)、黃杞有樹高> 8 m的單株(未發表數據)。

小苗組成、豐量及密度

南側試驗地20個小苗樣區首次調查記錄到51種495株前生苗(Table 1)，加上後續設置的24個樣區，前生苗共65種964株，其中55種試驗期間曾萌發新生苗。新生苗在調查9年期間共萌發64種1,688株(Table 1, TNR)。2011年最終調查時，整體小苗(前生苗及新生苗合計)存活65種，前生苗、新生苗的數量別為530、1,019株，合計1,549株。密度方面，首次調查時小苗密度為24.8 stem m^{-2}，整體小苗密度逐年提高，最終調查時達35.2 stem m^{-2} (Figure 2)。小苗物種豐度較高的科別包括樟科8種、茜草科(Rubiaceae) 7種、殼斗科5種，另有1種裸子植物竹柏(*Nageia nagi* (Thunb.) Kuntze) (Table 1)。成樹群聚中有12種未調查到小苗，例如松田氏冬青(*Ilex lonicerifolia* var. *matsudae* (Yamam.) Yamam.)、杏葉石櫟(*Lithocarpus amygdalifolius* (Skan) Hayata)、恆春山茶(*Camellia hengchunensis* C.E.Chang)等(Table 1)。試驗地成樹及整體小苗群聚的物種數分別為71、75種，小苗群聚中有16種不在成樹群聚中，兩群聚組成相同者59種，兩者的Dice-Sørensen coefficient為80.8%，兩群聚組成相似性高。

新生苗物種豐量的動態變化

新生苗豐量最高前5種分別為日本賽衛矛(喬木，268株)、恆春石斑木(*Rhaphiolepis indica* var. *hiiranensis* (Kaneh.) H.L.Li) (灌木，179株)、九節木(灌木，125株)、臺灣八角(喬木，102株)、大頭茶(喬木，95株)。新生苗豐量≥10株者有30種共1,603株(Table 2)，豐量< 10株者另有34種85株，其中14種僅發現1株(Table 1)。新生苗數量較多的30種中有28種在南、北兩試驗地都有分布，但細脈赤楠(*Syzygium euphlebium* (Hayata) Mori.)、頷垂豆(*Archidendron lucidum* (Benth.) I.C.Nielsen)僅出現在南側試驗地。

個別物種新生苗豐量逐年變化的樣式可歸為四型(Figure 3)，第一型為豐量逐年提高並維持高值，例如日本賽衛矛、倒卵葉冬青(*Ilex maximowicziana* Loes.)、雨傘仔(*Ardisia cornudentata* Mez)、橢圓葉赤楠(*Syzygium elliptifolium* (Merr.) Merr.)、江某(*Heptapleurum heptaphyllum* (L.) Y.F.Deng)、毛雞屎樹(*Lasianthus cyanocarpus* Jack) (Figure 3 a, d, j, m, n, s)；第二型其豐量也是逐年提高並維持高值數年，但之後緩慢減少，例如恆春石斑木、臺灣八角、九節木、大頭茶、大明橘(*Myrsine seguinii* H.Lév.)、山黃梔(*Gardenia jasminoides* J.Ellis)、小葉木犀(*Osmanthus marginatus* (Champ. ex Benth.) Hemsl.) (Figure 3 b, c, e, f, g, h, i)；第三型為新生苗豐量在7個年度大致維持穩定，奧氏虎皮楠(*Daphniphyllum glaucescen* subsp. *oldhamii* (Hemsl.) T.C.Huang)、武威山新木薑子(*Neolitsea buisanensis* Yamam. & Kamik.)、長尾尖葉櫧屬之(Figure 3 p, q, r)；第四型為新生苗豐量於某年度明顯增多，之後明顯降低，白匏仔(*Mallotus paniculatus* (Lam.) Müll.

Table 1. Abundance (stems) and shade-tolerance classes (STC) of trees with DBH ≥ 1 cm within 58 plots (25-m²) surveyed in July 2002 at the southern site of the windward slope of Nanjenshan Forest. Abundance of advanced seedlings at 20 seedling plots of 1-m² as of the initial census in July 2002 and the re-censuses of all seedlings in 44 seedling plots in August 2005, July 2007, 2009, and 2011. TNR: total newly recruited seedlings. INT: intolerant, MT: moderately tolerant, T: tolerant species

Species	Trees	Seedlings					
	Stems (STC)	2002	2005	2007	2009	2011	TNR
Podocarpaceae							
*Nageia nagi*竹柏EN[2,*5]	25 (T)	4	4	15	10	8	15
Aquifoliaceae							
*Ilex cochinchinensis*革葉冬青[6]	102 (T)	1	4	4	5	5	1
Ilex loniceri folia var. *matsudae*松田氏冬青#[1*]	94 (T)	0	0	0	0	0	0
*Ilex maximowicziana*倒卵葉冬青[*]	3 (T)	2	34	34	53	60	85
*Ilex rotunda*鐵冬青	1 (MT)	1	1	1	2	2	2
*Ilex uraiensis*烏來冬青	55 (T)	1	2	3	4	4	4
Araliaceae							
*Heptapleurum heptaphyllum*江某	6 (MT)	7	10	17	16	18	26
Celastraceae							
*Microtropis fokienensis*福建賽衛矛	0 (T)	1	10	6	6	5	0
*Microtropis japonica*日本賽衛矛[*]	121 (T)	116	172	188	220	258	268
Chloranthaceae							
*Sarcandra glabra*紅果金粟蘭	0 (T)	5	9	16	17	27	37
Clusiaceae							
*Garcinia multiflora*恆春福木	28 (T)	4	12	12	12	13	3
Daphniphyllaceae							
Daphniphyllum glaucescens subsp. *oldhamii* 奧氏虎皮楠	30 (T)	6	30	29	37	25	21
Ebenaceae							
*Diospyros eriantha*軟毛柿	10 (T)	2	4	4	4	3	2
*Diospyros morrisiana*山紅柿	14 (T)	0	1	1	1	1	0
Elaeocarpaceae							
*Elaeocarpus sylvestris*杜英	16 (MT)	2	8	8	9	12	7
Ericaceae							
*Rhododendron simsii*唐杜鵑[*]	28 (MT)	3	3	3	2	2	0
Euphorbiaceae							
*Macaranga tanarius*血桐	0 (INT)	0	1	0	0	0	1
*Mallotus paniculatus*白匏子	0 (INT)	0	40	44	39	19	85
*Melanolepis multiglandulosa*蟲屎	0 (INT)	0	10	13	4	0	31
*Triadica cochinchinensis*白桕	0 (INT)	0	40	32	23	14	35
Fabaceae							
*Archidendron lucidum*頷垂豆	54 (MT)	16	27	28	29	40	15
*Ormosia hengchuniana*恆春紅豆樹# NT[4]	11 (T)	1	1	1	1	0	0
Fagaceae							
Castanopsis cuspidata var. *carlesii*長尾尖葉櫧	101 (T)	18	37	40	37	33	20
*Lithocarpus amygdalifolius*杏葉石櫟	26 (T)	0	0	0	0	0	0
*Lithocarpus harlandii*短尾葉石櫟	6 (T)	0	0	0	0	0	1
*Quercus championii*嶺南青剛櫟[*]	27 (MT)	1	3	3	2	2	1
Quercus longinux var. *kuoi* 郭氏錐果櫟#	68 (T)	1	4	3	4	4	5
*Quercus pachyloma*捲斗櫟[*]	41 (MT)	5	5	5	6	7	4

Table 1. (continue)

Species	Trees	Seedlings				
	Stems (STC)	2002	2005	2007	2009	2011	TNR
Garryaceae							
*Aucuba chinensis*桃葉珊瑚	1 (T)	0	1	1	2	2	1
Hydrangeaceae							
*Hydrangea chinensis*華八仙	0 (T)	0	0	0	0	0	2
Juglandaceae							
*Engelhardia roxburghiana*黃杞	32 (T)	6	4	4	4	3	1
Lamiaceae							
*Callicarpa remotiflora*疏花紫珠# NT	0 (MT)	0	1	1	2	2	1
Lauraceae							
*Beilschmiedia erythrophloia*瓊楠	0 (T)	0	2	1	0	0	0
*Beilschmiedia tsangii*華河瓊楠	79 (MT)	4	18	12	14	16	2
*Cinnamomum brevipedunculatum*小葉樟#VU	13 (T)	6	11	8	8	7	1
*Cryptocarya chinensis*厚殼桂	5 (T)	0	0	0	0	0	0
*Litsea acutivena*銳脈木薑子	28 (T)	4	4	4	4	6	2
*Machilus thunbergii*紅楠	23 (T)	2	14	11	10	5	6
*Machilus obovatifolia*恆春楨楠#	1 (T)	0	0	0	1	1	1
*Machilus zuihoensis*香楠#	0 (MT)	12	10	8	9	11	15
*Neolitsea buisanensis*武威山新木薑子*	35 (T)	13	26	33	44	27	19
*Neolitsea hiiranensis*南仁山新木薑子# VU[3]	1 (T)	0	0	0	0	0	0
Magnoliaceae							
*Magnolia kachirachirai*烏心石舅# VU	33 (MT)	0	2	2	2	1	0
Michelia compressa var. *formosana*臺灣烏心石#	4 (MT)	0	1	1	1	1	0
Melastomataceae							
*Melastoma candidum*野牡丹	60 (INT)	0	1	12	44	33	54
Moraceae							
*Ficus formosana*天仙果	0 (MT)	1	6	7	6	8	3
Ficus superba var. *japonica*雀榕	1 (INT)	0	0	0	0	0	0
Myricaceae							
*Myrica adenophora*青楊梅EN	1 (MT)	0	0	0	0	0	1
Myrtaceae							
*Decaspermum gracilentum*十子木	2 (MT)	0	0	0	0	0	0
*Syzygium elliptifolum*橢圓葉赤楠#*	29 (T)	17	53	59	58	62	34
*Syzygium euphlebium*細脈赤楠	10 (T)	8	10	53	41	22	62
Oleaceae							
*Osmanthus marginatus*小葉木犀	26 (T)	7	17	38	37	35	50
Opiliaceae							
*Champereia manillana*山柚	3 (T)	0	0	0	0	0	0
Pentaphylacaceae							
*Adinandra formosana*臺灣楊桐#	6 (T)	0	0	0	0	0	0
Anneslea fragrans var. *lanceolata*細葉茶梨* #VU	29 (T)	1	0	0	1	1	1
*Cleyera japonica*紅淡比*	6 (T)	0	0	0	0	0	0
*Eurya nanjenshanensis*南仁山柃木# NT*	56 (T)	4	13	14	16	11	10
*Ternstroemia gymnanthera*厚皮香*	11 (T)	0	0	0	0	0	0

Table 1. (continue)

Species	Trees	Seedlings					
	Stems (STC)	2002	2005	2007	2009	2011	TNR
Phyllanthaceae							
*Antidesma hiiranense*南仁五月茶# NT	51 (T)	2	9	4	6	7	3
*Glochidion philippicum*菲律賓饅頭果	6 (INT)	0	5	5	2	2	0
*Glochidion rubrum*細葉饅頭果	5 (INT)	2	2	2	5	5	3
*Glochidion zeylanicum*錫蘭饅頭果	0 (INT)	0	0	0	3	3	3
Primulaceae							
*Ardisia quinquegona*小葉樹杞	26 (T)	0	2	2	2	1	1
*Ardisia sieboldii*樹杞	0 (T)	1	3	2	10	8	16
*Ardisia cornudentata*雨傘仔	25 (T)	43	73	74	69	80	43
*Myrsine seguinii*大明橘*	53 (T)	16	23	39	53	57	37
Proteaceae							
*Helicia rengetiensis*蓮華池山龍眼	4 (T)	0	0	0	0	0	0
Rosaceae							
*Prunus phaeosticta*墨點櫻桃	1 (MT)	0	1	1	1	1	0
Rhaphiolepis indica var. *hiiranensis*恆春石斑木#*	21 (MT)	48	137	139	110	103	179
Rubiaceae							
*Gardenia jasminoides*山黃梔	1 (MT)	5	9	17	39	37	47
*Lasianthus cyanocarpus*毛雞屎樹	0 (T)	2	14	15	16	28	21
*Lasianthus obliquinervis*雞屎樹	3 (T)	4	9	7	12	23	21
*Litosanthes biflora*壺冠木	0 (T)	0	2	2	1	3	2
*Psychotria rubra*九節木	108 (T)	33	85	94	108	113	125
*Tarenna gracilipes*薄葉玉心花#	8 (T)	0	2	2	3	0	3
*Tricalysia dubia*狗骨仔	40 (T)	1	6	10	8	7	5
Rutaceae							
*Melicope semecarpifolia*山刈葉	1 (MT)	0	1	3	2	3	6
*Tetradium glabrifolium*賊仔樹	0 (INT)	0	1	2	1	0	1
Sabiaceae							
*Meliosma squamulata*綠樟*	47 (T)	0	5	3	2	2	4
Schisandracea							
*Illicium arborescens*臺灣八角#	386 (T)	36	142	174	138	135	102
Symplocaceae							
*Symplocos congesta*楊桐葉灰木*	57 (T)	3	7	6	7	7	1
*Symplocos shilanensis*希蘭灰木# VU*	18 (T)	1	1	1	0	0	0
*Symplocos theophrastifolia*山豬肝	21 (T)	4	17	14	14	10	10
Theaceae							
*Camellia hengchunensis*恆春山茶# VU	3 (T)	0	0	0	0	0	0
*Polyspora axillaris*大頭茶*	58 (MT)	6	19	44	66	69	95
Schima superba var. *kankaoensis*港口木荷#	24 (MT)	2	2	2	2	2	0
Thymelaceae							
*Wikstroemia taiwanensis*臺灣蕘花#*	1 (T)	2	18	22	20	27	25
Total individuals	2,330	495	1,261	1,465	1,547	1,549	1,688
Total species	71	51	68	68	69	65	64

[1] #: Endemic to Taiwan, [2] EN: Endangered, [3] VU: Vulnerable, [4] NT: Near-threatened, [5] *: characteristic species of ridge-type community (Fan et al. 2005), [6] The underlined species are expected to persist in future forest composition.

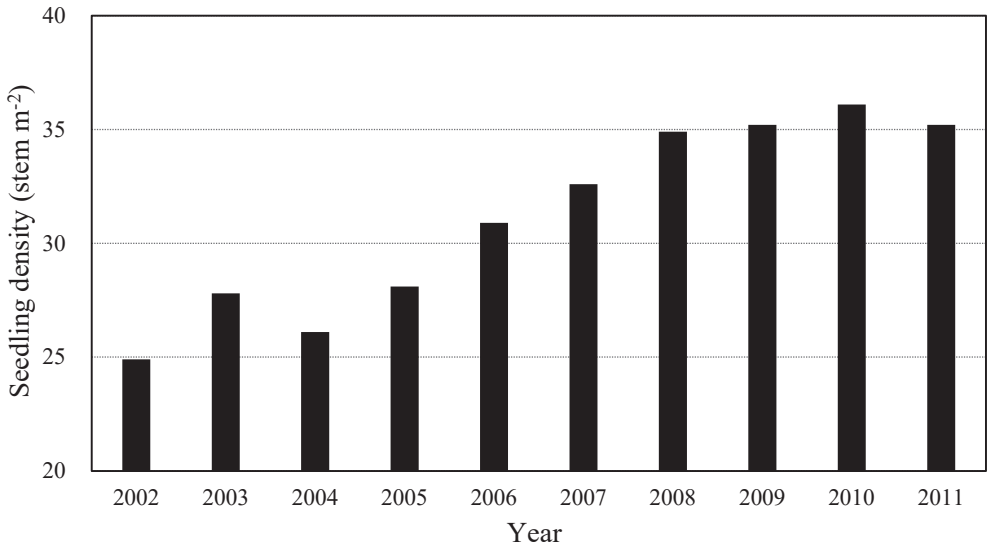

Figure 2. Density of advanced seedlings at the initial census (July 2002) and of all seedlings during subsequent re-censuses (July 2003–2011; August 2005) on the windward slopes of Nanjenshan Forest.

Arg.)、細脈赤楠、野牡丹(*Melastoma candidum* D.Don)、白柏(*Triadica cochinchinensis* Lour.)、蟲屎(*Melanolepis multiglandulosa* (Reinw. *ex* Blume) Rchb. & Zoll.)屬此類型(Figure 3 k, l, o, t, u)。

新生苗於不同苗齡的存活比例及存活中位時間

調查9年期間共記錄到新生苗1,688株，最終調查時仍存活1,019株，苗齡介於1~107個月。新生苗存活≥ 8年(96個月)者有12種19株，以臺灣八角5株，長尾尖葉櫧3株較多。新生苗≥ 10株之30物種，於苗齡分別為13~24, 25~36, 37~48, 49~60, 61~72, 73~84個月時，平均存活比例分別為70.3 ± 17.2、52.8 ± 17.3、42.3 ± 17.2、31.9 ±17.3、20.9 ± 13.6、12.2 ± 12.4% (Table 2, mean ± 1 SD)。苗齡13~24個月時存活比例< 50%者僅蟲屎、白匏仔；苗齡25~36, 37~48, 49~60個月時存活比例≥ 50%者分別有19、11、5種；苗齡73~84個月時雨傘仔、武威山新木薑子的存活比例分別高達40、38% (Table 2)。

整體64種1,688株新生苗，藉由Kaplan-Meier存活分析法估算的存活中位時間(MST值)為34個月(Figure 4)，不耐陰類群8物種的MST值為12個月，中等耐陰類群18種、耐陰類群38種的MST值分別為40、39個月。新生苗≥ 10株之30物種的MST值分布在6~80個月，以雨傘仔MST值最大，依序為武威山新木薑子71個月、大頭茶64個月；香楠(*Machilus zuihoensis* Hayata)、山黃梔、長尾尖葉櫧、大明橘、竹柏等5種為53~59個月；江某、奧氏虎皮楠、九節木、臺灣蕘花、小葉木犀、臺灣八角、南仁山柃木等7種則為40~49個月；新生苗數量較多的日本賽衛矛及恆春石斑木，MST值則分別為37、19個月(Table 2)。蟲屎、白匏仔、白柏、野牡丹等4種不耐陰物種的MST值較小，分別為6、11、19、17個月(Table 2)。此外，30物種的MST值，與各物種於苗齡25~36, 37~48, 49~60個月等3齡級的存活比例都具顯著正向關係($r^2 \geq 0.80$)，MST值與苗齡49~60個月存活比例的關係最密切($r^2 = 0.83$)。上述30物種中喬木類、灌木類物種分別有22、8種(Table 2)，前者MST值平均(± 1 SD)為40.1 ± 18.1個月，後者為37.1 ± 10.4個月，兩者的MST值不具顯著差異。

新生苗及前生苗的高生長

新生苗數量≥ 10株的30物種，初始苗高在4.0~7.4 cm範圍，以長尾尖葉櫧最高，而江某、樹杞(*Ardisia sieboldii* Miq.)、九節木、南仁山柃

Table 2. Survival proportion (%) of newly recruited seedlings within various age ranges for 30 woody species growing in the windward slopes of Nanjenshan Forest. *n*, sample size, numbers in brackets are surviving individuals at the final census. MST, median survival time (months). A_{max}, the maximum photosynthetic rate (μmol CO_2 m^{-2} s^{-1}, reported by Kuo et al. 2021). Growth form T: tree, S: shrub. Species are listed in descending order of A_{max} values

Species and growth form	*n*	Seedling age (months)						MST	A_{max}
		13~24	25~36	37~48	49~60	61~72	73~84		
Melanolepis multiglandulosa (蟲屎) T	31 (0)	10	7	3	0	0	0	6	31.0
Mallotus paniculatus (白匏仔) T	85 (15)	45	28	22	18	15	0	11	29.4
Triadica cochinchinensis (白桕) T	35 (4)	63	41	38	18	13	3	19	26.0
Melastoma candidum (野牡丹) S	54 (24)	53	27	23	15	7	3	17	24.6
Machilus zuihoensis (香楠) T	15 (7)	71	62	45	45	22	11	53	19.7
Polyspora axillaris (大頭茶) T	95 (51)	75	61	49	31	26	20	64	19.4
Rhaphiolepis indica [1] (恆春石斑木) S	179(58)	64	42	29	22	15	12	19	18.1
Heptapleurum heptaphyllum (江某) T	26 (14)	80	62	55	39	31	0	48	17.4
Gardenia jasminoides (山黃梔) T	47 (31)	91	64	50	44	11	11	59	16.5
Archidendron lucidum (頷垂豆) T	15 (8)	69	36	30	22	13	13	22	16.1
Ardisia cornudentata [2] (雨傘仔) S	43 (32)	90	81	76	68	57	40	80	15.2
Ardisia sieboldii (樹杞) T	16 (6)	64	43	25	9	9	9	20	15.0
Daphniphyllum glaucescens [3] (奧氏虎皮楠) T	21 (9)	75	65	47	42	37	33	47	14.5
Castanopsis cuspidata [4] (長尾尖葉櫧) T	20 (9)	85	63	58	50	41	31	57	14.1
Psychotria rubra (九節木) S	125 (67)	79	65	44	38	30	5	48	13.8
Wikstroemia taiwanensis (臺灣蕘花) S	25 (14)	76	63	50	29	21	15	44	13.7
Ilex maximowicziana (倒卵葉冬青) T	85 (38)	64	37	19	8	2	0	26	13.5
Syzygium elliptifolum (橢圓葉赤楠) T	34 (16)	64	50	38	36	25	5	33	13.3
Myrsine seguinii (大明橘) T	37 (22)	83	66	62	50	21	6	59	12.9
Symplocos theophrastifolia (山豬肝) T	10 (3)	60	44	33	22	22	22	26	12.8
Osmanthus marginatus (小葉木犀) T	50 (24)	82	61	55	41	19	4	49	12.6
Neolitsea buisanensis (武威山新木薑子) T	19 (11)	82	71	71	63	44	38	71	11.6
Syzygium euphlebium (細脈赤楠) T	62 (14)	85	69	47	25	20	4	33	10.9
Illicium arborescens (臺灣八角) T	102 (48)	74	58	53	46	32	22	49	10.3
Microtropis japonica (日本賽衛矛) T	268(150)	74	54	39	26	16	11	37	8.7
Nageia nagi (竹柏) T	15 (4)	80	73	67	50	18	9	54	8.3
Sarcandra glabra (紅果金粟蘭) S	37 (19)	69	54	50	35	18	10	37	-
Lasianthus cyanocarpus (毛雞屎樹) S	21 (13)	60	46	33	27	20	20	30	-
Lasianthus obliquinervis (雞屎樹) S	21 (10)	62	31	15	8	8	8	22	-
Eurya nanjenshanensis (南仁山柃木) T	10 (4)	80	60	50	29	14	0	40	-
Mean		70.3	52.8	42.5	31.9	20.9	12.2		

[1] var. *hiiranensis*, [2] subsp. *cornudentata*, [3] subsp. *oldhamii*, [4] var. *carlesii*.

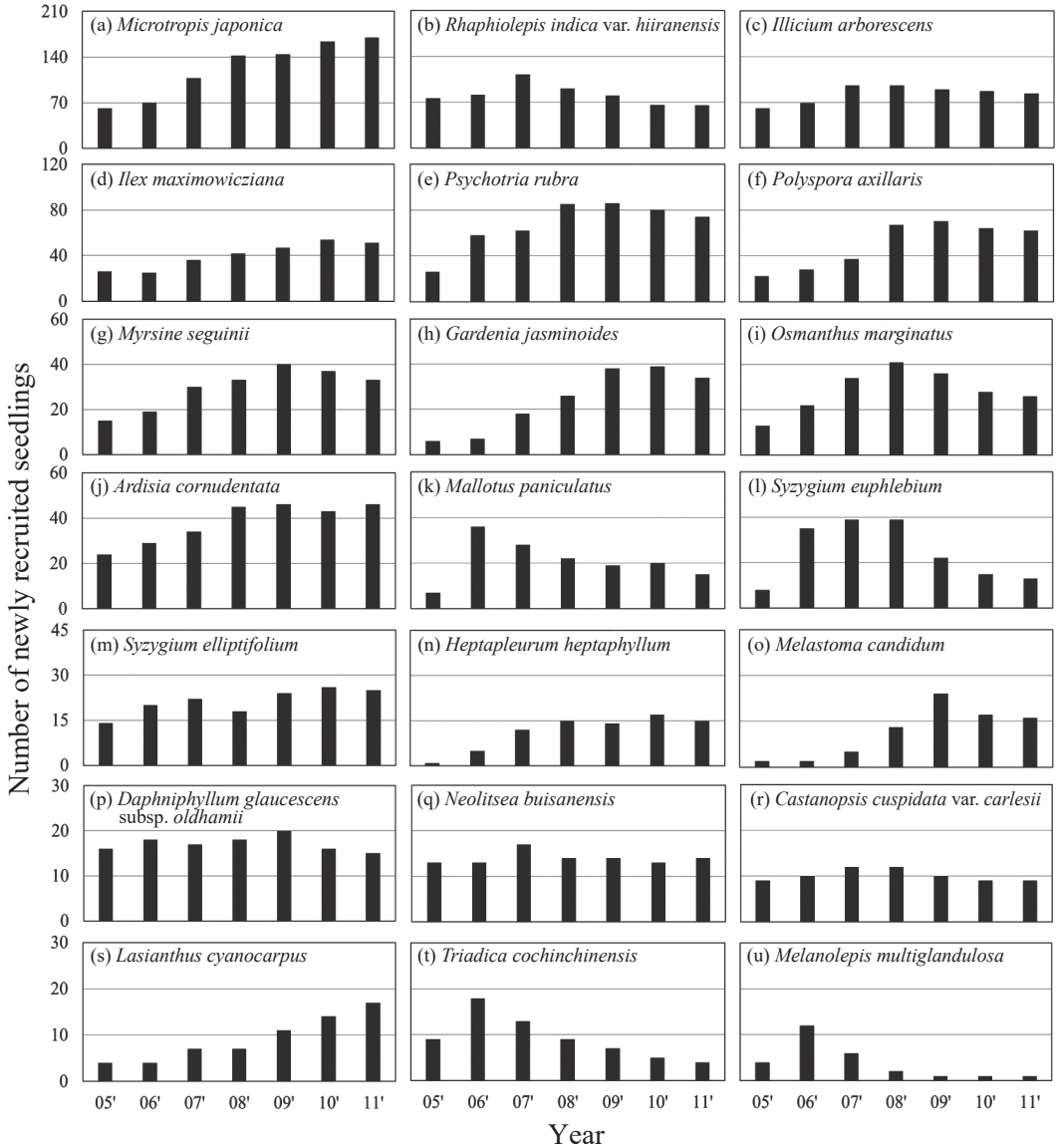

Figure 3. Annual abundance of newly recruited seedlings of 21 tree species during the July or August census (2005–2011) on the windward slopes of Nanjenshan Forest.

木(*Eurya nanjenshanensis* (C.F.Hsieh, L.K.Ling & Sheng Z.Yang) Sheng Z.Yang & S.Y.Lu) 初始苗高較低，都≤ 4.5 cm (Table 3)。不耐陰的白匏仔、白柏、野牡丹新生苗生長快，合併此3種，於苗齡24、48月時平均苗高分別為27.5 ± 6.3、58.9 ± 21.3 cm (± 1 SD)。紅果金粟蘭(*Sarcandra glabra* (Thunb.) Nakai)、毛雞屎樹、雞屎樹(*Lasianthus obliquinervis* Merr.)、南仁山柃木等4種雖尚未測得光合潛力數值(Table 2)，未能歸類其耐陰性等級，但依據其微生育地之光環境(個人觀察)都可歸類為耐陰物種。合併上述4種，試驗地26種耐陰物種於苗齡24、48月時的苗高平均值分別為8.6 ± 1.5、13.6 ± 5.1 cm，顯示高生長緩慢，但新生苗高生長種間差異大。香楠、奧氏虎皮楠、

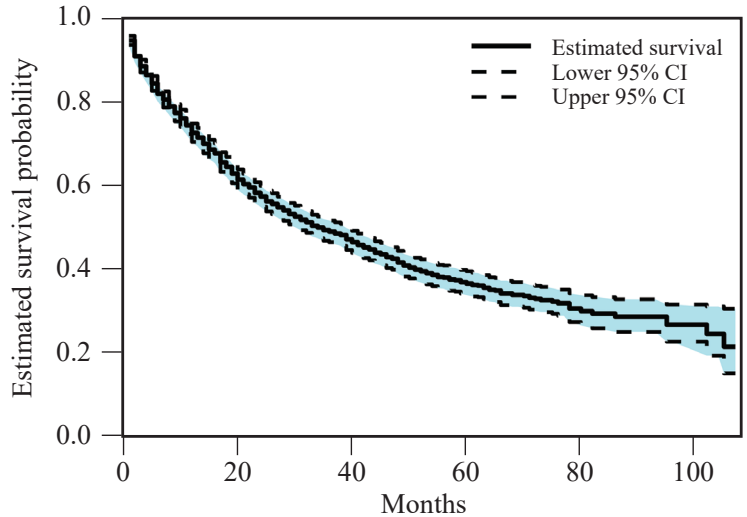

Figure 4. Estimated survival function of all new recruits combined on the windward slopes of Nanjenshan Forest based on monthly seedling censuses (July 2002–July 2011). Estimated survival average probability (solid lines) and 95% confidence interval (CI) (dotted lines) are shown.

長尾尖葉櫧、臺灣蕘花(*Wikstroemia taiwanensis* C.E.Chang)小苗高生長較快，此4種於苗齡48月時平均苗高都> 20 cm，苗齡72 月時可達33~53 cm；相對的，樹杞、九節木、小葉木犀、日本賽衛矛、紅果金粟蘭小苗的高生長極慢，各物種苗齡48 月時之平均高度都< 10 cm (Table 3)。新生苗於最終調查時存活1,019株，其中高度≥ 50 cm者14種40株。

首次調查於20個樣區記錄到495株前生苗，最終調查時存活215株；首次調查時苗高以< 10 cm者最多(40%)，苗高≥ 60 cm的數量僅6%；經過9年這些前生苗明顯長高，以高度級20~29 cm者居多，苗高≥ 60 cm的數量已提高到26% (Figure 5)。所有44個樣區的前生苗於最終調查時存活530株，高度≥ 100、200、300 cm者分別有108、13、3株。最終調查時前生苗與新生苗共存活1,549株，植株高度≥ 100、200、300 cm者分別有122、19、3株，最高的6株分別為野牡丹360 cm (前生苗)、奧氏虎皮楠363、312、288 cm (前生苗)、白柏297 cm (新生苗)、長尾尖葉櫧290 cm (前生苗)。

藉新生苗苗齡與苗高的迴歸關係(Figure 6)，估算同一物種小苗高度達20 cm所需的時間(Age_{20})，發現白匏仔、白柏、野牡丹於苗齡1.3~1.5年即可長至20 cm高(Table 3)。耐陰性物種中有20種的小苗，於苗齡2.7~10.3年苗高才會達20 cm，其中臺灣蕘花、奧氏虎皮楠、香楠的高生長相對較快，Age_{20}值分別為2.7、3.4、4.2年(Table 3)。調查期間有5種新生苗植株高度都未達20 cm，經線性外插(linear extrapolation)估計其Age_{20}值為10.4~21.0年，其中九節木、紅果金粟蘭高生長很慢，分別需 16.4、21.0年才可能長至20 cm高。毛雞屎樹之苗齡與苗高關係不顯著，無法估算Age_{20}值(Table 3)。

颱風擾動對小苗萌發及死亡的影響

試驗地於9年調查期間曾經歷4次明顯影響小苗之新生、死亡的颱風擾動事件，分別為2003年9月的強颱杜鵑、2005年7月的強颱海棠(Typhoon Haitang)、2006年7月中颱凱米(Typhoon Kaemi)，以及2009年8月的莫拉克颱風(Typhoon Morakot)。根據鄰近南仁山生態保護區的檳榔測候站資料，該4次颱風事件當月雨量依序分別為425、976、847、1,315 mm。前兩次颱風的擾動形式以風害為主，嚴重損傷森林樹冠層；凱米颱風帶來豪雨沖刷林地；莫拉克颱風帶來強風豪雨，對樹冠層及地被層都有嚴重負面影響。凱米及莫拉克颱風

Table 3. Mean height (cm) of newly recruited seedlings within various age ranges for 30 woody species growing in the windward slopes of Nanjenshan Forest. Numbers in brackets are sample size. Age_{20}, the age (years) when seedlings grow to 20 cm in height

Species and diaspore type	Initial	12 mo	24 mo	48 mo	72 mo	Age_{20}
Melanolepis multiglandulosa (capsule)	6.0 (31)	9.3 (9)	9.7 (3)	-	-	5.4 [3]
Mallotus paniculatus (capsule)	6.2 (85)	12.6 (41)	20.2 (20)	35.0 (12)	82.5 (9) [2]	1.3
Triadica cochinchinensis (capsule)	6.5 (35)	17.0 (24)	30.7 (15)	65.6 (8)	297 (1)	1.4
Melastoma candidum (capsule)	5.8 (54)	12.0 (25)	31.6 (12)	76.0 (5)	95 (1)	1.5
Machilus zuihoensis (drupe)	6.9 (15)	8.9 (11)	9.7 (9)	22.8 (6)	53.0 (1)	4.2
Polyspora axillaris (capsule)	5.1 (95)	5.6 (71)	8.1 (53)	11.7 (19)	14.3 (11)	6.2
Rhaphiolepis indica var. *hiiranensis* (pome)	5.7 (179)	6.7 (109)	8.1 (72)	13.4 (32)	26.4 (16)	4.9
Heptapleurum heptaphyllum (drupe)	4.3 (26)	6.3 (21)	10.3 (13)	17.1 (9)	20.6 (5) [2]	5.5
Gardenia jasminoides (berry)	4.8 (47)	6.6 (42)	7.3 (27)	10.1 (11)	21.5 (2)	6.4
Archidendron lucidum (legume)	6.1 (15)	8.5 (11)	9.5 (4)	12.5 (2)	16.1 (1)	10.4 [3]
Ardisia cornudentata (drupe)	5.8 (43)	7.7 (36)	9.5 (31)	12.3 (17)	20.8 (6)	6.5
Ardisia sieboldii (drupe)	4.0 (16)	4.8 (9)	6.3 (6)	7.3 (4)	9.0 (1)	12.8 [3]
Daphniphyllum glaucescens [1] (drupe)	6.2 (21)	8.8 (15)	11.6 (13)	22.3 (8)	53.1 (6)	3.4
Castanopsis cuspidata var. *carlesii* (nut)	7.4 (20)	7.9 (18)	9.4 (12)	22.4 (9)	32.8 (6)	4.7
Psychotria rubra (drupe)	4.5 (125)	5.3 (96)	6.3 (73)	8.6 (35)	11.2 (10)	16.4 [3]
Wikstroemia taiwanensis (drupe)	6.6 (25)	9.6 (20)	10.2 (12)	26.6 (4)	48.0 (2)	2.7
Ilex maximowicziana (drupe)	5.4 (85)	6.9 (49)	7.7 (27)	10.7 (7)	19.7 (1) [2]	5.6
Syzygium elliptifolum (berry)	5.6 (34)	7.4 (23)	9.2 (16)	12.0 (10)	15.9 (4)	7.8
Myrsine seguinii (drupe)	5.8 (37)	7.1 (29)	8.3 (21)	10.3 (13)	19.0 (1)	6.8
Symplocos theophrastifolia (drupe)	6.8 (10)	8.5 (6)	9.4 (5)	13.0 (2)	17.0 (2)	10.3
Osmanthus marginatus (drupe)	5.8 (50)	5.9 (40)	6.6 (30)	9.3 (16)	12.7 (3)	7.6
Neolitsea buisanensis (drupe)	6.4 (19)	6.6 (14)	7.8 (12)	12.9 (10)	14.0 (6)	8.0
Syzygium euphlebium (berry)	6.8 (62)	8.8 (53)	10.8 (41)	15.6 (17)	18.5 (2)	5.6
Illicium arborescens (follioles)	4.9 (102)	7.4 (73)	9.0 (59)	16.4 (40)	26.0 (13)	4.8
Microtropis japonica (capsule)	5.4 (268)	6.7 (180)	7.7 (108)	9.8 (43)	11.8 (15)	8.7
Nageia nagi (seed)	6.9 (15)	10.3 (11)	10.6 (11)	13.0 (8)	15.0 (1)	10.5 [3]
Sarcandra glabra (drupe)	4.9 (37)	5.7 (21)	6.5 (15)	8.1 (9)	8.0 (2)	21.0 [3]
Lasianthus cyanocarpus (drupe)	5.1 (21)	6.6 (10)	7.5 (6)	10.7 (3)	12.5 (2)	ns [4]
Lasianthus obliquinervis (drupe)	5.0 (21)	5.9 (8)	7.7 (4)	10.2 (1)	27.0 (1)	5.5
Eurya nanjenshanensis (berry)	4.2 (10)	6.7 (9)	9.7 (6)	18.7 (3)	33.0 (1) [2]	4.4

[1] subsp. *oldhamii*, [2] height of the 60-month-old seedlings, [3] values obtained by linear extrapolation, [4] not significant relationship.

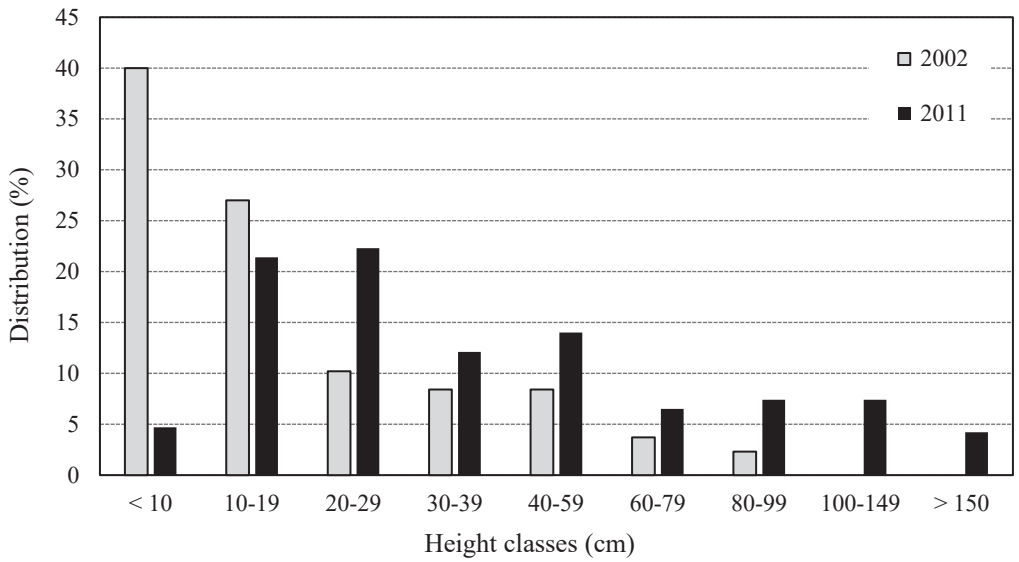

Figure 5. Height-class distributions for 215 advanced seedlings in 20 plots at the southern study site of Nanjenshan Forest (2002–2011).

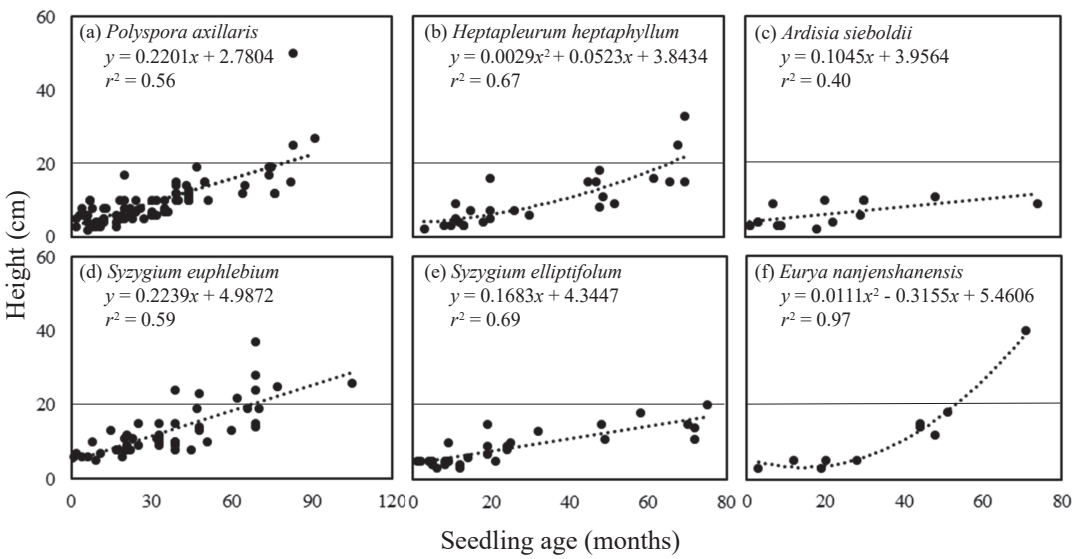

Figure 6. Seedling heights as a function of seedling ages for six representative species on the windward slopes of Nanjenshan Forest.

擾動過後半年內，整體小苗死亡數量都高於新生苗萌發數量，分別減少整體小苗密度2.6、4.5 stem m^{-2}；然而，杜鵑及海棠颱風過後卻是新生數量高於死亡數量，因為不耐陰的蟲屎、白柏、白匏仔大量萌發，造成整體小苗密度於兩次颱風過後半年內分別提高6.5、3.2 stem m^{-2}。海棠颱風過後8個月，蟲屎、白匏仔、白柏分別增加22、45、12株新生苗，但野牡丹的新增卻與颱風擾動無關。莫拉克颱風擾動前3個月整體小苗死亡26種105株；颱風擾動後3個月小苗死亡增加至41種205

株，小苗死亡總數之62%是植株遭上層掉落枝葉覆蓋無法尋獲而判定為死亡。試驗地2005~2011年於夏季、秋季新生苗出現數量(密度)接近，但小苗死亡數量於夏季明顯高於秋季(Figure 7)。

光環境方面，試驗地所有小苗樣區在2005年7月海棠颱風擾動前2週、擾動後4、8個月，平均相對光量分別為5.8、16.7、11.3%，顯示颱風擾動會提高林下光資源。2009年8月莫拉克颱風擾動前3個月、擾動後1、4個月，所有小苗樣區平均相對光量分別為7.5、12.2、7.6%。本研究9年期間共測定整體小苗樣區的光環境16日(次)，平均相對光量< 4.5%僅3次，5.8~9.8%者8次，11.3~16.7%者5次，小苗樣區16次相對光量測值平均為8.4 ± 3.9% (± 1 SD)。

討論

南仁山迎風生育地具獨特的生態環境

東北季風本質上是一個較冷的氣流，令局部地區氣溫降低，且因風吹降溫作用(wind chilling)，有季風作用的微環境氣溫會比無季風者低。因此南仁山區海拔高僅330 m的迎風坡森林，出現許多原本分布臺灣中海拔暖溫帶的冬青科及殼斗科樹種(Table 1)。東北季風長期慢性的逆境，形成南仁山迎風生育地獨特的生態環境，能忍受此處冬季強風、低溫、土壤貧瘠(Chen et al. 1997)等逆境的物種才能在此處生存，並容納許多臺灣地區性稀有物種(regionally rare species)在此環境建立(Ku et al. 2021)。試驗地71種成樹組成中的20種為臺灣特有種(endemics)，並有2種瀕危(endangered)、6種易危(vulnerable)、5種接近受脅(near threatened)等級的稀有物種(Editorial Committee of the Red List of Taiwan Plants 2017)；上述13種稀有物種中的11種在試驗地曾有小苗萌發 (Table 1)。南仁山的古湖樣區(Nanjen-Lake Plot)有20樹種為迎風稜脊型植群(ridge-type plant community)的特徵種(characteristic species) (Fan et al. 2005)，而該20種在本試驗地成樹樣區都有分布(Table 1)。Fan and Hsieh (2010)報導南仁山欖仁溪森林動態樣區(Lanjenchi Forest Dynamics Plot)下層小苗的空間分布，與上層成樹的分布十分吻合。本試驗地大多數成樹在小苗樣區出現更新苗(71種中的59種，83%)，此生態現象不同於大多數成樹種類缺少更新苗的福山森林(Chang-Yang et al. 2013)。

南仁山迎風坡森林可承載較高的小苗物種數及密度

本研究初設置小苗樣區時，是主觀的選取當時小苗(前生苗)物種數、小苗豐量較高之微生育地設置樣區，而Chang-Yang et al. (2013), Lin et al. (2017), Lin et al. (2024)小苗動態研究則是系統性的設置小苗樣區。本研究樣區設置方法雖不能代

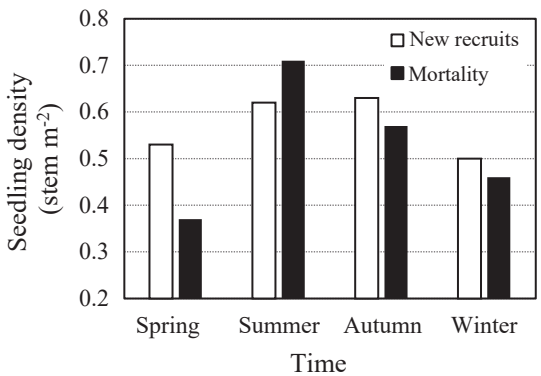

Figure 7. Seasonal variations in the seedling density of new recruits and mortality on the windward slopes of Nanjenshan Forest (2005–2011).

表當地小苗群聚種類及數量動態變化的全貌，但足以顯現此環境單位面積可承載之小苗物種豐度及小苗密度的潛力。小苗物種豐度方面，本研究首次調查時在20個1-m²小苗樣區即記錄到51種高度< 100 cm的前生苗，在整體44個小苗樣區記錄到65種前生苗，於9年期間共記錄到75種新生苗。最終調查時整體小苗存活65種，單一樣區小苗物種數介於7~21種，平均13.1種。相較之下，福山森林小苗樣區面積約為本研究的6倍(261 m²)，首次調查時記錄到DBH < 1 cm 的前生苗36種，8年期間新生苗僅記錄到28種(Chang-Yang et al. 2013)。墾丁高位珊瑚礁森林設置的小苗樣區面積約為本研究的5倍(216 m²)，於5年期間僅記錄到36種新生苗(Lin et al. 2017)。南仁山溪谷樣區設置的小苗樣區面積較本研究多出70% (75 m²)，在8.3年調查期間只記錄到43種新生苗(Lin et al. 2024)。相較於上述3處森林，本試驗地小苗群聚的物種豐度相對很高。小苗密度方面，本研究首次調查時高度< 100 cm的前生苗平均密度為24.8 stem m^{-2}， 9年期間包含前生與新生苗整體的小苗密度持續增高，最終時達35.2 stem m^{-2}，單一樣區小苗密度介於15~65 stem m^{-2}。與此相較，Tsai (2002)普查南仁山溪谷樣區1,284 個1-m²樣方，發現DBH < 1 cm 的小苗70種6,287株，小苗密度平均為4.9 stem m^{-2}；福山森林最終調查時小苗平均密度為 2 stem m^{-2} (Chang-Yang et al. 2013)。上述比較顯示本試驗地可承載的小苗密度相對很高。

試驗地成樹群聚與小苗群聚的關係

試驗地成樹群聚與小苗群聚，兩者的組成相似性很高，成樹群聚71種中有59種曾萌發更新苗，至最終調查時有54種的更新苗仍存活。比較同一物種成樹與小苗數量的差異(Table 1)，發現冬青科的革葉冬青、松田氏冬青、烏來冬青(*Ilex uraiensis* Mori & Yamamoto)有眾多成樹但更新苗數量極少，不利後續維持優勢；相反的，倒卵葉冬青成樹數量極少但更新苗數量多，將來應可提高其優勢度。殼斗科樹種：杏葉石櫟、嶺南青剛櫟、郭氏錐果櫟、捲斗櫟也是成樹多但更新苗極少，僅長尾尖葉櫧的成樹與更新苗豐量都高，後續可維持優勢。臺灣八角、日本賽衛矛成樹及更新苗數量都極多，將來應仍可維持其優勢度。此外，奧氏虎皮楠、頷垂豆、武威山新木薑子、大明橘、小葉木犀、大頭茶等樹種有數十株成樹及更新苗，將來仍會是成樹群聚的優勢組成。另一方面，黃杞、烏心石舅(*Magnolia kachirachirai* (Kanehira & Yamamoto) Dandy)、狗骨仔(*Tricalysia dubia* (Lindl.) Ohwi)、綠樟(*Meliosma squamulata* Hance)、楊桐葉灰木(*Symplocos congesta* Benth.)等5樹種在試驗地有≥ 30株成樹，但更新苗數都< 10株，將來不易維持目前的優勢程度。成樹群聚各組成物種若符合下列兩項評估準則之一，則判斷幾十年後該物種仍會是試驗地森林群聚的組成分子：(1) 2002年成樹數量≥ 10株者，無論最終調查時有無存活更新苗，因為有相當多數的母樹於幾十年期間可繁衍後代；(2) 2002年成樹數量<10株，但最終調查時仍存活的更新苗≥ 15株，因為有數量多的更新苗存活，有後繼者可成長，但排除新生苗存活時間短的白匏仔。經分析符合準則(1)、(2)者分別有46、7種，合計53種(Table 1畫底線物種)，將來有較大機會成為試驗地迎風坡森林群聚的組成物種。

試驗地喬木類與灌木類物種比較

試驗地新生苗數量較多的30物種中，喬木類物種數多於灌木類(22 vs. 8種) (Table 2)，喬木類新生苗總數也多於灌木類(1,133 vs. 480株)。最終調查時小苗樣區存活的整體小苗(前生苗及新生苗)共65種1,549株(Table 1)，其中喬木類有存活小苗者50種1,086株，灌木類為15種463株，喬木類存活物種數為整體存活小苗物種數的77%，數量則為整體存活小苗個體數的70%，顯示試驗地森林最終調查仍存活的小苗，在物種豐度及豐量兩方面都是以喬木類物種為主，有助於試驗地將來維持森林冠層群聚的組成。

更新物種的散殖體類型及傳播方式

森林小苗的更新，與更新物種的散殖體(diaspores)類型及其傳播方式(dispersal mode)關係密切。試驗地30種新生苗數量較多的物種，其散

殖體類型包括核果(drupes) 15種、蒴果(capsule) 6種、漿果(berry) 4種，另有梨果(pome) (恆春石斑木)、莢果(legume) (頷垂豆)、堅果(nut) (長尾尖葉櫧)、蓇葖果(follicle) (臺灣八角)的物種各一，裸子植物竹柏的散殖體為種子(seed) (Table3)。野牡丹蒴果肉質，開裂後可被動物取食傳播；大頭茶種子具翅，蒴果開裂後種子可風力傳播(anemochory)，東北季風期間試驗地可見此物種種子隨風散播。山黃梔、橢圓葉赤楠、細脈赤楠、南仁山柃木等4種散殖體為漿果，主要藉動物傳播(zoochory)。竹柏大粒的種子靠重力傳播(barochory)，試驗地新生苗附近常見其母樹。散殖體為核果的香楠、江某、樹杞、臺灣蕊花、倒卵葉冬青、紅果金粟蘭、毛雞屎樹、雞屎樹8物種，以及散殖體為漿果的山黃梔，在試驗地能繁殖的大植株甚少(0~6株)，但新生苗數量多(15~85株)且分散在> 10個小苗樣區，顯示這些物種多數的新生苗可能來自樣區外的散殖體。另一方面，野牡丹、大頭茶、恆春石斑木、雨傘仔、長尾尖葉櫧、九節木、大明橘、小葉木犀、臺灣八角、日本賽衛矛等10物種，原本即有許多大植株(21~386株) (Table3)，且各物種的新生苗皆分散在≥ 15個小苗樣區，顯示這些物種大多數新生苗可能來自上方母樹掉落的散殖體。不耐陰的蟲屎、白匏仔、白柏之散殖體為蒴果，試驗地並無能繁殖的大植株，小苗萌發時機與颱風擾動有關，其新生苗可能來自試驗地之外，並累積在土壤內的種子。

臺灣亞熱帶森林新生苗存活動態比較

南仁山樣帶(Nanjenshan Transect) (Lai 1996)、福山森林(Leu 2004)、南仁山溪谷樣區(Lin 2018)苗齡1年的小苗存活比例分別為22.5、33.0、22.3%；墾丁高位珊瑚礁森林苗齡0.5、2年的小苗存活比例分別為51、11% (Lin et al. 2017)，顯示該4處森林超過半數的新生苗萌發1年內即死亡。然而本試驗地30物種小苗於苗齡13~24個月的平均存活比例高達70.3% (Table 2)，不同於上述4處森林。此外在欖仁溪森林動態樣區(Li 1995)、南仁山樣帶(Liao 2019)苗齡1年的小苗存活比例分別為60、70%，新生苗並不會在萌發1年內即死亡過半。

負同種密度依存(NCDD)效應，會令某物種小苗的存活率，在同種小苗密度較高之處減低(Johnson et al. 2012, Zhu et al. 2018, Comita et al. 2024)。由此可推論：整體小苗的存活比例或存活中位時間(MST)，也會因NCDD效應而降低。本試驗地64種新生苗整體的MST值34個月，遠高於整體新生苗MST值都是6個月的福山森林、墾丁高位珊瑚礁森林、南仁山溪谷樣區(Chang-Yang et al. 2013, Lin et al. 2017, Lin et al. 2024)。由上述現象可預期本試驗地小苗群聚遭NCDD效應的影響應不明顯。在物種階層，福山森林大明橘、江某、裏白饅頭果(*Glochidion acuminatum* Müll.Arg.)新生苗數量分別為總數10,848株的63、11、9%，該3種小苗的MST值分別為7、6、4個月(Chang-Yang et al. 2013)；南仁山溪谷樣區茄苳(*Bischofia javanica* Blume)新生苗數量為總數1,810株的49%，苗齡1年時的存活比例僅4.5% (Lin 2018)。上述2處森林小苗豐量甚高的物種，可能因NCDD效應而令新生苗在短期內即大量死亡。然而，森林小苗群聚中不同物種對NCDD效應的反應並不相同(Comita and Hubbell 2009, Zhu et al. 2018)。本試驗地日本賽衛矛、恆春石斑木、九節木之新生苗數量分別為總數1,688株的16、11、7%，此3種小苗的MST值分別為37、19、48個月，苗齡13~24個月的存活比例分別為74、64、79% (Table 2)。然而，恆春石斑木新生苗各齡級的存活比例及MST值都低於日本賽衛矛及九節木(Table 2)。恆春石斑木於2002~2007年間，在一個小苗樣區即萌發60株新生苗，該60株至最終調查時，死亡植株的平均存活月數為21個月；在另 9個小苗樣區相同期間萌發的33株恆春石斑木新生苗，死亡植株的平均存活月數為32個月。上述分析顯示恆春石斑木小苗，在同種小苗密度較高的樣區其存活時間較短，具有NCDD效應。本試驗地新生苗數量較多的日本賽衛矛、九節木、臺灣八角、大頭茶、倒卵葉冬青、細脈赤楠等物種，在同種小苗密度較高的樣區，小苗平均存活時間並不會較短(數據未呈現)，NCDD效應並不明顯。

Sun et al. (1996)提出假說，認為南仁山遭長期風吹逆境的迎風生育地，植株生長率慢且存活率低。然而，在欖仁溪森林動態樣區苗齡1年的新生苗存活比例可達60% (Li 1995)，存活率並不低；南仁山樣帶的小苗動態研究也不支持上述假說，因為苗齡1、2年的新生苗存活比例分別可達70、61% (Liao 2019)。本研究也不支持上述假說，因為新生苗整體的存活中位時間為34個月，新生苗存活率高，且遠高於東北季風影響較輕微的南仁山溪谷樣區(MST值0.5年，Lin et al. 2024)小苗群聚，也高於有東北季風吹襲的福山森林(MST值0.52年，Chang-Yang et al. 2013)。在物種階層，本試驗地大明橘、江某、香楠、奧氏虎皮楠、橢圓葉赤楠、山豬肝(*Symplocos theophrastifolia* Siebold & Zucc.)之MST值分別為59、48、48、47、33、30個月(Table 2)，然而相同樹種在福山森林的小苗，其MST值分別僅為7、6、7、21、15、7個月(Chang-Yang et al. 2013)，本試驗地上述6種小苗的MST值比福山森林者高出52~17個月。福山森林MST值最大者為山龍眼(*Helicia formosana* Hemsl.) 38個月(Chang-Yang et al. 2013)，墾丁高位珊瑚礁森林MST值最大者為臺灣土沉香(*Excoecaria formosana* (Hayata) Hayata) 33個月(Lin et al. 2017)，而本試驗地有19種小苗MST值≥ 33個月，雨傘仔甚至高達80個月(Table 2)。根據上述生態現象可歸納出新的假說：南仁山迎風坡森林，相較於背風坡森林，更新小苗的存活比例較高、存活時間較長。此假說成立的可能機制如下述說明。

迎風坡森林小苗存活時間較長的可能機制

Grime (1979)將植物的生命史策略(life history strategy)歸納為三類：(1)在資源豐盛的生育地，不同物種具激烈交互作用，能建立者屬競爭性植物(competitive plant)策略；(2)在擾動(disturbance)事件頻繁的生育地建立者，屬於壽命短的雜生者(ruderal)策略；(3)在有強烈環境逆境的生育地，只有能忍受該逆境且成長緩慢、常綠性、對植食性動物不適口的耐逆境植物(stress-tolerant plant)才能建立。競爭、擾動、逆境三者嚴重程度的差異，形成多樣化的生態環境，容許具不同生命史策略的植物在各自適合的環境梯度分布(Grime 1979)。遭長期季風吹逆境的南仁山迎風生育地，小苗在生命史初期的存活率及存活時間相對很高，此現象可能的機制包括：(1)試驗地迎風坡小苗物種組成，大多與上層樹種相同，經歷長期的生態篩選(ecological filtering)已適應東北季風逆境，其生活史策略屬Grime (1979)倡議的耐逆境植物策略；為了抵抗外在環境逆境，小苗具相當高的生存韌性，其代價是生長緩慢，但連帶的也降低植株間(同種或異種)的競爭強度，此生活史策略最終可提高迎風坡小苗密度及存活時間。(2)試驗地一個小苗樣區有7~21種小苗，平均1-m²有年齡、體型各異的13種35株小苗共存。小苗植株密集生長彼此可相互保護，可減低強勁季風造成的機械損傷，因而提高小苗存活機會。(3)試驗地因有強勁季風吹襲，地被層草本植物並不茂盛(個人觀察)，不會嚴重攔阻上方入射光照；另一方面，相隔1或數年的颱風擾動，減損部分林冠，因而提高林下光資源，迎風坡森林下方平均相對光量可達8.4%，遠高於相對光量平均僅1.3%的背風溪谷樣區(Chao et al. 2022)。南仁山溪谷樣區因地被層生長著茂盛的草本植物，木本小苗可利用的光資源遭草本植物攔阻而減少24% (Chao et al. 2022)；福山森林冠層受頻繁的颱風擾動，林下入射光資源雖充足，但也是遭草本植物的負面影響，小苗可利用的光資源受限，因而不利小苗存活(Chang-Yang et al. 2013)。本試驗地森林下方相對較高的光資源，有利於小苗的新增、生長及存活(Kuo et al. 2007, Pen et al. 2007, Rüger et al. 2009, Chao et al. 2022)。

小苗存活比例與存活中位時間兩者的比較

森林下層大多數物種小苗族群的個體通常具多樣化的年齡，很少物種的小苗族群是由短時間內萌發的同齡群(age cohort)個體所組成，因此本研究計算各別物種某齡級新生苗的存活比例時，計算式分母並不是該物種小苗的總數，而是刪除最終調查時仍存活，但苗齡未達該齡級門檻月數的樣本。若是以小苗總數當計算式分母，會低估

該物種各齡級的存活比例。本研究藉由Kaplan-Meier存活分析法估算某物種新生苗存活中位月數(MST值)的結果，與該物種新生苗存活比例為50%的月數範圍(Table 2)大致吻合。例如橢圓葉赤楠新生苗存活比例50%的月數範圍為25~36個月，其MST值為33個月，MST值在該月數範圍內；紅果金粟蘭、南仁山柃木、臺灣蕘花存活比例50%都在37~48個月，其MST值分別為37、42、44個月，兩介量符合；長尾尖葉櫧、大明橘、竹柏存活比例50%都在49~60個月，而此3物種的MST值分別為57、59、59個月，兩介量也符合，其餘各物種的MST值大多位於存活比例接近50%的齡級，或前、後一個齡級的月數範圍(Table 2)。上述結果顯示，本研究計算各物種新生苗不同齡級存活比例的方法合邏輯。

小苗高生長

森林林下小苗的高生長都很慢嗎？這會因樹種及光環境而異(Kuo and Fan 2003, Kuo et al. 2007, Rüger et al. 2009)。生長在福山森林之大明橘、香楠、江某於苗齡1年的淨高生長分別為1.2、0.8、0.8 cm (Leu 2004)，上述相同樹種在本試驗地的淨高生長則都較高，分別為1.3、2.0、2.0 cm (Table 3)。福山森林新生苗平均每年淨高生長僅1.55 cm，8年調查期間只有4株之高度> 50 cm (Chang-Yang et al. 2013)。本研究9年調查期間新生苗高度≥ 50 cm者計14種40株，≥ 100 cm者4種14株，包括耐陰樹種奧氏虎皮楠3株(163、162、100 cm，苗齡71~76個月)，顯示該樹種有少數植株高生長快。試驗地不耐陰的白匏仔、白柏、野牡丹，苗齡48個月時平均淨增高生長52.8 cm，年淨高生長可達13.2 cm；相對的，26種耐陰物種新生苗高生長較緩慢，於苗齡48個月之淨增高生長僅8.2 cm，平均年淨高生長2.1 cm (Table 3)。然而，本試驗地耐陰物種小苗的年淨高生長(2.1 cm)高於福山森林小苗(1.55 cm)。另一方面，福山森林不同樹種新生苗需費時22~200年才能長到高度2 m、DBH ≥ 1 cm的稚樹階段(Chang- Yang et al. 2021)。本試驗地新生苗植株高度>2 m有2株，都是不耐陰樹種，分別為白柏297 cm (苗齡7.7年)、白匏仔211 cm (苗齡5.9年)，其DBH可能會≥ 1 cm，且至最終調查時該2株仍存活，應可由苗木晉級成為稚樹。

前生苗是森林群聚重要的後繼者

過去小苗動態研究著重在能確知年齡之新生苗的存活死亡動態，較少關注無法確知年齡之前生苗的動態。然而，這些較大齡但形體仍屬小苗階段的前生苗，因為其生命史已度過死亡率最高的幼齡階段，持續生存的機會較高(Green et al. 2014)，且植株淨高生長較快(Pan et al. 2007)，有機會在林下環境存活十幾年或數十年(Connell and Green 2000, Condit et al. 2025)。南側試驗地20個小苗樣區初設置時有495株前生苗，經過9年仍存活215株，存活率43%；最終調查時兩處試驗地前生苗共存活530株，平均1-m²存活12株，苗齡都>7年，而植株高度≥ 200 cm者已有13株，高度≥ 300 cm者3株。這些前生苗部分植株應會長到稚樹階段，成為維持森林組成結構的重要後繼者。

結論

南仁山迎風坡試驗地的71種成樹中有59種可產生小苗，顯示多數樹種的更新限制不高。最終調查時1-m²小苗樣區的物種數介於7~21種，平均13種，小苗密度介於15~65 stem m^{-2}，平均35 stem m^{-2}，顯示試驗地森林具有承載很高的小苗物種豐度及小苗豐量的潛力。試驗地整體新生苗的存活中位時間為34個月，中等耐陰、耐陰兩類群新生苗的存活中位時間分別為40、39個月，小苗並不會在萌發1年內即死亡過半。試驗地森林9年期間遭4次颱風擾動損傷林冠，但提高林下光資源，平均相對光量為8.4%，有利小苗新增及生長。每年長達6個月的東北季風強風逆境，抑制不耐風的草本植物在林下繁衍，降低其對已適應此環境的耐陰性木本小苗的競爭。在東北季風及颱風共同作用下，南仁山迎風坡森林小苗群聚的物種豐度、密度及存活時間，都高於福山森林動態樣區、墾丁高位珊瑚礁森林動態樣區、南仁山溪谷樣區之小苗群聚。

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