Taiwan J For Sci 40(2): 201-38, 2025
https://doi.org/10.7075/TJFS.202506_40(2).0004

Research paper

Responses of Photosynthetic Traits to CO_2 Concentrations in Seedlings with Different Levels of Shade Tolerance in the Nanjenshan Forest

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ABSTRACT

This research conducted two experiments comparing the responses of photosynthetic traits of various shade-tolerant plant species to naturally enriched CO_2 concentrations near the forest floor in the Nanjenshan Forest, southern Taiwan. The objective of this study was to investigate how seedlings of shade-tolerant species can maintain positive net photosynthetic rates (P_n) while those of shade-intolerant species cannot in understory low-light environments. In the first experiment, we measured the photosynthetic light responses of six species with different levels of shade tolerance under CO_2 concentrations of 360-420 ppm. Results showed that as the CO_2 concentration was elevated, the P_n and apparent quantum use efficiency increased while light compensation points (LCP) and dark respiration rates (R_d) decreased in most species, with significantly more changes in shade-tolerant seedlings. In the second experiment, we provided 350-430 ppm of CO_2 concentrations to seedlings of 40 woody and herbaceous species for photosynthesis by pumping the air at 5 and 100 cm above the forest floor. Results showed that under a low light of ≤ 12 μmol photon m^{-2} s^{-1}, seedlings with higher shade-tolerant levels had higher photosynthetic CO_2 use efficiency (the slope of regression lines between P_n and ambient CO_2 concentrations, C_aUE). Seedlings of 19 shade-tolerant species showed positive P_n values at 400 ppm of CO_2 (A_{400}), while seedlings of 10 shade-intolerant species showed negative A_{400} values. Furthermore, in the low-light environments of the understory, the CO_2 compensation point (the CO_2 concentration above which P_n shifts from a negative to a positive value, C_aCP) of shade-tolerant species were 105 ppm less than that of shade-intolerant species. This is an innovative finding. Seedlings of shade-tolerant species could maintain positive P_n values within the range of elevated CO_2 concentrations due to soil respiration. In conclusion, though the photosynthesis of understory woody or herbaceous species is limited by insufficient light availability, the seedlings of these shade-tolerant species could benefit from higher CO_2 concentrations near the forest floor through significantly decreasing their LCP, R_d, and C_aCP and increasing C_aUE to maintain positive carbon gain.

Keywords: photosynthetic CO_2 compensation point, photosynthetic CO_2 use efficiency, shade tolerance, soil respiration, understory low-light environmen

Cheng CT, Kuo YL. 2025. Responses of photosynthetic traits to CO_2 concentrations in seedlings with different levels of shade tolerance in the Nanjenshan Forest. Taiwan J For Sci 40(2):201-38.

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2025年3月送審，2025年5月通過。Received March 2025, Accepted May 2025.

INTRODUCTION

Seedlings naturally regenerating in the forest understory face extremely low light levels during the day. For example, in the Nanjenshan Forest of southern Taiwan, 94% of the photosynthetic photon flux density (PPFD, 400-700 nm) measured at the forest floor stays below 10 μmol photon m^{-2} s^{-1} (Cheng 2001). The average relative light intensity at 20 cm above the forest floor is only 1.3% of the light above the canopy, as has been observed for nine years (Chao et al. 2022). Understory seedlings in the deep shade develop physiological and morphological traits that reduce carbon consumption to maintain a positive carbon balance under photosynthetically limiting conditions (Reich et al. 2003, Craine and Reich 2005). Furthermore, the carbon balance of naturally regenerated seedlings in the understory benefits from elevated CO_2 concentrations near the forest floor, which primarily come from soil respiration (Bazzaz 1990, Osborne et al. 1997). Soil respiration includes both autotrophic respiration from roots and rhizosphere organisms, and heterotrophic respiration from soil microorganisms (Hanson et al. 2000). This process elevates CO_2 concentrations immediately above the forest floor, providing an accessible source of CO_2 for low-stature understory plants, as a common ecological phenomenon worldwide (Schlesinger and Andrews 2000, de Araujo et al. 2008). The contribution of soil respiration to the carbon balance of naturally regenerating seedlings in Taiwanese forest understories needs further study.

Since the Industrial Revolution, atmospheric CO_2 concentrations have increased substantially from 316.9 ppm in 1960 to 369.7 ppm in 2000 and reached 424.6 ppm by 2024 (NOAA 2025). However, these levels remain below the photosynthetic saturation point for C_3 plants (Körner 2015, Erwin and Gesick 2017, Ren et al. 2018). As the substrate for carbon fixation, CO_2 remains a limiting factor for Rubisco—the key carboxylation enzyme in C_3 plants. As a result, higher CO_2 concentrations improve Rubisco's carboxylation efficiency and competitively suppress its oxygenation activity, thereby reducing CO_2 losses through photorespiration (Ainsworth and Rogers 2007, Leakey et al. 2009, Cernusak et al. 2013). Consequently, both shade-tolerant and shade-intolerant C_3 plants have the potential to achieve significantly higher net photosynthetic rates (P_n) under elevated CO_2 concentrations (Sefcik et al. 2006, Bader et al. 2010, Kitao et al. 2016). This effect is also seen in seedlings growing in the low-light conditions of the forest understory, where rising CO_2 levels significantly increase P_n (Hättenschwiler et al. 2001, Holton and Winter 2001, Sefcik et al. 2006, Damasceno et al. 2024). In addition, elevated CO_2 improves quantum use efficiency (quantum yield) and CO_2 use efficiency (C_aUE) while reducing the dark respiration rate (R_d) and light compensation point (LCP) in C_3 plants (Teskey and Shrestha 1985, Springer and Thomas 2007, Leakey et al. 2009, Kitao et al. 2016).

During the day, active photosynthesis in the canopy foliage absorbs a significant amount of CO_2, creating a vertical gradient in atmospheric CO_2 concentrations, with the lowest concentration at the canopy and the highest at the forest floor (Buchmann et al. 1996, Brooks et al. 1997). For example, in the Nanjenshan Forest in 2000, annual daytime average CO_2 concentrations measured at 2, 10, and 20 cm above the forest floor were 62, 30, and 20 ppm higher, respectively, than the concentration above the canopy, which was 361 ppm (Cheng and Kuo 2004). This reflects

how the understory leaves situated at different heights above the forest floor are exposed to varying ambient CO_2 concentrations, which can influence their P_n (Bazzaz and Williams 1991).

Previous research in the Nanjenshan Forest has found a significant negative correlation between the light demanding index and the C_aUE of 30 naturally regenerating seedlings. Seedlings with lower light demanding indices, indicating greater shade tolerance, had higher C_aUE (Cheng and Kuo 2004). At that time, photosynthetic capacity (A_{max}) was not used to measure shade tolerance; instead, LCPs were used as a proxy for light demanding index. More recently, a database of physiological shade tolerance rankings based on A_{max} values has been developed for 434 native broadleaved tree species in Taiwan (Kuo et al. 2021). This database allows for more accurate comparisons of C_aUE among woody species with confirmed shade tolerance classifications. In addition, Hsu and Kuo (2021) found that under low-light conditions, seedlings with higher shade tolerance showed stronger photosynthetic responses to elevated CO_2 levels. While their study focused on 15 woody species with varying shade tolerance, the current study expands the scope to include plants with different growth forms, such as herbaceous species, woody lianas, bamboos, and shrubs. The aim is to determine whether photosynthetic responses to elevated CO_2 under low-light conditions differ among these growth forms and whether these differences are linked to shade tolerance. This study further explores the physiological mechanisms that enable shade-tolerant seedlings to maintain positive P_n under limited light conditions, in contrast to shade-intolerant seedlings. Based on these objectives, the following three research questions are proposed:

(1) Within a CO_2 concentration range of 360-420 ppm, do shade-tolerant seedlings show greater responsiveness in photosynthetic traits (including P_n, quantum use efficiency (apparent QUE), LCP, and R_d) compared to shade-intolerant seedlings?
(2) Under low-light conditions within CO_2 gradients naturally elevated by soil respiration, do shade-tolerant seedlings exhibit significantly higher photosynthetic C_aUE than shade-intolerant seedlings?
(3) Under low-light conditions, as CO_2 concentration increases, do shade-tolerant seedlings exhibit a significantly lower ambient CO_2 compensation point (C_aCP, meaning the CO_2 concentration level when P_n transitions from negative to positive) than shade-intolerant seedlings? If shade-tolerant seedlings under low-light conditions exhibit greater sensitivity in P_n, QUE, LCP, and R_d to elevated CO_2, along with significantly higher C_aUE and lower C_aCP than shade-intolerant seedlings, this would clarify the mechanisms enabling shade-tolerant seedlings to maintain positive P_n and those preventing shade-intolerant seedlings from maintaining positive P_n in shaded understory environments.

MATERIALS AND METHODS

Photosynthetic trait responses of six tree seedlings to varying CO_2 concentrations in the forest understory

This study was conducted in the Nanjenshan Ecological Reserve, a protected area of Kenting National Park (120° 51′ 37” E, 22° 02′ 51” N; Figure 1a). Measurements were conducted at a site located approximately 200 m southeast of the Nanshan Trail on a leeward forest slope at an elevation of approximately 190 m (Figure 1b). In 1995,

the corresponding author established two iron towers at this location to monitor canopy photosynthetic productivity (Kuo 2000). The forest canopy was dominated by *Ficus benjamina* L., *Machilus japonica* var. *kusanoi* (Hayata) J.C.Liao, *Michelia compressa* var. *formosana* (Kaneh.) Chien F.Chen, *Schefflera octophylla* (Lour.) Harms, and *Ilex rotunda* Thunb. The understory was dominated by *Psychotria rubra* Poir. and *Aglaia elliptifolia* Merr. A meteorological station, located 200 m from the towers at an elevation of 150 m, recorded a mean annual temperature of 23.9℃ and a total annual precipitation of 2800 mm during 2000 (the study period), with about 50% of the rainfall occurring between June and August (Cheng 2001).

Six tree species with varying shade tolerances were selected from the forest understory, with three seedlings per species used for measurements. The shade-intolerant species included *Mallotus paniculatus* (Lam.) Müll Arg. var. *paniculatus*, *Bischofia javanica* Blume, and *Dendrocnide meyeniana* (Walp.) Chew, while the shade-tolerant species included *Machilus japonica* var. *kusanoi*, *Ag. elliptifolia*, and *Drypetes karapinensis* (Hayata) Pax & K. Hoffm. Photosynthetic trait measurements in response to elevated CO_2 concentrations were conducted in July to August 2000. Seedlings of *Machilus paniculatus* var. *paniculatus* and *Bi. javanica* Blume germinated in December 1999, measuring 10-15 cm and 5-7 cm in height, respectively, at the time of sampling. *Machilus japonica* var. *kusanoi* germinated in September 1999 and reached 7-9 cm in height. Germination dates for *De. meyeniana*, *Ag. elliptifolia*, and *Dr. karapinensis* were unknown; *De. meyeniana* and *Ag. elliptifolia* were 8-10 cm tall, while *Dr. karapinensis* was 5-7 cm tall. *Mallotus paniculatus* var. *paniculatus* seedlings were located near canopy gaps receiving relatively higher light availability, while the other five species grew in low-light environments within the shaded understory. P_n was measured using an LI-6400XT portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA). During measurements, leaf temperature was maintained at 28 ℃, relative humidity at 60-70%, and CO_2 concentrations were measured at 360, 380, 400, and 420 ppm. P_n was measured on one leaf per seedling under each PPFD level of 0, 4, 8, 15, and 20 μmol photon m^{-2} s^{-1}. Light response curves were analyzed by the linear regression of P_n against PPFD to determine the LCP (defined as the PPFD at which $P_n = 0$), R_d (y-intercept at PPFD = 0), and apparent QUE as the slope of the regression line. Additionally, the value of P_n at PPFD =10 μmol photon m^{-2} s^{-1} (A_{10}) was calculated from the regression equation. For each CO_2 concentration level, the LCP, R_d, apparent QUE, and A_{10} values for a given tree species represented the mean values calculated from three seedlings.

Our team assessed the light response of P_n under higher light intensities in the seedlings of six tree species at the four CO_2 concentration levels, between 09:00 and 15:00 on different days during July and August 2000. At each CO_2 concentration (360, 380, 400, and 420 ppm), a seedling leaf from one species put into the leaf chamber was sequentially exposed to PPFD levels of 0, 50, 100, 200, 400, 600, 800, 1000, 1250, and 1500 μmol photon m^{-2} s^{-1}. After measurement of the first seedling, the second and third seedlings of the same species were measured under the same CO_2 concentration. Measurements at the next CO_2 level commenced only after all three seedlings had been measured at the preceding concentration. The mean P_n values of the three seedlings of the same species under each CO_2 concentration

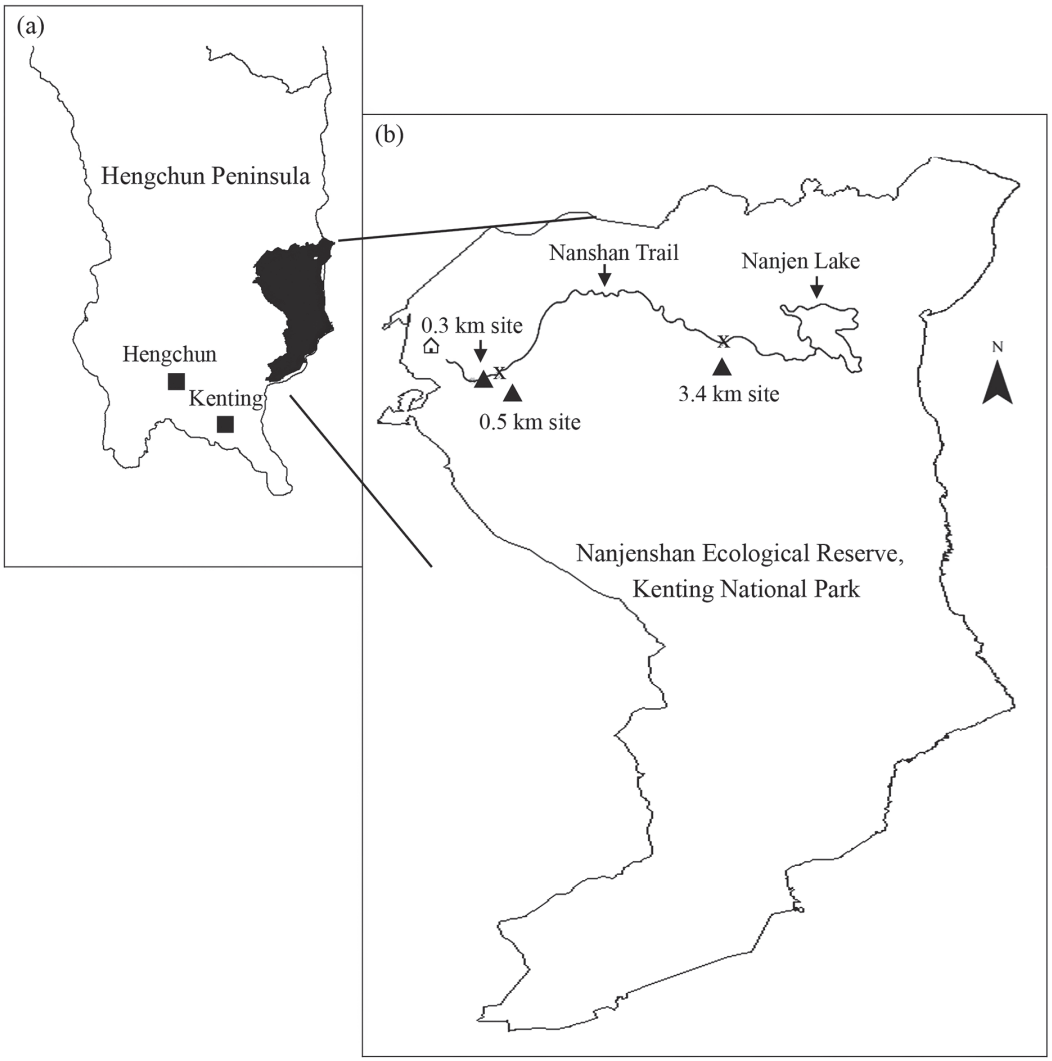

Figure 1. Sampling sites of this study were located in the Nanjenshan Ecological Reserve (南仁山生態保護區), Kenting National Park (墾丁國家公園) of southern Taiwan (a). Sampling site at 0.3 km was on an open field, while a 0.5 km site and a 3.4 km site were located respectively at a leeward and a windward forest along Nanshan Trail (b). ⌂ marks the control station.

and same light density were used to construct the photosynthetic light response curves for that species. The light-saturated photosynthetic rate (A_{sat}) for each species was defined by the mean maximum values of P_n of the three seedlings under each CO_2 level.

Photosynthetic responses of 40 plant species to naturally elevated CO_2 under low-light conditions

This study examined the photosynthetic responses to naturally elevated CO_2 concentrations of 40 naturally regenerated understory plant species, including 31 woody

trees and shrubs, four herbaceous species (*Crassocephalum crepidioides* (Benth.) S.Moore, *Alocasia odora* (Roxb.) Spach, *Elatostema lineolatum* var. *majus* (Wight) Wedd. var. *majus*, *Chloranthus oldhami* Solms), four woody lianas (*Kadsura japonica* (L.) Duna, *Piper kadsura* (Choisy) Ohwi, *Calamus formosanus* Becc., *Flagellaria indica* L.), and one climbing bamboo species (*Schizostachyum diffusum* (Blanco) Merr.). Seedlings were sampled from three distinct forest habitats: a tower plot, a relatively open site located at 0.3 km along the Nanshan Road Trail, and a windward forest slope at 3.4 km along the same trail. Specifically, seedlings of the following eight species were collected from the relatively open site at 0.3 km: *Mallotus paniculatus*, *Macaranga tanarius* (L.) Müll. Arg., *Melanolepis multiglandulosa* (Reinw. *ex* Blume) Rchb. & Zoll., *Lagerstroemia subcostata* Koehne, *Maesa perlaria* (Lour.) Merr. var. *formosana* (Mez) Yuen P.Yang, *Rhus javanica* L. var. *roxburghiana* (DC.) Rehd. & Wilson, *Stachytarpheta urticaefolia* Sims, and *Cra. crepidioides*. Seedlings of the following six species were sampled from the windward forest slope near the 3.4 km point: *Illicium arborescens* Hayata, *Machilus obovatifolia* (Hayata) Kaneh. & Sasaki var. *obovatifolia* *Beilschmiedia tsangii* Merr., *Aucuba chinensis* Benth., *Daphniphyllum glauescens* subsp. *oldhamii* (Hemsl.) T.C.Huang, and *Microtropis japonicus* (Franch. & Sav.) Hallier f. The remaining 26 species were collected from the tower plot. Photosynthetic measurements were conducted using natural irradiance as the light source. PPFD at the measured leaves was $\leq$ 12 μmol photon m^{-2} s^{-1}, with the majority of measurements between 4-9 μmol photon m^{-2} s^{-1}. For seedlings growing in a relatively open area at 0.3 km along Nanshan Road, simulated understory light conditions were created by covering the leaf chamber of the instrument with one or two layers of *Al. odora* leaves, adjusting the PPFD to approximately 5-8 μmol photon m^{-2} s^{-1}. This study used ambient air instead of artificially supplying different CO_2 concentrations. Air was drawn from two vertical heights above the forest floor into the leaf chamber to provide leaves with ambient CO_2 at different concentrations during photosynthetic measurements. A silicone tube connected the air inlet of an LI-6400XT gas exchange system, with the other end on a metal rod 1.5 m away from the instrument at 5 cm or 100 cm off the ground. The 5 cm height corresponded to the typical height of seedling leaves; air at this height contained CO_2 concentrations ranging from 380 to 430 ppm. At 100 cm, CO_2 concentrations were generally lower, ranging from 350 to 380 ppm, depending on the time of day. During measurements, the leaf chamber was maintained at 28℃ with a relative humidity of 60-70%. First, the air intake tube was positioned at 100 cm height and recorded 6-8 P_n measurements. Subsequently, the tube was repositioned horizontally at 5 cm above the ground on a metal pole near the instrument to draw air, and another 6-8 P_n measurements were recorded. The instrument was then moved to measure another nearby seedling. Measurements were conducted between late September and early November 2000, on five measurement days between 09:00 and 15:00, completing the sampling for three seedlings across all 40 species. The P_n data from three seedlings were averaged across the corresponding ambient CO_2 concentration. A linear regression was fitted to these combined data, and the slope of the regression line was used as an indicator of photosynthetic ambient C_aUE under low-light conditions (Teskey and Shrestha 1985, Hsu and Kuo

2021). The ambient CO_2 compensation point (C_aCP), defined as the CO_2 concentration where net photosynthesis equals zero (i.e., $P_n = 0$), was determined from the regression line under low-light conditions. Positive P_n values showed when ambient CO_2 concentrations exceeded the C_aCP.

RESULTS

Changes in the photosynthetic traits of six tree species under different CO_2 concentrations in the forest understory

Photosynthetic light-response curves differed among the six species under CO_2 concentrations of 360, 380, 400, and 420 ppm (Figure 2). Under high-light conditions (PPFD 1000-1500 μmol photon m^{-2} s^{-1}), the light-saturated photosynthetic rates (A_{sat}) of the three shade-intolerant species (*Mallotus paniculatus*, *Bi. javanica*, and *De. meyeniana*) consistently exceeded those of the three shade-tolerant species (*Machilus japonica* var. *kusanoi*, *Ag. elliptifolia* and *Dr. karapinensis*) across all CO_2 levels (Table 1). A_{sat} values increased significantly ($p < 0.05$) with rising CO_2 concentrations in five of the six species (all except *Bi. javanica*). Elevating CO_2 from 360 to 420 ppm increased A_{sat} by 47-83% in shade-tolerant species, compared to only 13-28% in shade-intolerant species (Table 1). Under low-light conditions (PPFD 0-20 μmol photon m^{-2} s^{-1}), the apparent QUE increased

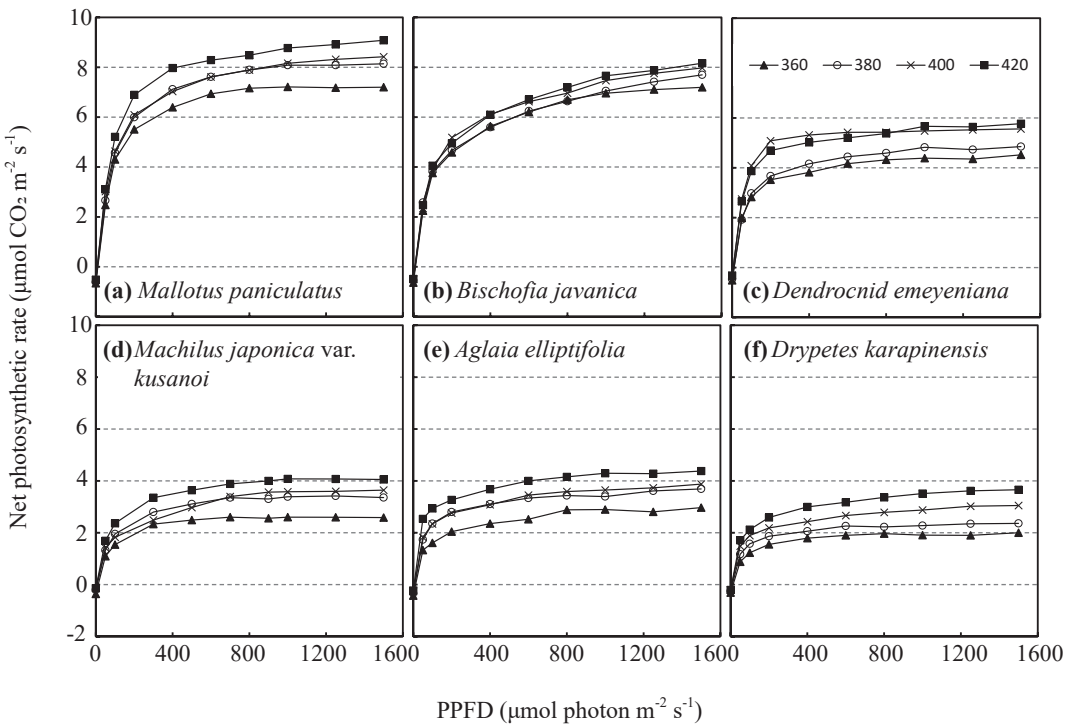

Figure 2. Photosynthetic light responses measured at ambient CO_2 concentrations of 360, 380, 400, and 420 ppm, respectively, and photosynthetic photon flux density (PPFD) of 0, 50, 100, 200, 400, 600, 800, 1000, 1250, and 1500 μmol photon m^{-2} s^{-1} in seedlings of six tree species growing in the Nanjenshan Forest (南仁山森林). Each point is the mean of 3 replicates.

significantly with elevated CO_2 concentrations in five species (all except *Bi. javanica*), while LCP and R_d decreased significantly in all six species (Table 1). When CO_2 increased from 360 to 420 ppm, QUE showed the greatest improvement in *Ag. elliptifolia* (77%) and *De. meyeniana* (68%). Reductions in LCP and R_d were most pronounced in *Machilus japonica* var. *kusanoi* and *Ag. elliptifolia*, whereas the pioneer species *Mallotus paniculatus* exhibited the smallest reductions (Table 1). Furthermore, at a low PPFD of 10 μmol

Table 1. Comparisons of the light-saturated photosynthetic rate, apparent quantum use efficiency, light compensation point, and dark respiration rate measured at various CO_2 concentrations in seedlings of six tree species growing in the Nanjenshan Forest (mean ± standard error, n = 3). 420/360 denote the ratio of photosynthetic traits measured between CO_2 concentrations at 420 and 360 ppm of each species

	CO_2 concentration (ppm)				
	360	**380**	**400**	**420**	**420/3600**
Light-saturated photosynthetic rate (μmol CO_2 m^{-2} s^{-1})					
Mallotus paniculatus	7.24 ± 0.40[b1]	8.14 ± 0.14[ab]	8.42 ± 0.03[ab]	9.08 ± 0.31[a]	+25%
Bischofia javanica	7.20 ± 0.04[a]	7.70 ± 0.46[a]	7.97 ± 0.19[a]	8.16 ± 0.28[a]	+13%
Dendrocnide meyeniana	4.52 ± 0.36[a]	4.85 ± 0.40[a]	5.56 ± 0.60[a]	5.77 ± 0.58[a]	+28%
Machilus japonica [2]	2.59 ± 0.09[b]	3.36 ± 0.04[ab]	3.64 ± 0.08[ab]	4.05 ± 0.08[a]	+53%
Aglaia elliptifolia	2.97 ± 0.30[b]	3.69 ± 0.1[ab]	3.88 ± 0.23[ab]	4.38 ± 0.17[a]	+47%
Drypetes karapinensis	2.00 ± 0.08[c]	2.36 ± 0.08[bc]	3.05 ± 0.25[ab]	3.66 ± 0.07[a]	+83%
Apparent quantum use efficiency (μmol CO_2 (μmol photon)$^{-1}$)					
Mallotus paniculatus	0.079 ± 0.004[b]	0.083 ± 0.002[b]	0.088 ± 0.002[ab]	0.100 ± 0.002[a]	+27%
Bischofia javanica	0.061 ± 0.002[a]	0.063 ± 0.004[a]	0.063 ± 0.002[a]	0.059 ± 0.001[a]	-3%
Dendrocnide meyeniana	0.041 ± 0.002[b]	0.045 ± 0.004[b]	0.061 ± 0.004[a]	0.069 ± 0.003[a]	+68%
Machilus japonica [2]	0.041 ± 0.001[c]	0.046 ± 0.003[bc]	0.051 ± 0.002[ab]	0.058 ± 0.001[a]	+41%
Aglaia elliptifolia	0.048 ± 0.003[c]	0.050 ± 0.001[bc]	0.068 ± 0.002[ab]	0.085 ± 0.006[a]	+77%
Drypetes karapinensis	0.042 ± 0.004[b]	0.043 ± 0.003[b]	0.050 ± 0.002[ab]	0.064 ± 0.004[a]	+52%
Light compensation point (μmol photon m^{-2} s^{-1})					
Mallotus paniculatus	8.47 ± 0.24[a]	7.71 ± 0.05[ab]	6.45 ± 0.08[b]	6.05 ± 0.06[b]	-31%
Bischofia javanica	10.08 ± 0.10[a]	7.17 ± 0.28[b]	6.21 ± 0.12[c]	5.60 ± 0.07[c]	-44%
Dendrocnide meyeniana	10.15 ± 0.49[a]	8.74 ± 0.72[b]	4.73 ± 0.54[c]	4.29 ± 0.21[c]	-58%
Machilus japonica [2]	7.16 ± 0.12[a]	3.97 ± 0.24[b]	3.56 ± 0.26[bc]	2.80 ± 0.15[c]	-61%
Aglaia elliptifolia	7.35 ± 0.25[a]	5.79 ± 0.12[b]	3.74 ± 0.15[c]	2.84 ± 0.08[d]	-61%
Drypetes karapinensis	7.07 ± 0.56[a]	5.14 ± 0.42[b]	4.08 ± 0.03[b]	3.49 ± 0.14[b]	-51%
Dark respiration rate (μmol CO_2 m^{-2} s^{-1})					
Mallotus paniculatus	0.66 ± 0.03[a]	0.62 ± 0.02[ab]	0.54 ± 0.02[b]	0.52 ± 0.02[b]	-21%
Bischofia javanica	0.64 ± 0.03[a]	0.55 ± 0.01[ab]	0.51 ± 0.03[b]	0.49 ± 0.03[b]	-23%
Dendrocnide meyeniana	0.51 ± 0.03[a]	0.47 ± 0.04[ab]	0.36 ± 0.01[bc]	0.32 ± 0.02[c]	-37%
Machilus japonica [2]	0.36 ± 0.02[a]	0.20 ± 0.02[b]	0.15 ± 0.03[b]	0.14 ± 0.02[b]	-61%
Aglaia elliptifolia	0.42 ± 0.03[a]	0.33 ± 0.02[ab]	0.26 ± 0.02[b]	0.23 ± 0.01[b]	-45%
Drypetes karapinensis	0.31 ± 0.01[a]	0.25 ± 0.02[b]	0.21 ± 0.01[b]	0.21 ± 0.01[b]	-32%

[1] Different letters among CO_2 concentrations denote a significant difference by Scheffe's test at $p < 0.05$.
[2] *Machilus japonica* var. *kusanoi*.

photon m^{-2} s^{-1}, P_n increased significantly with rising CO_2 concentrations in all six species (Figure 3). Across CO_2 concentrations, P_n values were generally higher in shade-tolerant species than in shade-intolerant species. Collectively, these results demonstrated that under low light (PPFD 0-20 μmol photon m^{-2} s^{-1}) and across the CO_2 range of 360-420 ppm, seedlings of more shade-tolerant species generally exhibited greater responsiveness in key photosynthetic traits, such as P_n, QUE, LCP, and R_d, when compared to shade-intolerant seedlings.

Photosynthetic responses of 40 seedling species to naturally elevated CO_2 under low-light conditions

Under low-light understory conditions (PPFD ≤ 12 μmol photon m^{-2} s^{-1}), the P_n of seedlings from all 40 species generally increased with rising atmospheric CO_2 concentrations near the forest floor (Figure 4). Regression analysis revealed a significant positive linear relationship ($p < 0.05$) between P_n and CO_2 concentrations for 25 species. The relationship was marginally significant ($0.05 \leq p < 0.10$) for eight species, and non-significant ($p \geq 0.10$) for the remaining seven species, which were predominantly shade-intolerant (Table 2). The slope of the linear regression of P_n against CO_2 concentration was used as an indicator of photosynthetic C_aUE under low-light conditions. Species with the highest C_aUE (≥ 0.02 μmol CO_2 m^{-2} ppm^{-1} s^{-1}) included *Ardisia sieboldii* Miq., *Be. erythrophloia* Hayara, *P. rubra*, *E. lineolatum* var. *majus*, *Machilus japonica* var. *kusanoi*, *Castanopsis indica* (Roxb. *ex* Lindl.) A.DC., and *Dr. karapinensis* (Table 2). By contrast, highly intolerant species (*Macaranga tanarius*, *Melanolepis multiglandulosa*, *R. javanica* var. *roxburghiana*, *Mallotus paniculatus*) and intolerant species (*Lagerstroemia subcostata*, *B. javanica*, *De. meyeniana*) exhibited the

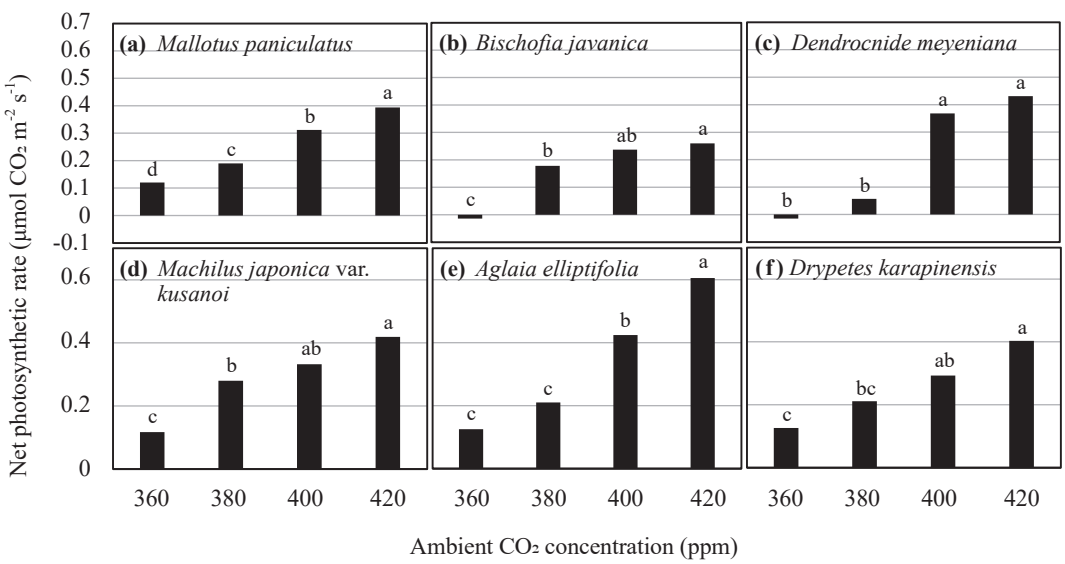

Figure 3. Net photosynthetic rates measured under photosynthetic photon flux density (PPFD) of 10 μmol photon m^{-2} s^{-1} at ambient CO_2 concentrations of 360, 380, 400, and 420 ppm for seedlings of six tree species growing in the Nanjenshan Forest. Different letters among various CO_2 concentrations for each species denote a significant difference by Scheffe's test at $p < 0.05$.

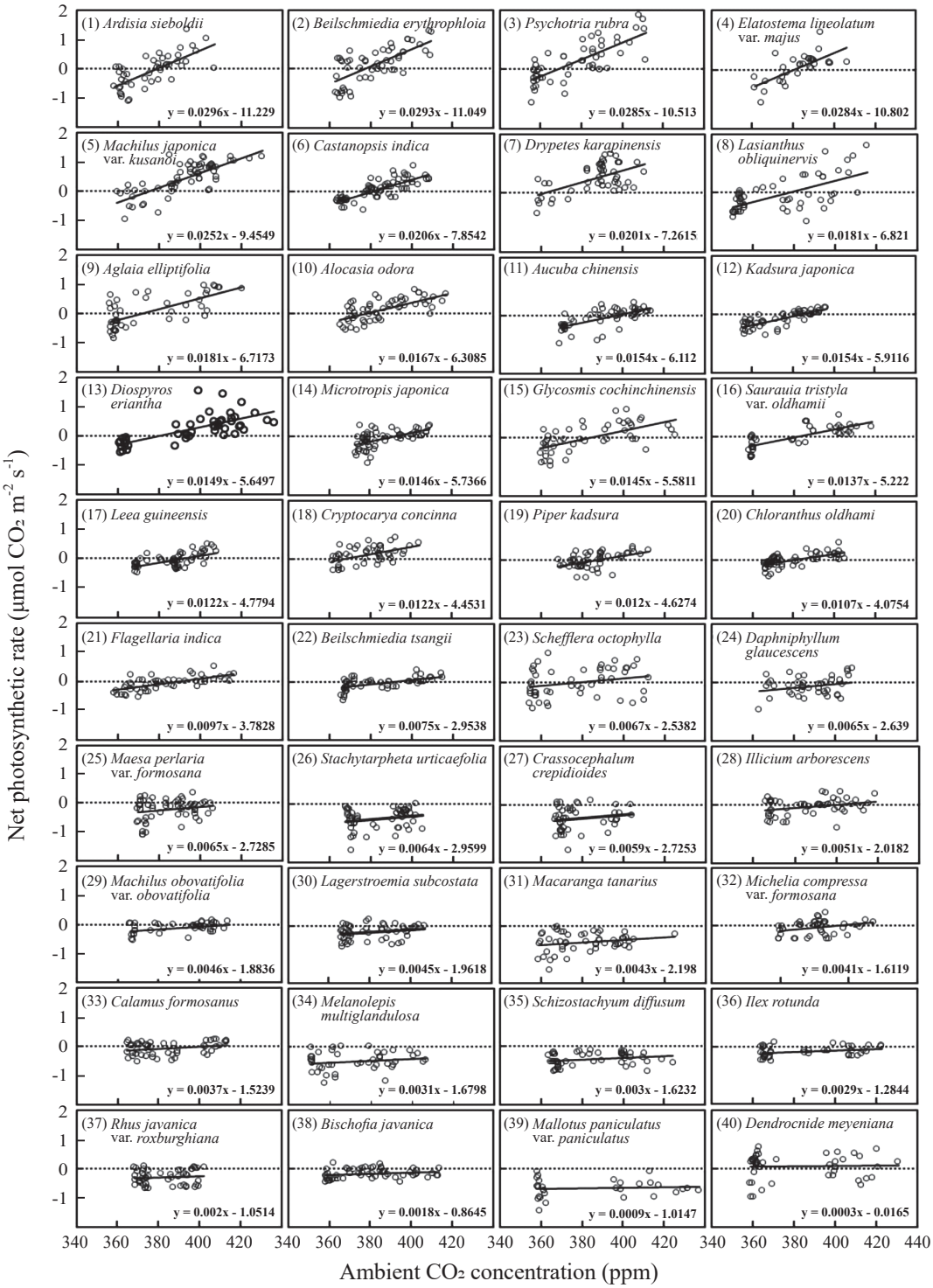

Figure 4. Responses of net photosynthetic rates to the in situ CO_2 concentrations above the forest floor for seedlings of 40 species growing in the Nanjenshan Forest. Measurements were made under photosynthetic photon flux density of 3-12 μmol photon m^{-2} s^{-1}.

Table 2. Photosynthetic ambient CO_2 use efficiency (C_aUE, μmol CO_2 m^{-2} ppm^{-1} s^{-1}), ambient CO_2 compensation point (C_aCP), calculated net photosynthetic rates at CO_2 concentrations of 360 ppm (A_{360}) and 400 ppm (A_{400}), and the maximum photosynthetic rate (A_{max}, reported by Kuo et al. 2021) of each tested species, which are listed in descending order of C_aUE values

Species	C_aUE	C_aCP	A_{360}	A_{400}	A_{max}
		(ppm)	(μmol CO_2 m^{-2} s^{-1})		
(1) *Ardisia sieboldii* (樹杞)	0.0296*** [1]	379	-0.57	0.61	15.0
(2) *Beilschmiedia erythrophloia* (瓊楠)	0.0293***	377	-0.50	0.67	13.5
(3) *Psychotria rubra* (九節木)	0.0285***	369	-0.25	0.89	13.8
(4) *Elatostema lineolatum* var. *majus* (冷清草)	0.0284***	386	-0.65	0.56	-
(5) *Machilus japonica* var. *kusanoi* (大葉楠)	0.0252***	375	-0.38	0.63	14.9
(6) *Castanopsis indica* (印度苦櫧)	0.0206***	381	-0.44	0.39	14.2
(7) *Drypetes karapinensis* (交力坪鐵色)	0.0201***	363	-0.03	0.78	7.8
(8) *Lasianthus obliquinervis* (雞屎樹)	0.0181***	377	-0.31	0.52	-
(9) *Aglaia elliptifolia* (大葉樹蘭)	0.0181***	371	-0.20	0.42	13.1
(10) *Alocasia odora* (姑婆芋)	0.0167***	378	-0.30	0.37	-
(11) *Aucuba chinensis* (桃葉珊瑚)	0.0154***	397	-0.57	0.05	-
(12) *Kadsura japonica* (南五味子)	0.0154***	384	-0.37	0.25	-
(13) *Diospyros eriantha* (軟毛柿)	0.0149***	379	-0.29	0.31	12.7
(14) *Microtropis japonica* (日本賽衛矛)	0.0146***	393	-0.48	0.10	8.7
(15) *Glycosmis cochinchinensis* (石苓舅)	0.0145***	385	-0.36	0.22	10.7
(16) *Saurauia tristyla* var. *oldhamii* (水冬瓜)	0.0137***	381	-0.29	0.26	13.8
(17) *Leea guineensis* (火筒樹)	0.0122***	392	-0.39	0.10	20.1
(18) *Cryptocarya concinna* (土楠)	0.0122***	365	-0.06	0.43	12.5
(19) *Piper kadsura* (風藤)	0.0120***	386	-0.31	0.17	-
(20) *Chloranthus oldhami* (臺灣及己)	0.0107***	381	-0.22	0.21	-
(21) *Flagellaria indica* (印度鞭藤)	0.0097***	390	-0.29	0.10	-
(22) *Beilschmiedia tsangii* (華河瓊楠)	0.0075***	394	-0.25	0.05	17.5
(23) *Schefflera octophylla* (江某)	0.0067*	379	-0.13	0.14	17.4
(24) *Daphniphyllum glaucescens* (奧氏虎皮楠) [2]	0.0065*	406	-0.39	-0.04	14.5
(25) *Maesa perlaria* var. *formosana* (臺灣山桂花)	0.0065*	420	-0.30	-0.13	15.1
(26) *Stachytarpheta urticaefolia* (長穗木)	0.0064*	463	-0.66	-0.40	26.0 [3]
(27) *Crassocephalum crepidioides* (昭和草)	0.0059NS	462	-0.60	-0.37	-
(28) *Illicium arborescens* (臺灣八角)	0.0051**	395	-0.18	0.02	10.3
(29) *Machilus obovatifolia* var. *obovatifolia* (恆春楨楠)	0.0046***	409	-0.23	-0.04	15.9
(30) *Lagerstroemia subcostata* (九芎)	0.0045*	436	-0.34	-0.16	25.7
(31) *Macaranga tanarius* (血桐)	0.0043NS	511	-0.65	-0.48	31.9
(32) *Michelia compressa* var. *formosana* (烏心石)	0.0041*	393	-0.14	0.03	17.5
(33) *Calamus formosanus* (黃藤)	0.0037*	412	-0.19	-0.04	-
(34) *Melanolepis multiglandulosa* (蟲屎)	0.0031NS	542	-0.56	-0.44	31.0
(35) *Schizostachyum diffusum* (莎勒竹)	0.0030*	541	-0.54	-0.42	-
(36) *Ilex rotunda* (鐵冬青)	0.0029**	443	-0.24	-0.12	17.4
(37) *Rhus javanica* var. *roxburghiana* (羅氏鹽膚木)	0.0020NS	526	-0.33	-0.25	26.0
(38) *Bischofia javanica* (茄苳)	0.0018NS	481	-0.22	-0.15	22.7
(39) *Mallotus paniculatus* var. *paniculatus* (白匏仔)	0.0009NS	-	-0.69	-0.66	29.4
(40) *Dendrocnide meyeniana* (咬人狗)	0.0003NS	-	0.09	0.10	23.0

[1] NS: $p \geq 0.10$, * $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$.
[2] *Daphniphyllum glaucescens* subsp. *oldhamii.*
[3] Reported by Kuo et al. (2001).

lowest C_aUE (≤ 0.0045 μmol CO_2 m^{-2} ppm^{-1} s^{-1}) (Table 2).

Regarding the C_aCP, seedlings of 25 species exhibited positive P_n at CO_2 concentrations below 400 ppm. Conversely, seven species had C_aCP above 460 ppm to achieve positive P_n, with *Macaranga tanarius*, *Melanolepis multiglandulosa*, *R. javanica* var. *roxburghiana*, and *Schizostachyum diffusum* displaying notably high C_aCP values (511-542 ppm; Table 2). For *Mallotus paniculatus* and *De. meyeniana*, the near-zero slopes of their P_n vs. CO_2 regression lines rendered the calculated C_aCP (1127 ppm and 55 ppm, respectively) unreliable. For the remaining 38 species, C_aCP was significantly negatively correlated with C_aUE (r^2 = 0.65; Figure 5a), indicating that species with higher C_aUE generally possess lower C_aCP. Furthermore, using the regression equations (Figure 4), P_n values were calculated at CO_2 concentrations of 360 and 400 ppm. At 360 ppm, P_n was negative for all 39 species excluding *De. meyeniana*. When CO_2 increased to 400 ppm, the P_n became positive for 25 of these 39 species (Table 2).

For 29 woody species of the 40 tested species, the maximum photosynthetic capacity (A_{max}) values were available from a previous study (Kuo et al. 2021; Table 2). These species included 8 shade-intolerant species, 8 moderately shade-tolerant species, and 13 shade-tolerant species. Excluding *De. meyeniana*, when CO_2 increased from 360 to 400 ppm, the mean P_n of the 7 shade-intolerant species increased by 28% (from -0.46 to -0.33 μmol CO_2 m^{-2} s^{-1}) but remained negative. The eight moderately shade-tolerant species showed a 69% mean increase in P_n (from -0.29 to +0.09 μmol CO_2 m^{-2} s^{-1}), shifting from negative to positive values. The 13 shade-tolerant species exhibited a mean 233% increase in P_n (from -0.29 to +0.38 μmol CO_2 m^{-2} s^{-1}), a rate nearly three times that of the moderately shade-tolerant group. Among these 29 woody species, C_aUE exhibited a significant negative linear relationship with A_{max} (r^2 = 0.36, Figure 5b), indicating that higher A_{max} is associated with lower photosynthetic C_aUE under low-light conditions. Conversely, when excluding *Mallotus paniculatus* and *De. meyeniana* (*n*

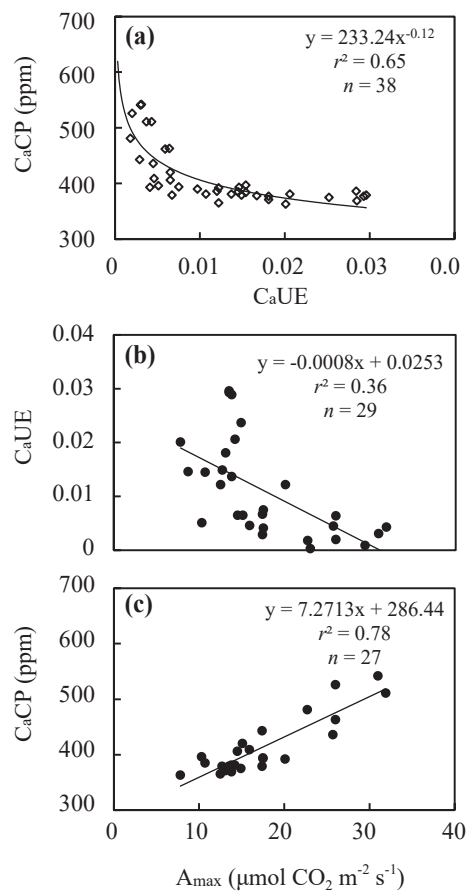

Figure 5. Relationships between the photosynthetic ambient CO_2 compensation point (C_aCP) and the photosynthetic ambient CO_2 use efficiency (C_aUE, μmol CO_2 m^{-2} ppm^{-1} s^{-1}) (a), C_aUE and the maximum photosynthetic rate (A_{max}) (b), and C_aCP and A_{max} (c) for seedlings growing in the Nanjenshan Forest. Data of A_{max} are from Kuo et al. (2021).

= 27), C_aCP showed a strong positive linear correlation with A_{max} (r^2 = 0.78; Figure 5c), suggesting that species with higher shade tolerance (i.e., lower A_{max}) tend to have lower C_aCP.

DISCUSSIONS

Photosynthetic trait responses of six tree seedlings to elevated CO_2

A vertical gradient in atmospheric CO_2 concentration characterizes forest canopies, with concentrations increasing toward the forest floor. This gradient was quantified in the Nanjenshan Forest in 2000, with annual daytime mean CO_2 concentrations of 423, 391, and 381 ppm at 2, 10, and 20 cm above the forest floor, respectively (Cheng and Kuo 2004). Similarly, measurements conducted between September 2019 and June 2020 in an experimental plantation at the National Pingtung University of Science and Technology recorded even higher averages of 459, 447, and 436 ppm at the same heights (Hsu and Kuo 2021). These consistent findings suggested that leaves located closer to the forest floor are exposed to elevated CO_2 availability. In a valley plot of the Nanjenshan lowland rainforest, 44% of 5,786 ground-layer plants (≤ 100 cm tall) were 1-10 cm in height, comprising 18% at 1-5 cm and 26% at 6-10 cm (Tsai Jun-Miao, personal communication). This indicated that a substantial proportion of juvenile plants occupy microenvironments near the forest floor, where CO_2 concentrations are naturally elevated. Among the 40 species studied, seedlings of 25 species had a mean height of < 10 cm, while those of the remaining 15 species averaged 10-18 cm. The leaves measured for photosynthesis were typically situated below the seedling apex and thus closer to the forest floor; they likely utilized the naturally elevated CO_2 concentrations prevalent during morning hours for photosynthesis (Buchmann et al. 1996, Brooks et al. 1997, Hsu and Kuo 2021). Previous research (Cheng and Kuo 2004) has found that elevating CO_2 from 360 to 400 ppm reduced mean LCP and R_d by 25% among 24 shade-tolerant seedlings growing under low-light understory conditions. By contrast, six shade-intolerant species exhibited smaller reductions of 13% in LCP and 5% in R_d. Consistent with these findings, our data (Table 1) showed that a 40 ppm CO_2 increase led to mean reductions of 50% in LCP and 43% in R_d in three shade-tolerant species, compared to 34% and 22%, respectively, in three shade-intolerant species. Collectively, the results from both studies demonstrated that shade-tolerant plants exhibited greater physiological responsiveness in LCP and R_d to moderate increases in ambient CO_2 than their shade-intolerant counterparts. For shade-tolerant plants, the additional CO_2 available near the forest floor significantly enhanced their QUE and P_n, thereby contributing to lower LCP values (Table 1). This physiological adaptation conferred a substantial advantage, enhancing the survival and growth of their regenerating seedlings within the light-limited but CO_2 enriched forest understory (Osborne et al. 1997, Würth et al. 1998, Springer and Thomas 2007, Damasceno et al. 2024).

Shade tolerance levels for species without measured photosynthetic capacity

The distribution of juvenile plants along light gradients within forest habitats generally corresponds with their species' shade tolerance levels, which are assessed via A_{max} values (Kuo et al. 2024). Seedlings of shade-intolerant species primarily establish themselves in high-light habitats and are

rarely found in low-light conditions, while those of shade-tolerant species are mostly confined to shaded understory environments. In the Nanjenshan valley plot, Chao et al. (2022) further observed that seedlings in their established stage with different shade tolerances are distributed along different light gradients. The shade-intolerant seedlings are established across a broad range of microsites, including both high-light and low-light conditions, whereas more shade-tolerant seedlings are restricted to deeply shaded areas. In this study, seedlings of eight species (*Mallotus paniculatus*, *Macaranga tanarius*, *Melanolepis multiglandulosa*, *Lagerstroemia subcostata*, *Maesa perlaria* var. *formosana*, *R. javanica* var. *roxburghiana*, *Stachytarpheta urticaefolia*, and *Cra. crepidioides*) were predominantly sampled from open, high-light habitats, indicating their adaptation to bright environments. By contrast, the remaining 32 species were collected from shaded forest understories, which is consistent with greater shade tolerance. The primary objective of this study was to investigate whether photosynthetic responses to elevated CO_2 vary among seedlings of different growth forms, including herbs, lianas, bamboos, and woody plants, and whether these differences correspond with their shade tolerance levels under low-light conditions. However, A_{max} data were unavailable for 11 of the 40 species, precluding their shade tolerance classification based on this metric. To address this, we propose utilizing the P_n measured under low light at 400 ppm CO_2 (A_{400}) as a proxy for shade tolerance. This proposal is grounded in our observation that species classified as shade tolerance levels IV (tolerant) and V (highly tolerant) (A_{max} < 15.0 μmol CO_2 m^{-2} s^{-1}) (Kuo et al. 2021) predominantly exhibited positive A_{400} values (Table 2). Consequently, the sign (positive or negative) of A_{400} serves as a suitable threshold for differentiating shade tolerance levels. Therefore, for species with unknown shade tolerance levels, the first classification criterion was the sign of A_{400}: species with positive A_{400} values were assigned to the "shade-tolerant group," while those with negative A_{400} values were assigned to the "shade-intolerant group." The second criterion was the magnitude of the A_{400} value: a more positive A_{400} value indicated a higher shade tolerance capacity, while a more negative value indicated a lower shade tolerance capacity (i.e., greater light demand). Applying these criteria: *Schizostachyum diffusum* and *Cra. crepidioides* (A_{400} = -0.42 and -0.37 μmol CO_2 m^{-2} s^{-1}, respectively) were classified as shade tolerance Class I (highly intolerant); *Cal. formosanus* (A_{400} = -0.04 μmol CO_2 m^{-2} s^{-1}) as Class II; *Au. chinensis* (A_{400} = 0.05 μmol CO_2 m^{-2} s^{-1}) as Class III; *Al. odora*, *Flagellaria indica*, *Kadsura japonica*, *Piper kadsura*, and *Chl.oldhami* (A_{400} = 0.10 to 0.37 μmol CO_2 m^{-2} s^{-1}) as Class IV; and *E. lineolatum* var. *majus* and *Lasianthus obliquinervis* Merr. var. *obliquinervis* (A_{400} = 0.56 and 0.52 μmol CO_2 m^{-2} s^{-1}, respectively) as Class V (highly shade-tolerant).

Differences in photosynthetic C_aUE among shade-tolerant groups

Based on the classification described above, the 40 plant species examined in this study were assigned to five shade tolerance classes: Seven species in Class I, 4 in Class II, 9 in Class III, 14 in Class IV and 6 in Class V. Due to the small sample sizes in Classes II and V, we combined Classes I and II into a "shade-intolerant group" (n = 11) and Classes IV and V into a "shade-tolerant group" (n = 20), while Class III (n = 9) was retained as an "intermediate group" for statistical comparison. Statistical analysis showed that the mean C_aUE values were 0.0033 ±

0.0006 μmol CO_2 m^{-2} ppm^{-1} s^{-1} for the shade-intolerant group and 0.0099 ± 0.0027 μmol CO_2 m^{-2} ppm^{-1} s^{-1} for the intermediate group. Both values were significantly lower than that of the shade-tolerant group, which averaged 0.0167 ± 0.0018 μmol CO_2 m^{-2} ppm^{-1} s^{-1} ($p < 0.001$; Figure 6a). Within the intermediate group (Class III) in the boxplot (Figure 6a), *Ar. sieboldii* was an outlier, with a C_aUE reaching 0.0296 μmol CO_2 m^{-2} ppm^{-1} s^{-1}, the highest among all 40 species examined. Its A_{max} was 15.0 μmol CO_2 m^{-2} s^{-1}, corresponding exactly to the lower threshold for the "moderately shade-tolerant" level (Class III) as defined by Kuo et al. (2021). If this A_{max} threshold were adjusted to >15.0 μmol CO_2 m^{-2} s^{-1}, this species would be classified as shade-tolerant (Class IV), and its C_aUE value would fall within the typical range observed for the shade-tolerant group (Figure 6a). Regardless of classification boundaries, its exceptional responsiveness of net photosynthesis to elevated CO_2 warrants further physiological investigation. Previous research (Hsu and Kuo 2021) has reported divergent patterns of C_aUE between shade-tolerant and shade-intolerant seedlings under varying light regimes. Under low-light conditions (PPFD ≤ 60 μmol photon m^{-2} s^{-1}), shade-tolerant seedlings tend to exhibit significantly higher C_aUE, while under high light (≥ 250 μmol photon m^{-2} s^{-1}), shade-intolerant seedlings generally show superior CO_2 responsiveness (Hsu and Kuo 2021). Conducted under low-light understory conditions similar to the low-light regime described above, our study similarly found that seedlings of the shade-tolerant group possessed significantly higher C_aUE than those of the shade-intolerant group (Figure 6a). The low C_aUE values observed in shade-intolerant seedlings under such low-light conditions may have resulted from limited activation of photosynthetic enzymes and reduced stomatal conductance, both of which would have constrained the ability of shade-intolerant seedlings to utilize increased CO_2 concentrations (Way and Pearcy 2012).

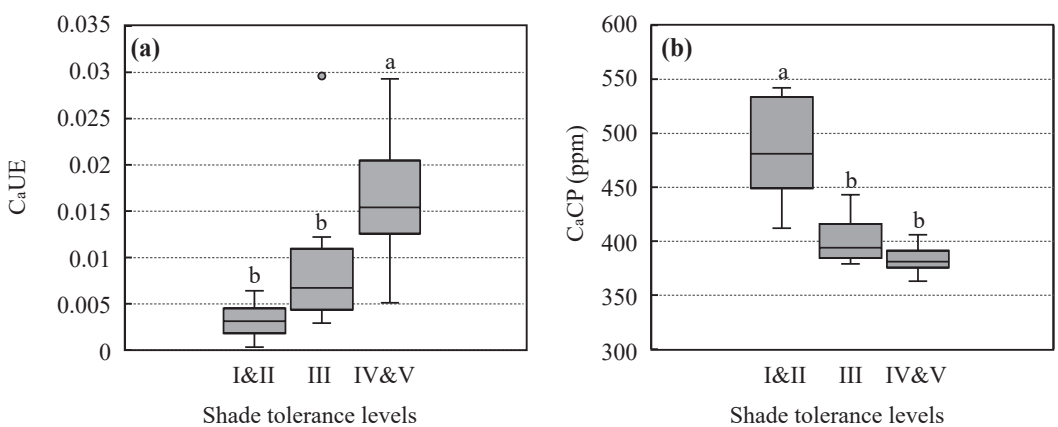

Figure 6. Boxplots showing the photosynthetic ambient CO_2 use efficiency (C_aUE, μmol CO_2 m^{-2} ppm^{-1} s^{-1}) (a) and ambient CO_2 compensation point (C_aCP) (b) of species with various levels of shade tolerance. I: highly intolerant, II: intolerant, III: moderate tolerant, IV: tolerant, V: highly tolerant species. Different letters among shade tolerance levels denote a significant difference by Scheffe's test at $p < 0.05$.

Differences in photosynthetic C_aCP among shade-tolerant groups

This study found that the mean photosynthetic C_aCP of shade-intolerant species was 486 ± 16 ppm, significantly higher than those of the moderately shade-tolerant group (Class III, 401 ± 7 ppm) and the shade-tolerant group (Class IV + V, 381 ± 4 ppm) ($p < 0.001$, Figure 6b). This corresponds to mean reductions in C_aCP of 85 ppm and 105 ppm for the moderately shade-tolerant and shade-tolerant groups, respectively, compared to that of the shade-intolerant group. Consequently, seedlings with higher shade tolerance are more likely to experience ambient CO_2 concentrations above their C_aCP during daytime. Therefore, they are likely to maintain positive P_n for longer durations than shade-intolerant seedlings. The absolute increase in P_n caused by elevated near-ground CO_2 is modest. For instance, P_n for shade-tolerant seedlings at 400 ppm CO_2 ranged from only 0.05 to 0.89 μmol CO_2 m^{-2} s^{-1} (Table 2). However, for understory seedlings enduring chronically low light and sustaining assimilation rates barely above respiration rates, this enhancement of carbon assimilation via soil-respired CO_2 is critically important. This benefit not only enhances seedling shade tolerance, likely by facilitating a lower LCP compared to that of less tolerant species, but is also essential for maintaining long-term positive carbon balance, thereby conferring significant ecological significance (Osborne et al. 1997, Kerstins 1998, Sefcik et al. 2006, Kitao et al. 2016, Valladares et al. 2016).

In plant ecophysiology, the photosynthetic CO_2 compensation point (CCP) is defined as the intercellular CO_2 concentration at which the rate of photosynthetic CO_2 assimilation equals the rate of CO_2 release from respiration, resulting in a P_n of zero. Under saturating light, the intercellular CCP for C_3 plants is approximately 40-50 ppm (Lambers et al. 1998). However, the ambient CO_2 concentration surrounding leaves is generally much higher than this intercellular CCP. Consequently, P_n does not become negative solely because ambient CO_2 falls below the compensation point itself. Negative P_n occurs only when extremely low light availability reduces CO_2 assimilation rates below the rate of respiratory CO_2 release. Under identical low-light conditions, increasing the CO_2 concentration can elevate CO_2 assimilation rates sufficiently to meet or exceed rates of respiratory CO_2 release. In this study, under very low understory light conditions (PPFD 3-12 μmol photon m^{-2} s^{-1}), we measured the P_n of seedlings of 40 species across ambient CO_2 concentrations (350-430 ppm) characteristic of the forest floor (Figure 4). At CO_2 concentrations below 360 ppm, the P_n was negative for the vast majority of species. A modest increase to 400 ppm shifted the P_n to positive values for some species, while others, predominantly those in the shade-intolerant group, remained negative (Table 2). This specific eco-physiological context provided a unique opportunity to calculate species-specific ambient C_aCP under these conditions using the linear regression of P_n against ambient CO_2 concentrations. As previously reported and illustrated in Figure 6b, the C_aCP of the shade-tolerant group was significantly lower than that of the shade-intolerant group. Crucially, under low-light understory conditions, seedlings of shade-tolerant and moderately shade-tolerant species in the Nanjenshan Forest achieved positive net photosynthesis at significantly lower ambient CO_2 concentrations than shade-intolerant seedlings required. The average difference was 105 ppm lower for shade-tolerant species (Figure 6b). This finding

demonstrated a substantial difference in C_aCP intrinsically linked to shade tolerance under natural understory light. To our knowledge, this represents the first report of such a phenomenon in forest tree ecophysiology. We propose that through long-term evolutionary adaptation, shade-tolerant plants have developed specific physiological traits: higher photosynthetic ambient C_aUE and lower ambient C_aCP. These traits enhance their capacity to utilize the elevated CO_2 resources near the forest floor originating from soil respiration. This adaptation enables them to achieve positive carbon gain under lower light availability. Such gain is sufficient to sustain growth and ensure the survival of their naturally regenerating seedlings in the deeply shaded forest understory. Conversely, shade-intolerant seedlings primarily regenerate in high-light habitats. During establishment, abundant light resources support assimilation rates sufficient for positive carbon gain without substantial dependence on elevated soil-respired CO_2. Consequently, they lack the specific photosynthetic traits evolved for efficient CO_2 utilization under deep shade conditions, namely high C_aUE and low C_aCP.

Responses of photosynthetic traits to elevated CO_2 in herbaceous and woody vine species with differing shade tolerances

This study investigated whether herbaceous plants and woody lianas exhibit the same shade-tolerance-dependent photosynthetic response to elevated CO_2 observed in woody species, where shade-tolerant individuals show greater sensitivity in key photosynthetic traits compared to shade-intolerant counterparts. Among the four herbaceous species studied, *Cra. crepidioides* was classified as shade-intolerant (Class I) and exhibited a photosynthetic C_aUE of 0.0059 μmol CO_2 m^{-2} ppm^{-1} s^{-1}. This value was less than half of the average C_aUE of the other three species *E. lineolatum* var. *majus*, *Al. odora*, and *Chl. oldhami*, which were classified as tolerant and highly tolerant species (Class IV and V) and had a mean C_aUE of 0.0186 μmol CO_2 m^{-2} ppm^{-1} s^{-1}. Photosynthetic C_aCP of *Cra. crepidioides* was 462 ppm, approximately 80 ppm higher than the average C_aCP of 382 ppm in the other three species (Table 2). For woody lianas, species classified as shade tolerance Classes I, II, and IV, *Schizostachyum diffusum*, *Cal. formosanus*, and *Flagellaria indica*, showed increasing C_aUE values (0.0030, 0.0037, and 0.0097 μmol CO_2 m^{-2} ppm^{-1} s^{-1}) and decreasing C_aCP values (541, 412, and 390 ppm) with increasing shade tolerance. By contrast, two shade-tolerant lianas (Class IV), *K. japonica* and *Piper kadsura*, exhibited higher C_aUE (0.0154 and 0.0120 μmol CO_2 m^{-2} ppm^{-1} s^{-1}) and lower C_aCP (384 and 386 ppm) than the less shade-tolerant lianas (Table 2). These results indicated that within herbaceous and woody liana growth forms, more shade-tolerant species have photosynthetic traits (C_aUE and C_aCP) that respond more sensitively to elevated CO_2 than shade-intolerant species.

In the Nanjenshan Forest, *Cal. formosanus* and *Schizostachyum diffusum* seedlings can tolerate low-light understory conditions but exhibit strong phototropism and rapidly colonize canopy gaps created by disturbances, extending from forest edges into higher-light microsites (Chao 2001, Kuo and Fan 2003). In addition, *De. meyeniana*, classified as shade-intolerant (Class II), regenerates in both shaded understory and canopy gaps, making up as much as 33% of seedlings in understory sites with < 4% relative light intensity (Kuo et al. 2024). Its P_n at a PPFD of 8-12 μmol photon m^{-2} s^{-1} and a CO_2 concentration of 355-370 ppm was about 50% positive (Figure

4, species #40), resulting in a positive mean A_{360} value, unlike other shade-intolerant species, which exhibited negative values. Its photosynthetic traits—QUE, LCP, and R_d—under increasing CO_2 resembled those of shade-tolerant species (Table 1), supporting its particularity as a light-demanding species with shade-tolerant traits (Kuo et al. 2024). By contrast, *Maesa perlaria* var. *formosana* was classified as moderately shade-tolerant based on its A_{max} (15.1 μmol CO_2 m^{-2} s^{-1}), but its seedlings were primarily found in higher-light habitats. Natural regeneration in landslide areas of Taiwan's central and southern mountains (Chang et al. 2017, Chen et al. 2022, Chung et al. 2022) also suggested that this species could acclimate to higher light conditions. Meanwhile, *Dr. karapinensis*, with the lowest A_{max} (7.8 μmol CO_2 m^{-2} s^{-1}) among 440 woody species studied (Kuo et al. 2021), demonstrated classic shade-tolerant traits. Its C_aUE ranked seventh highest among all tested species (0.0201 μmol CO_2 m^{-2} ppm^{-1} s^{-1}), and it had the lowest C_aCP (363 ppm), underscoring its strong photosynthetic responsiveness to elevated CO_2 under low light. Excluding *De. meyeniana, Dr. karapinensis* had the least negative A_{360} (-0.03 μmol CO_2 m^{-2} s^{-1}) and the second highest A_{400} (0.78 μmol CO_2 m^{-2} s^{-1}), consistent with traits of an extreme shade-tolerant species.

As atmospheric CO_2 continues to rise, seedlings of shade-tolerant herbaceous and woody species in forest understories may increasingly benefit from enhanced CO_2 availability. This advantage could enhance their competitive ability under low light, potentially altering forest species composition and successional dynamics (Kubiske and Pregitzer 1996, Valladares et al. 2016). From a practical standpoint, incorporating organic materials into nursery soils to enhance microbial respiration and local CO_2 levels may improve growth performance for shade-tolerant seedlings in shaded cultivation environments.

CONCLUSIONS

In the Nanjenshan Forest, elevated ambient CO_2 concentrations enhanced photosynthetic performance in seedlings with varying degrees of shade tolerance. Among the six woody species analyzed in detail, both P_n and apparent QUE increased as CO_2 levels rose. By contrast, the LCP and R_d decreased significantly. Similarly, for 40 woody and herbaceous plant species growing in the shaded understory, higher near-ground CO_2 concentrations were associated with increased P_n values under low-light conditions. In addition to the known pattern that shade-tolerant species exhibit higher photosynthetic C_aUE, this study provides novel evidence that they also possess significantly lower C_aCP than shade-intolerant species. Under low-light conditions, many shade-intolerant species exhibit negative P_n values at 400 ppm CO_2. By contrast, most shade-tolerant species had already achieved positive P_n values at the same concentration. Among herbaceous and woody liana species, individuals with greater shade tolerance exhibited stronger photosynthetic responses to elevated CO_2 compared to their shade-intolerant counterparts. CO_2 released through soil respiration may help reduce the LCP of understory seedlings, thereby enhancing their shade tolerance and increasing their likelihood of maintaining a positive carbon balance. This CO_2-mediated mechanism plays an important role in supporting the survival and growth of seedlings in deeply shaded forest environments.

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研究報告

南仁山森林不同耐陰性小苗在不同CO_2濃度下的光合性狀反應

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摘 要

本研究比較南仁山森林不同耐陰性植物小苗，光合作用性狀對林床上方自然提高之CO_2濃度的反應，目的在於探討為何耐陰植物的小苗，在林下低光環境能維持正值淨光合作用率(P_n)，而不耐陰植物則不具此特性的原因。第一項試驗測定6種不同耐陰性樹苗在CO_2濃度360~420 ppm的光合作用光反應。結果發現大多數樹苗於低光條件下的P_n及光量子利用效率會隨CO_2濃度升高而顯著提高，而光補償點(LCP)、暗呼吸率(R_d)則會顯著降低，然而耐陰性較高的樹苗光合性狀改變的程度較大。第二項試驗藉抽取林床上方5及100 cm的空氣，提供濃度350~430 ppm的CO_2供40種木本及草本植物小苗光合作用。結果發現在≤ 12 μmol photon m^{-2} s^{-1}的低光環境下，耐陰性高的木本及草本植物有較高的光合作用CO_2利用效率(P_n值隨空氣CO_2濃度改變之迴歸式的斜率，C_aUE)。耐陰的19種植物於CO_2濃度400 ppm時的P_n值(A_{400})都呈正值，不耐陰的10種植物其A_{400}值都是負值。此外，本研究也首次發現於林下低光環境，耐陰植物小苗的CO_2補償點(P_n值由負轉正的CO_2濃度，C_aCP)顯著比不耐陰者低105 ppm，在林下因土壤呼吸而提高的CO_2濃度範圍下可有正的P_n值。本文結論為生長在樹冠底層耐陰性較高的小苗，光合作用雖受限於光資源不足，但受益於土壤呼吸釋出較高的CO_2資源，可明顯降低其LCP、R_d、C_aCP，並有較高的C_aUE，有利於耐陰小苗維持正的碳收穫。

關鍵詞：光合作用CO_2補償點、光合作用CO_2利用效率、耐陰性、土壤呼吸、林下低光環境

鄭鈞騰、郭耀綸。2025。南仁山森林不同耐陰性小苗在不同CO_2濃度下的光合性狀反應。台灣林業科學 40(2):201-38。

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2025年3月送審，2025年5月通過。Received March 2025, Accepted May 2025.

緒言

生長在森林下層的天然更新小苗，白天能接受到的光資源甚低，例如南仁山森林底層白天入射的光合作用有效光子量(photosynthetic photon flux density, PPFD, 400~700 nm)有94%是低於10 μmol photon m^{-2} s^{-1} (Cheng 2001)；南仁山溪谷樣區林床上方20 cm處，9年期間平均相對光量僅為林冠上方的1.3% (Chao et al. 2022)。研究顯示生長在森林下層的幼齡植株，因長期處在低光環境，在生理及形態上已具備減少碳支出的性狀，以維持正值的碳平衡(carbon balance) (Reich et al. 2003, Craine and Reich 2005)。另一方面，森林下層天然更新小苗的碳平衡，亦會直接受益於林地土壤呼吸(soil respiration)釋出較高的CO_2資源(Bazzaz 1990, Osborne et al. 1997)。土壤呼吸為根系與根域(rhizosphere)的自營性呼吸作用，以及微生物的異營性呼吸作用之總和(Hanson et al. 2000)，過程中會將產物CO_2釋放到林床上方大氣，成為低矮植株可利用的CO_2來源，此為普遍的生態現象(Schlesinger and Andrews 2000, de Araujo et al. 2008)，土壤呼吸對臺灣森林下層幼齡植株碳平衡的貢獻，值得探討。

隨著工業革命的影響，大氣CO_2濃度年平均值由1960年的316.9 ppm，至2000年提升為369.7 ppm，2024年更增至424.6 ppm (NOAA 2025)。然而，當前大氣CO_2濃度仍未達C_3植物的光合作用CO_2飽和點(Körner 2015, Erwin and Gesick 2017, Ren et al. 2018)。CO_2是植物碳固定反應(carbon fixation)的受質(substrate)，C_3植物在目前大氣CO_2條件，碳固定的主要酵素Rubisco仍是受CO_2不足之限制，因此提高CO_2濃度可增進Rubisco酵素的羧化作用(carboxylation)效率，同時競爭性的抑制該酵素的氧化作用(oxylation)，使光呼吸作用(photorespiration)造成的CO_2損失降低(Ainsworth and Rogers 2007, Leakey et al. 2009, Cernusak et al. 2013)。因此，無論耐陰或不耐陰的C_3植物，其淨光合作用率都具有隨CO_2濃度增大而顯著提高的潛力(Sefcik et al. 2006, Bader et al. 2010, Kitao et al. 2016)。生長在森林下層低光環境的小苗，其淨光合作用率也會因CO_2濃度升高而顯著提高(Hättenschwiler et al. 2001, Holton and Winter 2001, Sefcik et al. 2006, Damasceno et al. 2024)。此外，CO_2濃度增大也可促進C_3植物的光合作用光量子利用效率(quantum use efficiency or quantum yield)及CO_2利用效率(CO_2 use efficiency)，並降低暗呼吸率(dark respiration)及光補償點(light compensation point) (Teskey and Shrestha 1985, Springer and Thomas 2007, Leakey et al. 2009, Kitao et al. 2016)。

樹冠層葉片白天光合作用旺盛，會大量吸收(消耗) CO_2，因此森林垂直剖面的CO_2濃度是以樹冠層最低，林地表面最高(Buchmann et al. 1996, Brooks et al. 1997)。例如南仁山森林於2000年林床上方2、10、20 cm處，白天的大氣年平均CO_2濃度分別比樹冠層上方(361 ppm)高出62、30、20 ppm (Cheng and Kuo 2004)。森林下層距林床表面不同高度的葉片，因其周遭空氣中可用的CO_2濃度具差異，進而影響葉片的淨光合作用率(Bazzaz and Williams 1991)。

過去研究發現南仁山森林30種天然更新小苗的需光指標值(light demanding index)與其CO_2利用效率有顯著負向關係，需光指標值越低(耐陰性等級越高)的小苗，其CO_2利用效率越高(Cheng and Kuo 2004)。當時尚無藉光合潛力數值(photosynthetic capacity, A_{max})量化各種植物生理耐陰性的基本資料，而是藉光補償點數值當作各植物的需光指標值。近年來藉由A_{max}數值已建立434種臺灣原生闊葉樹種生理耐陰性等級的資料庫(Kuo et al. 2021)；本研究可藉此資料庫，比較已確認耐陰性等級的木本植物是否也是越耐陰者，其CO_2利用效率越高。此外，Hsu and Kuo (2021)發現於低光條件下，耐陰性等級較高的樹苗其光合性狀對CO_2濃度提高的反應較敏銳。上述研究是以耐陰性等級相異的15種木本植物為材料，而本研究除了喬、灌木類之外，也增加草本、木質藤本、竹類等不同生長型(growth form)的植物當材料，目的在於探討於林下低光條件，除了木本植物小苗外，其他類別生長型植物的小苗因為耐陰性不同，其光合作用性狀對CO_2濃度變化的反

應是否均具顯著差異，並進一步探討耐陰植物小苗在林下低光環境能有正值淨光合作用率，而不耐陰植物卻不具此特性的生理機制。基於上述目的，本研究提出3項問題：(1)在CO_2濃度360~420 ppm範圍，較耐陰的樹苗其淨光合作用率(P_n)、光量子利用效率(apparent QUE)、光補償點(LCP)、暗呼吸率(R_d)等光合作用性狀反應的程度，是否會高於較不耐陰的樹苗？(2)在林下低光條件，於土壤呼吸自然提高的CO_2濃度梯度範圍，較耐陰植物的小苗其光合作用CO_2利用效率(C_aUE)是否會顯著高於較不耐陰植物的小苗？(3)在林下低光條件，隨著CO_2濃度提高，較耐陰植物的小苗其P_n由負值轉成正值的CO_2濃度，意即光合作用CO_2補償點(ambient-CO_2 compensation point, C_aCP)是否會顯著低於較不耐陰植物的小苗？若耐陰植物的小苗於林下低光條件，其P_n, apparent QUE, LCP, R_d等光合性狀對CO_2濃度的反應較敏銳，且比不耐陰者有顯著較高的C_aUE與顯著較低的C_aCP，如此即可說明「為何耐陰植物小苗在林下低光條件能有正的P_n值，而不耐陰植物小苗卻不具此性狀」的可能原因。

材料與方法

森林下層6種樹苗於不同CO_2濃度級光合性狀的改變

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 1a)，由保護區管制站前往南仁湖的步道(南山路) 0.5 km東南方200 m、海拔高約190 m的背風坡森林內進行測定(Figure 1b)。通訊作者曾於1995年在該處設置二座鐵塔，測定樹冠層光合作用生產力(Kuo 2000)。該森林冠層主要組成樹種為白榕(*Ficus benjamina* L.)、大葉楠(*Machilus japonica* var. *kusanoi* (Hayata) J.C.Liao)、烏心石(*Michelia compressa* var. *formosana* (Kaneh.) Chien F.Chen)、江某(*Schefflera octophylla* (Lour.) Harms)、鐵冬青(*Ilex rotunda* Thunb.)等；灌木層以九節木(*Psychotria rubra* Poir.)、大葉樹蘭(*Aglaia elliptifolia* Merr.)為主。與鐵塔相距200 m處(海拔150 m)設有簡易氣象站，研究期間2000年的年均溫為23.9℃，年雨量2800 mm，6~8月累積雨量達全年雨量的50% (Cheng 2001)。

於森林下層選定6種耐陰性不同的樹種小苗各3株，分別為不耐陰的白匏仔(*Mallotus paniculatus* (Lam.) Müll. Arg. var. *paniculatus*)、茄苳(*Bischofia javanica* Blume)、咬人狗(*Dendrocnide meyeniana* (Walp.) Chew)，較耐陰的大葉楠、大葉樹蘭、交力坪鐵色(*Drypetes karapinensis* (Hayata) Pax & K. Hoffm.)，於2000年7~8月測定各樹種小苗光合作用性狀隨CO_2濃度提高的變化。白匏仔、茄苳小苗於1999年12月萌發，測定時前者苗高10~15 cm，後者苗高5~7 cm；大葉楠為1999年9月萌發，苗高7~9 cm；咬人狗、大葉樹蘭、交力坪鐵色小苗的萌發時間未知，前兩者苗高都在8~10 cm，後者苗高5~7 cm。白匏仔小苗生長在光量稍高的樹冠孔隙邊緣，其餘5種小苗生長在森林下層的低光環境。使用LI-6400系統(LI-6400XT, LI-COR, Lincoln, USA)測定其葉片之光合作用速率。測定時將葉溫控制在28℃，相對濕度60~70%，CO_2濃度分別設定在360、380、400、420 ppm，於光合作用有效光子量(PPFD)分別為0、4、8、15、20 μmol photon m^{-2} s^{-1}的條件下，各植株測定一個葉片的淨光合作用率(P_n值)，繪製P_n vs. PPFD關係圖，並求得兩者的直線迴歸式，計算P_n值為0之時的PPFD數值，此即為該葉片的光合作用光補償點(LCP)；由迴歸式計算PPFD為0之時的CO_2釋出率，即為其暗呼吸率(R_d)；光量子利用效率(apparent QUE)為該直線迴歸式的斜率。此外，藉上述直線迴歸式計算PPFD為10 μmol photon m^{-2} s^{-1}之時的P_n值(A_{10})。同一樹種在各CO_2濃度級的LCP、R_d、apparent QUE、A_{10}值為3株小苗的平均值。

另外也於2000年7~8月不同測定日的09:00~15:00測定供試6樹種小苗分別在上述4等級CO_2濃度下，其P_n對較高光量的光反應。由CO_2濃度360 ppm開始，某樹種一株小苗葉片夾入葉箱後，依序分別照以0、50、100、200、400、600、800、1000、1250、1500 μmol photon m^{-2} s^{-1}等不同PPFD

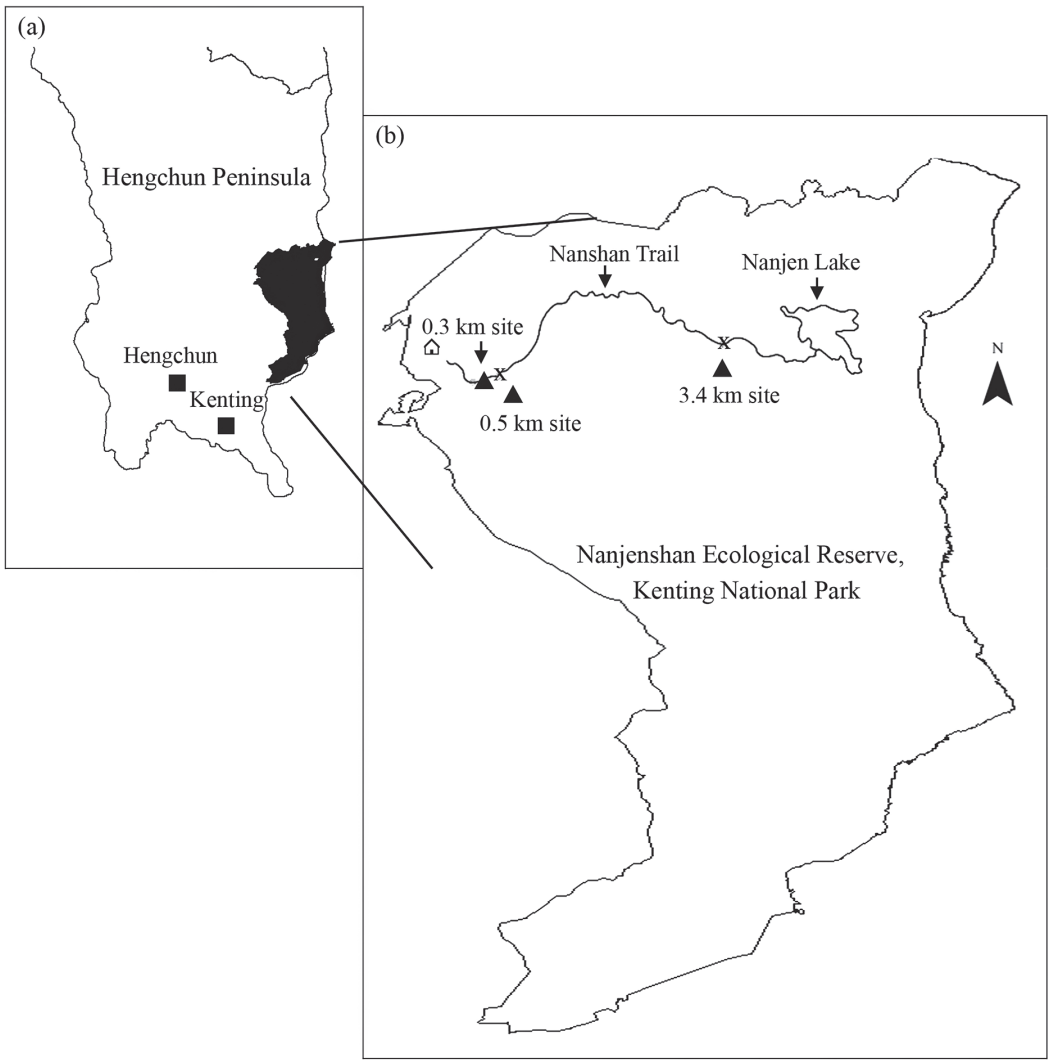

Figure 1. Sampling sites of this study were located in the Nanjenshan Ecological Reserve (南仁山生態保護區), Kenting National Park (墾丁國家公園) of southern Taiwan (a). Sampling site at 0.3 km was on an open field, while a 0.5 km site and a 3.4 km site were located respectively at a leeward and a windward forest along Nanshan Trail (b). ⌂ marks the control station.

值。其中一株小苗於CO_2濃度360 ppm條件完成光合作用光反應測定後，換同種另一株小苗進行相同CO_2濃度級的光反應測定，待3株小苗相同CO_2濃度級的光反應測定完成後，再換另一個較高的CO_2濃度級。將同種3株小苗在同一CO_2濃度、同一光量條件下的P_n值平均，可繪製該樹種小苗的光合作用光反應曲線。將各樹種3株小苗在各CO_2濃度條件最高的P_n值平均，得該樹種小苗的光飽和光合作用率(light-saturated photosynthetic rate, A_{sat})。

低光條件下40種植物小苗的淨光合作用率對CO_2濃度自然提高的反應

本研究分別在上述試驗的鐵塔樣區、南山路

步道0.3 km較空曠處，以及步道3.4 km附近的迎風坡森林內三處生育地(Figure 1b)，共選定31種喬木灌木，4種草本植物：昭和草(*Crassocephalum crepidioides* (Benth.) S.Moore)、姑婆芋(*Alocasia odora* (Roxb.) Spach)、冷清草(*Elatostema lineolatum* var. *majus* (Wight) Wedd.)、臺灣及己(*Chloranthus oldhami* Solms)；4種雙子葉木質藤本：南五味子(*Kadsura japonica* (L.) Dunal)、風藤(*Piper kadsura* (Choisy) Ohwi)、黃藤(*Calamus formosanus* Becc.)、印度鞭藤(*Flagellaria indica* L.)，以及1種攀緣性竹類莎勒竹(*Schizostachyum diffusum* (Blanco) Merr.)，合計40種植物，比較此多樣化的天然更新小苗在林下低光條件，其光合作用對近林床自然提高的較高濃度CO_2反應的差異。白匏仔、血桐(*Macaranga tanarius* (L.) Müll. Arg.)、蟲屎(*Melanolepis multiglandulosa* (Reinw. ex Blume) Rchb. & Zoll.)、九芎(*Lagerstroemia subcostata* Koehne)、臺灣山桂花(*Maesa perlaria* (Lour.) Merr. var. *formosana* (Mez) Yuen P.Yang)、羅氏鹽膚木(*Rhus javanica* L. var. *roxburghiana* (DC.) Rehd. & Wilson)、長穗木(*Stachytarpheta urticaefolia* Sims)、昭和草等8種植物的小苗，是於南山路步道0.3 km較空曠處尋獲。臺灣八角(*IIIicium arborescens* Hayata)、恆春楨楠(*Machilus obovatifolius* (Hayata) Kaneh. & Sasaki)、華河瓊楠(*Beilschmiedia tsangii* Merr.)、桃葉珊瑚(*Aucuba chinensis* Benth.)、奧氏虎皮楠(*Daphniphyllum glauescens* subsp. *oldhamii* (Hemsl.) T.C.Huang)、日本賽衛矛(*Microtropis japonicus* (Franch. & Sav.) Hallier f.)等6種小苗，是在步道3.4 km附近的迎風緩坡森林內尋獲，其餘26種植物的小苗是在鐵塔樣區尋獲。測定時是以現地的太陽輻射為光源，植株葉片在森林下接受到的PPFD值都 ≤ 12 μmol photon m^{-2} s^{-1}，然而大多數植株葉片照到的PPFD值在4~9 μmol photon m^{-2} s^{-1}範圍。生長在南山路0.3 km較空曠處的小苗，為模擬森林下方的光環境，以姑婆芋1~2層葉片覆蓋測量儀器葉箱，將PPFD值調整在5~8 μmol photon m^{-2} s^{-1}範圍。本研究並未人為提供不同濃度的CO_2資源，而是藉抽取林床上方兩處高度的空氣進入葉室，以提供夾在葉室內之葉片不同濃度的CO_2進行光合作用。本研究將矽膠管線一端連結在LI-6400光合作用系統的進氣口，另一端置於與儀器相距1.5 m處之鐵柱，離地表5 cm或100 cm處，前者為多數小苗葉片的高度，抽取的空氣中有380~430 ppm的CO_2，後者空氣內CO_2濃度約在350~380 ppm範圍，因測定時間而異。光合作用測定時將葉箱加熱板溫度控制在28℃，相對濕度60~70%。先將管線置於高度100 cm處抽取小苗光合作用所需CO_2資源，測定6~8筆P_n數值後，將管線取下橫向置於鐵桿離地5 cm處，抽取該處空氣再測定6~8筆P_n數值，之後移動儀器再測定鄰近另一株小苗。在2000年9月下旬至11月上旬，於5個測定日的09:00至15:00，完成40種植物各3株小苗的測定。合併同種植物3個植株在不同空氣CO_2濃度(ambient CO_2)測得的P_n數據，繪製P_n vs. CO_2濃度關係圖，獲得直線迴歸式，其斜率可供指示該植物在低光條件下的光合作用CO_2利用效率(C_aUE值) (Teskey and Shrestha 1985, Hsu and Kuo 2021)。此外，本研究藉各植物上述直線迴歸式計算P_n值為0之時的空氣CO_2濃度值，代表該植物在低光條件下的光合作用CO_2補償點(C_aCP)，葉片在CO_2濃度高於此C_aCP值時，即會有正的P_n值。

結果

森林下層6種樹苗於不同CO_2濃度級光合性狀的改變

供測定6樹種小苗葉片在CO_2濃度分別為360、380、400、420 ppm的測定條件下，其光合作用光反應曲線有所差異(Figure 2)。在高光(PPFD值 1000~1500 μmol photon m^{-2} s^{-1})條件下，不耐陰的白匏仔、茄苳、咬人狗在各CO_2濃度測定條件下的光飽和光合作用速率(A_{sat})都高於耐陰性較高的大葉楠、大葉樹蘭、交力坪鐵色(Table 1)。除了茄苳之外，另5種樹苗隨CO_2濃度上升其A_{sat}值均顯著增加($p < 0.05$) (Table 1)。當CO_2濃度由360 ppm提高至420 ppm時，大葉楠、大葉樹蘭、交力坪鐵色的A_{sat}值可提高47~83%，而3種不

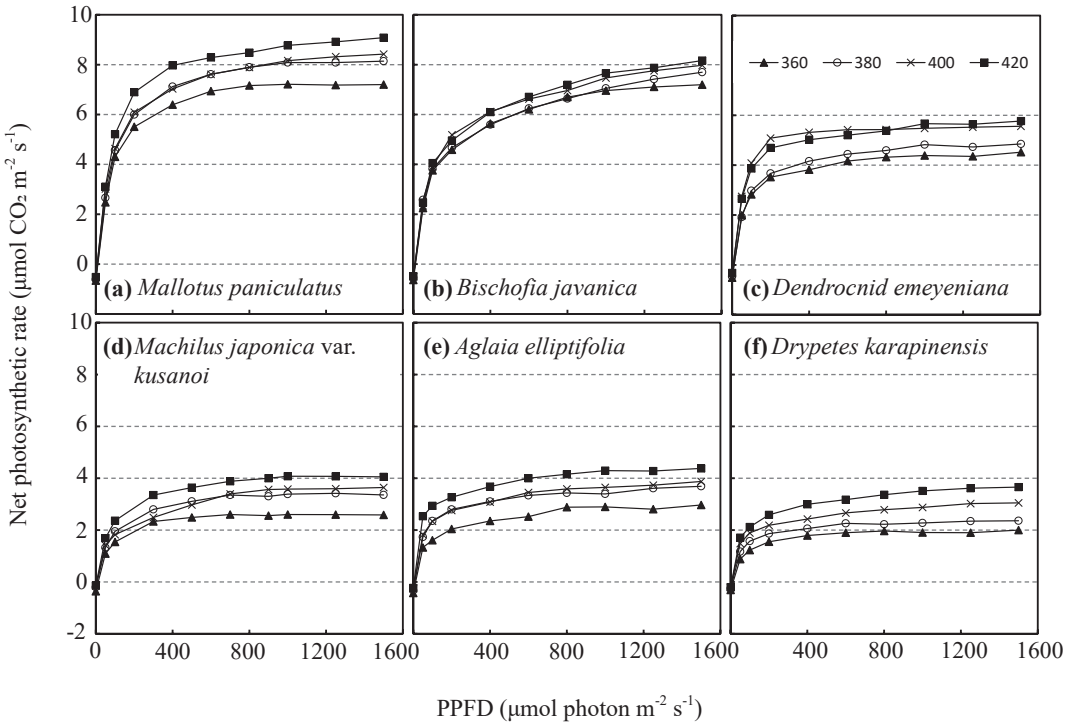

Figure 2. Photosynthetic light responses measured at ambient CO_2 concentrations of 360, 380, 400, and 420 ppm, respectively, and photosynthetic photon flux density (PPFD) of 0, 50, 100, 200, 400, 600, 800, 1000, 1250, and 1500 μmol photon m^{-2} s^{-1} in seedlings of six tree species growing in the Nanjenshan Forest (南仁山森林). Each point is the mean of 3 replicates.

耐陰樹苗只提高13~28% (Table 1)。在低光(PPFD值0~20 μmol photon m^{-2} s^{-1})條件下測得的光合作用光反應顯示，除了茄苳之外，另5種樹苗的光量子利用效率(QUE)均隨著CO_2濃度的上升而顯著提高，而所有6種樹苗的光補償點(LCP)及暗呼吸率(R_d)均隨著CO_2濃度上升而顯著降低(Table 1)。當CO_2濃度由360 ppm提高至420 ppm，QUE提高的程度以大葉樹蘭(77%)、咬人狗(68%)較大；LCP與R_d降低的程度都以大葉楠、大葉樹蘭最大；相反的，隨著CO_2濃度上升，先驅種白匏仔LCP及R_d降低的程度均最小(Table 1)。另一方面，在PPFD為10 μmol photon m^{-2} s^{-1}的低光條件，6種樹苗的P_n值也均隨著CO_2濃度的上升而顯著提高(Figure 3)，然而3種耐陰樹苗在各CO_2濃度的P_n值大多高於另3種不耐陰樹苗。上述結果顯示，在PPFD值0~20 μmol photon m^{-2} s^{-1}，以及CO_2濃度360~420 ppm兩項條件下，隨著CO_2濃度上升，耐陰性等級較高的樹苗其P_n、QUE、LCP、R_d等光合性狀改變的程度，大多高於較不耐陰的樹苗。

低光條件下40種植物小苗的淨光合作用率對CO_2濃度自然提高的反應

在南仁山森林於PPFD ≤ 12 μmol photon m^{-2} s^{-1}的低光條件下，本研究測定的40物種小苗，淨光合作用率(P_n值)大多隨林床上方大氣CO_2濃度增加而提高(Figure 4)。分析供測植物葉片其P_n vs. CO_2濃度的迴歸相關係數，發現具顯著($p < 0.05$)正向關係者有25種，迴歸相關係數p值在0.05~0.10間有8種，而有7種不耐陰的植物其p值> 0.10 (Table 2)。各種植物P_n vs. CO_2濃度直線迴歸式的斜率，可當作該植物在低光條件下光合作用CO_2利用效率(C_aUE)的指標。CO_2利用效率最高者依序為

Table 1. Comparisons of the light-saturated photosynthetic rate, apparent quantum use efficiency, light compensation point, and dark respiration rate measured at various CO_2 concentrations in seedlings of six tree species growing in the Nanjenshan Forest (mean ± standard error, n = 3). 420/360 denote the ratio of photosynthetic traits measured between CO_2 concentrations at 420 and 360 ppm of each species

	CO_2 concentration (ppm)				
	360	380	400	420	420/3600
Light-saturated photosynthetic rate (μmol CO_2 m^{-2} s^{-1})					
Mallotus paniculatus	7.24 ± 0.40[b1]	8.14 ± 0.14[ab]	8.42 ± 0.03[ab]	9.08 ± 0.31[a]	+25%
Bischofia javanica	7.20 ± 0.04[a]	7.70 ± 0.46[a]	7.97 ± 0.19[a]	8.16 ± 0.28[a]	+13%
Dendrocnide meyeniana	4.52 ± 0.36[a]	4.85 ± 0.40[a]	5.56 ± 0.60[a]	5.77 ± 0.58[a]	+28%
Machilus japonica [2]	2.59 ± 0.09[b]	3.36 ± 0.04[ab]	3.64 ± 0.08[ab]	4.05 ± 0.08[a]	+53%
Aglaia elliptifolia	2.97 ± 0.30[b]	3.69 ± 0.1[ab]	3.88 ± 0.23[ab]	4.38 ± 0.17[a]	+47%
Drypetes karapinensis	2.00 ± 0.08[c]	2.36 ± 0.08[bc]	3.05 ± 0.25[ab]	3.66 ± 0.07[a]	+83%
Apparent quantum use efficiency (μmol CO_2 (μmol photon)$^{-1}$)					
Mallotus paniculatus	0.079 ± 0.004[b]	0.083 ± 0.002[b]	0.088 ± 0.002[ab]	0.100 ± 0.002[a]	+27%
Bischofia javanica	0.061 ± 0.002[a]	0.063 ± 0.004[a]	0.063 ± 0.002[a]	0.059 ± 0.001[a]	-3%
Dendrocnide meyeniana	0.041 ± 0.002[b]	0.045 ± 0.004[b]	0.061 ± 0.004[a]	0.069 ± 0.003[a]	+68%
Machilus japonica [2]	0.041 ± 0.001[c]	0.046 ± 0.003[bc]	0.051 ± 0.002[ab]	0.058 ± 0.001[a]	+41%
Aglaia elliptifolia	0.048 ± 0.003[c]	0.050 ± 0.001[bc]	0.068 ± 0.002[ab]	0.085 ± 0.006[a]	+77%
Drypetes karapinensis	0.042 ± 0.004[b]	0.043 ± 0.003[b]	0.050 ± 0.002[ab]	0.064 ± 0.004[a]	+52%
Light compensation point (μmol photon m^{-2} s^{-1})					
Mallotus paniculatus	8.47 ± 0.24[a]	7.71 ± 0.05[ab]	6.45 ± 0.08[b]	6.05 ± 0.06[b]	-31%
Bischofia javanica	10.08 ± 0.10[a]	7.17 ± 0.28[b]	6.21 ± 0.12[c]	5.60 ± 0.07[c]	-44%
Dendrocnide meyeniana	10.15 ± 0.49[a]	8.74 ± 0.72[b]	4.73 ± 0.54[c]	4.29 ± 0.21[c]	-58%
Machilus japonica [2]	7.16 ± 0.12[a]	3.97 ± 0.24[b]	3.56 ± 0.26[bc]	2.80 ± 0.15[c]	-61%
Aglaia elliptifolia	7.35 ± 0.25[a]	5.79 ± 0.12[b]	3.74 ± 0.15[c]	2.84 ± 0.08[d]	-61%
Drypetes karapinensis	7.07 ± 0.56[a]	5.14 ± 0.42[b]	4.08 ± 0.03[b]	3.49 ± 0.14[b]	-51%
Dark respiration rate (μmol CO_2 m^{-2} s^{-1})					
Mallotus paniculatus	0.66 ± 0.03[a]	0.62 ± 0.02[ab]	0.54 ± 0.02[b]	0.52 ± 0.02[b]	-21%
Bischofia javanica	0.64 ± 0.03[a]	0.55 ± 0.01[ab]	0.51 ± 0.03[b]	0.49 ± 0.03[b]	-23%
Dendrocnide meyeniana	0.51 ± 0.03[a]	0.47 ± 0.04[ab]	0.36 ± 0.01[bc]	0.32 ± 0.02[c]	-37%
Machilus japonica [2]	0.36 ± 0.02[a]	0.20 ± 0.02[b]	0.15 ± 0.03[b]	0.14 ± 0.02[b]	-61%
Aglaia elliptifolia	0.42 ± 0.03[a]	0.33 ± 0.02[ab]	0.26 ± 0.02[b]	0.23 ± 0.01[b]	-45%
Drypetes karapinensis	0.31 ± 0.01[a]	0.25 ± 0.02[b]	0.21 ± 0.01[b]	0.21 ± 0.01[b]	-32%

[1] Different letters among CO_2 concentrations denote a significant difference by Scheffe's test at $p < 0.05$.
[2] *Machilus japonica* var. *kusanoi*.

樹杞(*Ardisia sieboldii* Miq.)、瓊楠(*Beilschmiedia erythrophloia* Hayata)、九節木、冷清草、大葉楠、印度苦櫧(*Castanopsis indica* (Roxb. *ex* Lindl.) A.DC.)、交力坪鐵色，其C_aUE值均≥ 0.02 μmol CO_2 m^{-2} ppm^{-1} s^{-1}；先驅樹種血桐、蟲屎、羅氏鹽膚木、白匏仔，陽性樹種九芎、茄苳、咬人狗之CO_2利用效率偏低，C_aUE值均≤ 0.0045 μmol CO_2 m^{-2} ppm^{-1} s^{-1} (Table 2)。

在光合作用CO_2補償點(C_aCP)方面，有25種植物在CO_2 < 400 ppm時即有正的P_n值；相反的，有7種植物C_aCP值須> 460 ppm，才會有正的P_n值，其中血桐、蟲屎、羅氏鹽膚木、莎勒竹的

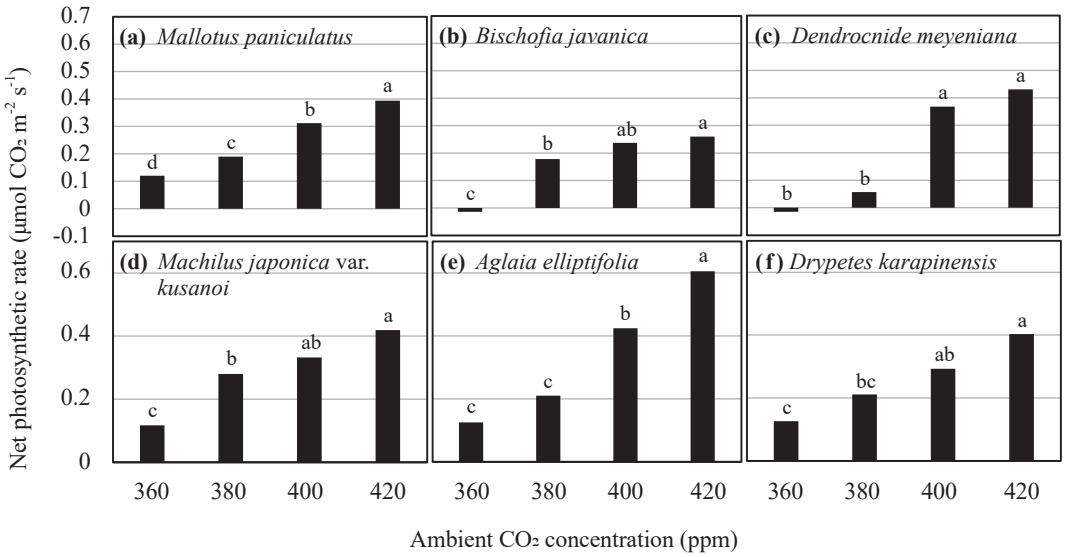

Figure 3. Net photosynthetic rates measured under photosynthetic photon flux density (PPFD) of 10 μmol photon m^{-2} s^{-1} at ambient CO_2 concentrations of 360, 380, 400, and 420 ppm for seedlings of six tree species growing in the Nanjenshan Forest. Different letters among various CO_2 concentrations for each species denote a significant difference by Scheffe's test at $p < 0.05$.

C_aCP值高達511~542 ppm (Table 2)。白匏仔、咬人狗之P_n 值隨CO_2濃度變化之迴歸線斜率接近於0，計算所得之C_aCP值(分別為1127、55 ppm)並不合理，其餘38種植物之C_aCP值與C_aUE值兩者具指數負向關係(r^2 = 0.65, Figure 5a)，CO_2利用效率較高者，有較低的CO_2補償點。此外，藉上述直線迴歸式(Figure 4)計算各種植物分別於CO_2濃度360及400 ppm時的P_n值，發現除了咬人狗之外，其他39種植物於CO_2濃度360 ppm時的P_n值都呈負值，但CO_2濃度提高至400 ppm時，該39種植物中有25種會有正的P_n值(Table 2)。

本研究測定的40種植物中，在先前研究(Kuo et al. 2021)已測得其中29種木本植物之光合潛力A_{max}值(Table 2)，其中先驅性與陽性不耐陰樹種合計8種，中等耐陰等級也有8種，耐陰與極耐陰等級合計13種。若排除咬人狗，當CO_2濃度由360提高到400 ppm，7種不耐陰樹種的P_n值平均提高28% (由-0.46提高至-0.33 μmol CO_2 m^{-2} s^{-1})，但其P_n值仍為負值；8種中等耐陰樹種的P_n值平均提高69% (由-0.29提高到0.09 μmol CO_2 m^{-2} s^{-1})，且已由負值轉變成正值；13種耐陰樹種的P_n值平均可提高233% (由-0.29提高到0.38 μmol CO_2 m^{-2} s^{-1})，且P_n值提高的速率度為中等耐陰樹種的3倍。本研究也發現已測得A_{max}值的29種木本植物小苗，其C_aUE值與其A_{max}值兩者具線性負向關係(r^2 = 0.36, Figure 5b)，A_{max}值較高的樹種具較低的光合作用CO_2利用效率。相對的，上述小苗(排除白匏仔及咬人狗)的C_aCP值與A_{max}值兩者具線性正向關係(r^2 = 0.78, n = 27, Figure 5c)，耐陰性較高(有較低的A_{max}值)的樹種其光合作用CO_2補償點也較低。

討論

6種樹苗於不同CO_2濃度下光合性狀的改變

森林樹冠層垂直剖面的空氣存在CO_2濃度梯度，越靠近地表CO_2濃度越高。南仁山森林於2000年監測到林床上方2、10、20 cm處，年平均白天CO_2濃度分別為423、391、381 ppm (Cheng and Kuo 2004)；2019年9月至2020年6月在屏科大校園人工林，於上述相同高度測得年平均CO_2濃度分別為459、447、436 ppm (Hsu and Kuo

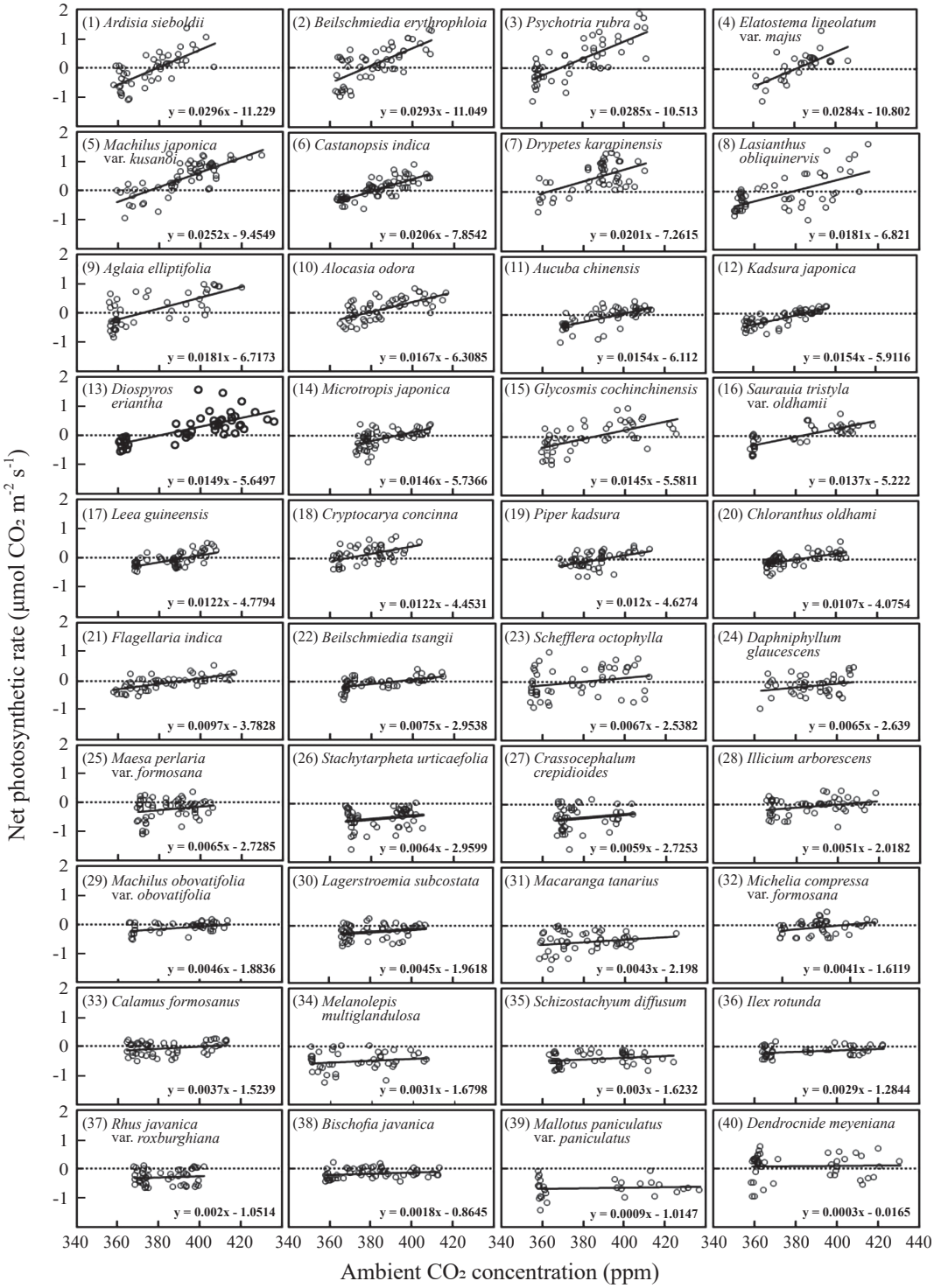

Figure 4. Responses of net photosynthetic rates to the in situ CO_2 concentrations above the forest floor for seedlings of 40 species growing in the Nanjenshan Forest. Measurements were made under photosynthetic photon flux density of 3-12 μmol photon m^{-2} s^{-1}.

Table 2. Photosynthetic ambient CO_2 use efficiency (C_aUE, μmol CO_2 m^{-2} ppm^{-1} s^{-1}), ambient CO_2 compensation point (C_aCP), calculated net photosynthetic rates at CO_2 concentrations of 360 ppm (A_{360}) and 400 ppm (A_{400}), and the maximum photosynthetic rate (A_{max}, reported by Kuo et al. 2021) of each tested species, which are listed in descending order of C_aUE values

Species	C_aUE	C_aCP	A_{360}	A_{400}	A_{max}
		(ppm)	(μmol CO_2 m^{-2} s^{-1})		
(1) *Ardisia sieboldii* (樹杞)	0.0296*** [1]	379	-0.57	0.61	15.0
(2) *Beilschmiedia erythrophloia* (瓊楠)	0.0293***	377	-0.50	0.67	13.5
(3) *Psychotria rubra* (九節木)	0.0285***	369	-0.25	0.89	13.8
(4) *Elatostema lineolatum* var. *majus* (冷清草)	0.0284***	386	-0.65	0.56	-
(5) *Machilus japonica* var. *kusanoi* (大葉楠)	0.0252***	375	-0.38	0.63	14.9
(6) *Castanopsis indica* (印度苦櫧)	0.0206***	381	-0.44	0.39	14.2
(7) *Drypetes karapinensis* (交力坪鐵色)	0.0201***	363	-0.03	0.78	7.8
(8) *Lasianthus obliquinervis* (雞屎樹)	0.0181***	377	-0.31	0.52	-
(9) *Aglaia elliptifolia* (大葉樹蘭)	0.0181***	371	-0.20	0.42	13.1
(10) *Alocasia odora* (姑婆芋)	0.0167***	378	-0.30	0.37	-
(11) *Aucuba chinensis* (桃葉珊瑚)	0.0154***	397	-0.57	0.05	-
(12) *Kadsura japonica* (南五味子)	0.0154***	384	-0.37	0.25	-
(13) *Diospyros eriantha* (軟毛柿)	0.0149***	379	-0.29	0.31	12.7
(14) *Microtropis japonica* (日本賽衛矛)	0.0146***	393	-0.48	0.10	8.7
(15) *Glycosmis cochinchinensis* (石苓舅)	0.0145***	385	-0.36	0.22	10.7
(16) *Saurauia tristyla* var. *oldhamii* (水冬瓜)	0.0137***	381	-0.29	0.26	13.8
(17) *Leea guineensis* (火筒樹)	0.0122***	392	-0.39	0.10	20.1
(18) *Cryptocarya concinna* (土楠)	0.0122***	365	-0.06	0.43	12.5
(19) *Piper kadsura* (風藤)	0.0120***	386	-0.31	0.17	-
(20) *Chloranthus oldhami* (臺灣及己)	0.0107***	381	-0.22	0.21	-
(21) *Flagellaria indica* (印度鞭藤)	0.0097***	390	-0.29	0.10	-
(22) *Beilschmiedia tsangii* (華河瓊楠)	0.0075***	394	-0.25	0.05	17.5
(23) *Schefflera octophylla* (江某)	0.0067*	379	-0.13	0.14	17.4
(24) *Daphniphyllum glaucescens* (奧氏虎皮楠) [2]	0.0065*	406	-0.39	-0.04	14.5
(25) *Maesa perlaria* var. *formosana* (臺灣山桂花)	0.0065*	420	-0.30	-0.13	15.1
(26) *Stachytarpheta urticaefolia* (長穗木)	0.0064*	463	-0.66	-0.40	26.0 [3]
(27) *Crassocephalum crepidioides* (昭和草)	0.0059NS	462	-0.60	-0.37	-
(28) *Illicium arborescens* (臺灣八角)	0.0051**	395	-0.18	0.02	10.3
(29) *Machilus obovatifolia* var. *obovatifolia* (恆春楨楠)	0.0046***	409	-0.23	-0.04	15.9
(30) *Lagerstroemia subcostata* (九芎)	0.0045*	436	-0.34	-0.16	25.7
(31) *Macaranga tanarius* (血桐)	0.0043NS	511	-0.65	-0.48	31.9
(32) *Michelia compressa* var. *formosana* (烏心石)	0.0041*	393	-0.14	0.03	17.5
(33) *Calamus formosanus* (黃藤)	0.0037*	412	-0.19	-0.04	-
(34) *Melanolepis multiglandulosa* (蟲屎)	0.0031NS	542	-0.56	-0.44	31.0
(35) *Schizostachyum diffusum* (莎勒竹)	0.0030*	541	-0.54	-0.42	-
(36) *Ilex rotunda* (鐵冬青)	0.0029**	443	-0.24	-0.12	17.4
(37) *Rhus javanica* var. *roxburghiana* (羅氏鹽膚木)	0.0020NS	526	-0.33	-0.25	26.0
(38) *Bischofia javanica* (茄苳)	0.0018NS	481	-0.22	-0.15	22.7
(39) *Mallotus paniculatus* var. *paniculatus* (白匏仔)	0.0009NS	-	-0.69	-0.66	29.4
(40) *Dendrocnide meyeniana* (咬人狗)	0.0003NS	-	0.09	0.10	23.0

[1] NS: $p \geq 0.10$, * $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$.
[2] *Daphniphyllum glaucescens* subsp. *oldhamii.*
[3] Reported by Kuo et al. (2001).

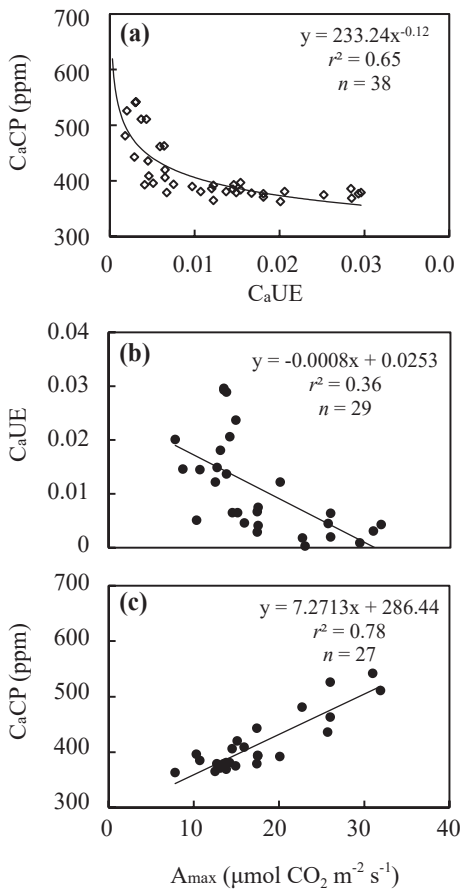

Figure 5. Relationships between the photosynthetic ambient CO_2 compensation point (C_aCP) and the photosynthetic ambient CO_2 use efficiency (C_aUE, μmol CO_2 m^{-2} ppm^{-1} s^{-1}) (a), C_aUE and the maximum photosynthetic rate (A_{max}) (b), and C_aCP and A_{max} (c) for seedlings growing in the Nanjenshan Forest. Data of A_{max} are from Kuo et al. (2021).

2021)，兩研究均顯示植株較靠近林地表面的葉片，可利用的CO_2資源會較高。南仁山低地雨林的溪谷樣區，高度≤ 100 cm的5786株地被層植物中，植株高度1~5、6~10 cm的株數比例分別為18、26%，合計44% (蔡潤苗個人通訊)，顯示有相當多的幼齡植株會生長在林床表面CO_2濃度增高的微環境。本研究測定的40種植物中，小苗平均高度< 10 cm者有25種，另15種高度在10~18 cm，測定光合作用的葉片較植株高度更低，更接近林地表面，葉片在黎明後數小時期間會利用濃度自然增高的CO_2資源進行光合作用(Buchmann et al. 1996, Brooks et al. 1997, Hsu and Kuo 2021)。過去研究發現生長在林下低光環境、耐陰性較高的24種小苗，當CO_2濃度由360 ppm提高至400 ppm時，LCP及R_d的平均值會降低25%，而6種不耐陰的小苗其LCP及R_d則改變不多，分別只降低13%及5% (Cheng and Kuo 2004)。本研究由Table 1計算CO_2濃度由360 ppm提高至400 ppm，3種較耐陰的小苗其LCP、R_d平均分別降低50、43%，而3種不耐陰的小苗該二性狀分別僅降低34、22%。兩研究的結果均顯示，耐陰性較高的植物，其LCP及R_d對CO_2濃度提高40 ppm的反應均高於較不耐陰的植物。耐陰性較高的植物因環境中額外增加的CO_2資源，可大幅增進其光量子利用效率，提高淨光合作用率，以致於有較低的LCP值(Table 1)，對其更新小苗在林下低光環境生存及成長會有很大助益(Osborne et al. 1997, Würth et al. 1998, Springer and Thomas 2007, Damasceno et al. 2024)。

尚未測定光合潛力植物之耐陰性等級的判斷

不同樹種幼齡植株其生態分布棲地的光環境差異，與其藉由光合潛力評估得到的耐陰性有一致的表現(Kuo et al. 2024)，不耐陰樹種的苗木主要分布在高光環境，甚少出現在低光環境，反之亦然。Chao et al. (2022)發現南仁山溪谷樣區小苗在建立階段(established stage)，不同耐陰性樹種小苗沿著光梯度(light gradient)的分布並不同，不耐陰的小苗可在高光與低光環境建立，較耐陰植物的小苗則侷限在低光環境。本研究白匏仔、血桐、蟲屎、九芎、臺灣山桂花、羅氏鹽膚木、長穗木、昭和草等8種植物，所測定的小苗主要生長在高光空曠地，顯示這些植物小苗能適應高光環境；另外32種植物的小苗樣本則是生長在森林下層光資源受限的生育地，顯示其較能適應低光環境。本研究目的在於探討「於林下低光條件下，除了木本樹苗外，其他類別生長型植物的小苗因為耐陰性不同，其光合作用性狀對CO_2濃

度變化的反應是否均具顯著差異」。然而，本研究所選擇的40種植物中，有11種其A_{max}值未知，因此不能用A_{max}歸類這11種植物的耐陰性等級。作者提出藉物種於低光條件、CO_2為400 ppm下測得的A_{400}數值來判斷其耐陰性，因為本研究已知耐陰性等級屬於第IV與第V兩級的植物(A_{max} < 15.0 μmol CO_2 m^{-2} s^{-1}) (Kuo et al. 2021)，在CO_2為400 ppm下測得的A_{400}值大多為正值(Table 2)，適合當作區別耐陰性等級的門檻。因此判斷本研究未知耐陰性等級物種，依據的第一個準則為A_{400}值為正值或負值，A_{400}為正值者屬「耐陰類群」植物，A_{400}為負值者屬「不耐陰類群」植物；依據的第二個準則為A_{400}數值高低，該值越正者(more positive)耐陰能力越高，該值越負者(more negative)越不耐陰。依據上述準則，將莎勒竹、昭和草(A_{400}值分別為-0.42、-0.37 μmol CO_2 m^{-2} s^{-1})判斷為耐陰等級I (極不耐陰)；黃藤(A_{400}值 -0.04 μmol CO_2 m^{-2} s^{-1})判斷為耐陰等級II；桃葉珊瑚(A_{400}值0.05 μmol CO_2 m^{-2} s^{-1})判斷為耐陰等級III；姑婆芋、南五味子、風藤、臺灣及己、印度鞭藤等5種植物的A_{400}值界於0.10~0.37 μmol CO_2 m^{-2} s^{-1}間，判斷為耐陰等級IV；冷清草、雞屎樹(*Lasianthus obliquinervis* Merr. var. *obliquinervis*)的A_{400}值分別為0.56、0.52 μmol CO_2 m^{-2} s^{-1}，判斷為耐陰等級V (極耐陰)。

不同耐陰類群植物光合作用CO_2利用效率(C_aUE)的差異

依上述結果歸納，本研究供測40種植物屬於耐陰等級I者7種，等級II者4種，等級III者9種，等級IV者14種，等級V者6種。因為等級II、V的取樣物種數較少，故將I、II兩級合併為「不耐陰類群」(n = 11)，IV、V兩級合併為「耐陰類群」(n = 20)。經過統計分析，不耐陰、中等耐陰兩類群的C_aUE平均值分別為0.0033 ± 0.0006、0.0099 ± 0.0027 μmol CO_2 m^{-2} ppm^{-1} s^{-1}，都顯著低於耐陰類群者(0.0167 ± 0.0018 μmol CO_2 m^{-2} ppm^{-1} s^{-1}) (p < 0.001, Figure 6a)。Figure 6a的中等耐陰類群(等級III)有一個離群值(outlier)為樹杞，其C_aUE值高達0.0296 μmol CO_2 m^{-2} ppm^{-1} s^{-1}，且為所有40種植物中最高者。樹杞的A_{max}值為15.0 μmol CO_2 m^{-2} s^{-1}，剛好是區分「中等耐陰」等級最低的門檻值(Kuo et al. 2021)，若將該A_{max}門檻值提高至> 15.0 μmol CO_2 m^{-2} s^{-1}，則本樹種會歸類在「耐陰」等級(等級VI)，其C_aUE值即會落在「耐陰類群」植物的分布範圍(Figure 6a)。無論如何，樹杞淨光合

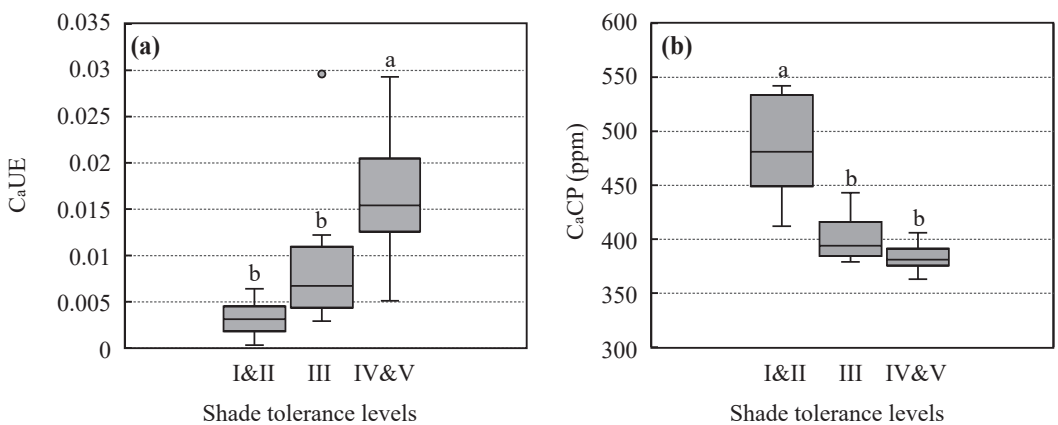

Figure 6. Boxplots showing the photosynthetic ambient CO_2 use efficiency (C_aUE, μmol CO_2 m^{-2} ppm^{-1} s^{-1}) (a) and ambient CO_2 compensation point (C_aCP) (b) of species with various levels of shade tolerance. I: highly intolerant, II: intolerant, III: moderate tolerant, IV: tolerant, V: highly tolerant species. Different letters among shade tolerance levels denote a significant difference by Scheffe's test at p < 0.05.

作用率對CO_2濃度提高的反應極為敏銳，其機制值得探討。前人研究發現不同耐陰性等級樹苗的C_aUE值，於低光或高光條件下有相反的表現；耐陰樹苗在PPFD ≤ 60 μmol photon m^{-2} s^{-1}的低光條件下，其C_aUE值顯著高於不耐陰樹種，但後者在≥ 250 μmol photon m^{-2} s^{-1}的高光條件下，其C_aUE值卻顯著高於耐陰樹苗(Hsu and Kuo 2021)。本研究是在林下低光環境進行，結果也是耐陰類群植物小苗的C_aUE值，顯著高於不耐陰類群植物(Figure 6a)。不耐陰的植物在過低的光資源下，其光合作用主要酵素受光活化(activate)的程度可能不足，且氣孔張開程度也受限(Way and Pearcy 2012)，導致不耐陰植物的光合作用對CO_2資源提高的反應不敏感，因此呈現極低的C_aUE值。

不同耐陰類群植物光合作用CO_2補償點(C_aCP)的差異

本研究發現，不耐陰類群植物的C_aCP平均值486 ± 16 ppm，顯著高於中等耐陰、耐陰二類群植物(分別為401 ± 7、381 ± 4 ppm) ($p < 0.001$, Figure 6b)；中等耐陰及耐陰兩類群植物，淨光合作用率由負值轉變成正值所需的CO_2濃度(CO_2補償點)，比不耐陰類群植物平均分別低85、105 ppm，顯示耐陰性較高的小苗，白天葉片經歷到超過其光合作用CO_2補償點之CO_2濃度的機會較大，因此白天P_n值為正值的時間應會長於不耐陰的植物。雖然因林床上方CO_2濃度增大，令小苗P_n值提高的絕對量並不高，例如耐陰類群植物小苗在CO_2濃度400 ppm時的P_n值僅在0.05~0.89 μmol CO_2 m^{-2} s^{-1}範圍(Table 2)，然而就長期處於光資源極低，勉強維持同化(assimilation)速率稍高於呼吸速率的林下小苗而言，此項因土壤呼吸提高同化作用的益處，不但可增強林下小苗的耐陰性(光補償點下降更低)，且對小苗長期維持碳平衡極為重要，具有重要的生態意義(Osborne et al. 1997, Kerstins 1998, Sefcik et al. 2006, Kitao et al. 2016, Valladares et al. 2016)。

植物生態生理學所謂的光合作用CO_2補償點(CCP)，是指在光合作用過程同化(吸收CO_2)速率與呼吸(釋出CO_2)速率達到平衡時的CO_2濃度，於飽和光照下C_3植物的CCP值約為葉片內細胞間隙(intercellular) 40~50 ppm的CO_2 (Lambers et al. 1998)。然而，植物葉片接觸到的空氣中CO_2濃度遠高於上述CCP值，淨光合作用率(P_n值)不會因未達到CO_2補償點濃度而成為負值，除非葉片獲得的光資源極低，令CO_2同化速率低於CO_2釋出速率。在相同的低光條件下，CO_2濃度提高即可能令不同植物的CO_2同化速率等於或高於CO_2釋出速率。本研究在林下光量極低(PPFD 3~12 μmol photon m^{-2} s^{-1})的條件下，測定40種植物小苗於林床上方CO_2濃度範圍(350~430 ppm)的P_n值(Figure 4)，發現絕大多數物種在CO_2 < 360 ppm時的P_n值會是負值，CO_2濃度微幅提高至400 ppm，部分物種的P_n可成為正值，但仍有部分物種(多屬不耐陰類群)仍為負值(Table 2)。此生態生理現象提供特別的機會，可藉個別物種P_n vs. CO_2濃度的直線迴歸式計算在此條件下的C_aCP值。結果顯示耐陰類群植物的C_aCP值顯著低於不耐陰類群者(Figure 6b)。於林下低光環境，南仁山森林耐陰與中等耐陰兩類群植物的小苗，比不耐陰類群者在顯著較低的CO_2濃度下(前者比後者平均低105 ppm) (Figure 6b)，就具有正的淨光合作用率，此現象是在林木生態生理學領域首次報導。本研究認為：耐陰性植物於長期演化過程，在生理上可能已經發展出能有效利用土壤呼吸釋出之較高CO_2資源的光合作用性狀，包括較高的光合作用CO_2利用效率(C_aUE)，以及較低的光合作用CO_2補償點(C_aCP)，因而在較低的光資源下也可有正的碳收穫足以維持其生長，所以在光資源極低的森林底層其天然更新小苗仍能生存。相對的，原本即在高光環境更新的不耐陰植物小苗，於建立階段可獲得充足的光資源供同化作用，不必依賴土壤呼吸提高的CO_2資源即可有正的碳收穫，因此不具上述耐陰性植物特性。

不同耐陰性草本、木質藤本植物光合性狀對CO_2濃度提高的反應

生長型為草本或木質藤本的植物，是否也具有「較耐陰者光合性狀對CO_2濃度提高的反應，高於不耐陰者」的現象？就4種草本植物而言，昭

和草歸類為耐陰等級I，其C_aUE值低於3種歸類為耐陰等級IV的冷清草、姑婆芋、臺灣及己C_aUE平均值的一半(0.0059 vs. 0.0186 μmol CO_2 m^{-2} ppm^{-1} s^{-1})；昭和草的C_aCP值462 ppm，則較另3種草本植物C_aCP平均值382 ppm高出80 ppm (Table 2)。另一方面，大型木質藤本莎勒竹、黃藤、印度鞭藤，其耐陰等級分別為第I、II、IV級，其C_aUE值隨耐陰性提高而增大(分別為0.0030、0.0037、0.0097 μmol CO_2 m^{-2} ppm^{-1} s^{-1})，C_aCP值則隨耐陰性提高而降低(分別為541、412、390 ppm) (Table 2)；相較於此3種較不耐陰的木質藤本，另2種耐陰等級VI的木質藤本南五味子、風藤，其C_aUE值分別為0.0154、0.0120 μmol CO_2 m^{-2} ppm^{-1} s^{-1}，比前3種的C_aUE值都高，而其C_aCP值分別為384、386 ppm，則較前3種都低。上述結果顯示，本研究取樣的草本或木質藤本植物，同一生長型較耐陰的植物，其光合性狀(C_aUE及C_aCP)對CO_2濃度提高的反應確實較不耐陰的植物敏感。

在南仁山森林，黃藤、莎勒竹在小苗階段可忍受低光，可在森林下層低光環境建立，然而森林若遭擾動形成林冠孔隙(canopy gaps)，此兩木質藤本趨光性強且可快速生長(現地觀察)，可由森林邊緣延伸進入孔隙內，佔據較高光的生育地(Chao 2001, Kuo and Fan 2003)。另一方面，由光合潛力表現判斷咬人狗為陽性樹種(耐陰等級II) (Kuo et al. 2021)，但在森林中咬人狗在林下及孔隙環境都可更新(Chao 2001)；在相對於林冠上方光量< 4%的林下低光環境，咬人狗幼齡植株分布比例可高達33% (Kuo et al. 2024)。本研究咬人狗的P_n隨CO_2濃度改變的形式，與其他陽性或先驅樹種並不同，在PPFD 8~12 μmol photon m^{-2} s^{-1}、CO_2濃度355~370 ppm的條件下，其P_n量測值約有一半為正值(Figure 4 #40)，因此其A_{360}值的平均值為正值，不同於其他39種植物A_{360}值都是負值。此外，在森林下層建立的咬人狗小苗，隨著CO_2濃度增大其QUE、LCP、R_d改變的程度都較接近耐陰樹種的反應(Table 1)。上述結果顯示咬人狗在光合作用生理上馴化低光的能力頗高，顯示其為「能耐陰的陽性樹種」(Kuo et al. 2024)的特殊性。相反的，臺灣山桂花依其光合潛力(15.1 μmol CO_2 m^{-2} s^{-1})歸類為中等耐陰樹種，但本研究是在較高光的環境尋獲其樹苗；在臺灣中、南部山區崩塌地也都可發現臺灣山桂花的天然更新植株(Chang et al. 2017, Chen et al. 2022, Chung et al. 2022)，顯示本樹種具有馴化高光的潛力。另一方面，前人研究測定440種木本植物的光合潛力A_{max}值，其中交力坪鐵色有最低的A_{max}值(7.8 μmol CO_2 m^{-2} s^{-1}) (Kuo et al. 2021)，顯示其耐陰性甚高。本研究結果發現交力坪鐵色的C_aUE值(0.0201 μmol CO_2 m^{-2} ppm^{-1} s^{-1})為供試40種植物中排序第7高者，而其C_aCP值363 ppm則為所有物種中最低者，此結果支持「耐陰性較高的物種其光合性狀對CO_2濃度提高的反應較明顯」(Hsu and Kuo 2021)的論點。排除咬人狗後，交力坪鐵色之A_{360}值(-0.03 μmol CO_2 m^{-2} s^{-1})為本研究測量植物中負值最少者，其A_{400}值(0.78 μmol CO_2 m^{-2} s^{-1})則排序第2高，符合極耐陰樹種之生理特性。

隨著大氣CO_2濃度逐年提高，森林下層木本及草本植物的幼齡植株可利用的CO_2資源也會隨之提高，此趨勢對耐陰性較高的物種較有利，其光合作用性狀對提高的CO_2資源較敏感，可促進其在低光環境下的競爭力。長此以往，有可能影響森林植群的組成及其動態變化(Kubiske and Pregitzer 1996, Valladares et al. 2016)。在應用方面，於陰棚下培育耐陰樹種苗木時，可於介質或土表增添有機質，促進土壤呼吸釋出額外的CO_2資源，應有助於苗木生長。

結論

南仁山森林6種不同耐陰性樹苗，其淨光合作用率、光量子利用效率多會隨環境中CO_2 (ambient CO_2)濃度的增加而提高，而光補償點、暗呼吸率則都顯著降低。在林下低光環境，40種木本及草本植物小苗的淨光合作用率，也會因林床上方較高的CO_2濃度而提高。耐陰性較高的植物除了有顯著較高的光合作用CO_2利用效率，本研究創新的發現這些植物的光合作用CO_2補償點也顯著比不耐陰的植物低。在低光條件下不耐陰的植物在CO_2濃度400 ppm時其淨光合作用率仍

為負值，而較耐陰的植物已具有正的淨光合作用率。生長型為木質藤本或草本的植物，耐陰性較高者其光合性狀對CO_2濃度提高的反應也高於不耐陰者。土壤呼吸釋出較多的CO_2資源，可降低林下木本及草本植物小苗的光補償點，增進其耐陰性，且有正淨光合作用率的機會提高，此現象對小苗維持正值碳平衡有重要貢獻，有利於小苗在林下低光環境的生長及生存。

謝誌

本研究獲國科會NSC 89-2621-B-020-007-A10補助計畫經費；初稿承蒙王相華及張勵婉兩位博士提供寶貴意見，並獲兩位審查人的審閱指教，提高稿件品質，謹此敬表謝意。徐露玉、吳家慈、王淑敏三位協助繪製稿件圖表，於此一併致謝。

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