Research paper

Photosynthetic Capacity and Shade Tolerance of 180 Native Broadleaf Tree Species in Taiwan

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【Summary】

Understanding the shade-tolerance ability of a species is crucial for the successful tending of young seedlings and selecting forestation species. Yet, no systematic investigations about the shade tolerance of native tree species have been carried out so far by foresters in Taiwan. In this study, we cultivated numerous seedlings of native broadleaf tree species in a nursery at National Pingtung University of Science and Technology. We measured the photosynthetic capacity (A_{max}) of 180 species during the rainy seasons of 2009~2014. The quantified data were applied as a physiological index for determining the shade-tolerance ability of a species and thereby classifying the species into 5 different shade-tolerance levels. To validate the suitability of this application, 6 experts of dendrology with years of field experience were asked to fill out a questionnaire for the tested species. The questionnaire inquired about the most likely light environment for natural recruits of each species. Then we compared the A_{max} results with the experts' opinions. Results showed that A_{max} of the 180 species ranged 35.8~9.1 μmol CO_2 m^{-2} s^{-1}; the first 5 species with the highest A_{max} values included *Hibiscus taiwanensis*, *Melia azedarach*, *Mallotus japonicus*, *Hibiscus tiliaceus*, and *Broussonetia papyrifera*, while *Garcinia subelliptica* showed the lowest. With reference to the experts' opinions, we divided A_{max} into 5 levels: ≧ 26.0, 25.9~21.0, 20.9~15.0, 14.9~12.5, and < 12.5 μmol CO_2 m^{-2} s^{-1}, corresponding to shade-tolerance levels 1, 2, 3, 4, and 5 (namely very intolerant, intolerant, moderately tolerant, tolerant, and very tolerant). By the A_{max} classification, numbers of species belonging to levels 1 to 5 were 18, 37, 70, 33, and 22; while according to the experts' opinions, respective numbers were 21, 52, 63, 40, and 4. Few species were considered to be very tolerant by the experts. The 2 sets of results showed a significant positive relationship with a Pearson's correlation coefficient of 0.92. Out of the 180 species, 131 (73%) species were classified into the same level by the 2 methods, and 49 species showed only 1 rank difference. Thus, employing A_{max} to classify the shade tolerance of subtropical broadleaf tree species is objective and practical. With these physiological data, we have established a database of shade-tolerance levels of subtropical broadleaf tree species of Taiwan. It provides references for forestation, ecological restoration, and ornamental applications.

Key words: expert opinion, light environment, photosynthetic capacity, shade-tolerance level, subtropical broadleaf tree.

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研究報告

台灣180種原生闊葉樹種光合潛力及耐陰性

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摘 要

瞭解樹種的耐陰性對苗木培育或造林樹種的選擇都很重要，然而林業界目前尚未針對眾多台灣原生樹種的耐陰性進行系統性的調查。本研究將台灣原生闊葉樹種栽植在屏東科技大學苗圃，在2009~2014年的雨季期間測定180種稚樹的光合潛力，藉此量化數據當作樹種耐陰性的生理指標，將這些樹種的耐陰性區分為五等級。為了檢驗藉各樹種光合潛力判斷耐陰性的適用性，我們邀請6位具野外經驗的樹木學專家填寫問卷，判定各樹種天然更新植株最常出現的光環境，比較專家意見與光合潛力判斷此180種樹種耐陰性等級的異同。結果發現，所有樹種光合潛力範圍在35.8~9.1 μmol CO_2 m^{-2} s^{-1}之間，最高的前5種分別為山芙蓉、苦楝、野桐、黃槿及構樹，最低者為菲島福木。參考專家意見，我們將光合潛力區分為(1) ≧ 26.0；(2) 25.9~21.0；(3) 20.9~15.0；(4) 14.9~12.5；(5) < 12.5 μmol CO_2 m^{-2} s^{-1}等五個等級，分別歸屬耐陰性第1、2、3、4、5級(先驅樹種、陽性樹種、中等耐陰樹種、耐陰樹種、極耐陰樹種)。供試180樹種根據上述光合潛力分級，歸類為耐陰性第1、2、3、4、5級的樹種分別有18、37、70、33、22種。專家意見對應上述五級光環境，由高光至低光分別有21、52、63、40、4種，專家意見認定的極耐陰樹種較少。此兩種判斷樹種耐陰性的結果，其皮耳森相關係數達0.92，兩者具極顯著正相關，其中有49種的分級僅差1級，而有131種(73%)藉此兩方法分類結果一致，顯示藉光合潛力來區分亞熱帶闊葉樹種的耐陰性，是合理且具有實用性。本研究已建立台灣原生闊葉樹種180種的耐陰性名錄，可供育林、生態復育及景觀植栽參考。

關鍵詞：專家意見、光環境、耐陰性等級、亞熱帶闊葉樹種、光合潛力。

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INTRODUCTION

Shade tolerance, an ecological concept, indicates the ability by which a plant can survive in the deep shade (Walters and Reich 1999). Tree species were classified into 2 functional groups, namely pioneer and non-pioneer, by Swaine and Whitmore (1989). Seeds of non-pioneer species can germinate and their seedlings can thrive under a closed canopy, thereby forming a seedling bank and can survive for years in low-light environments. Conversely, seeds of pioneer species can only germinate in open fields or if several hours of direct sunlight through forest gaps are available. Thus, seedlings of pioneer species cannot grow under a closed canopy. In recent years, researchers have redefined shade tolerance as a capacity for growth in the shade (Niinemets and Valladares 2006), emphasizing not only seedlings survival but also their capability for sustainable growth in low-light environments. For forest management, shade tolerance is also viewed as an important issue. Different levels of shading, either full sunlight or partial shading, are provided to seedlings in nurseries according to their shade-tolerance ability to achieve healthy growth. Forest operations such as establishing coastal stands, rehabilitation of degraded sites, ecological planting in industrial zones, creating multi-story stands, understory planting, and planting after thinning practices, all need to consider the light requirements of planted species. Matching the shade-tolerance ability of each chosen species to light conditions at planting sites will greatly improve the success of forestation.

The shade tolerance of plants was classified into 3 levels as intolerant, intermediate, and tolerant (Walters and Reich 1999, Ellis et al. 2000, Lusk 2004, Craine and Reich 2005), while others classified it into 5 levels as very intolerant, intolerant, moderately tolerant, tolerant, and very tolerant (Baker 1949, Niinemets and Valladares 2006), or even into 9 levels (Humbert et al. 2007). The shade-tolerance ability is usually assessed by the minimum light availability at a site where natural recruits of a species appear in the field (Baker 1949). With reference to experts' experiences or opinions in this aspect, researchers have characterized the shade tolerance of species into different rankings or levels. For example, a study of shrubs and trees in temperate forests of the northern hemisphere (Niinemets and Valladares 2006) and one of understory species of northeastern North America (Humbert et al. 2007) were all based on field experiences of experts. However, this kind of judgment on classifying shade-tolerance levels of a species depends on experts' opinions, which may or may not be accurate, and is relatively subjective. Ellis et al. (2000), by observing population dynamics over decades, classified tree species of a tropical moist forest in Panama into functional types of pioneer, moderate shade tolerance, and shade tolerance, and found that the photosynthetic capacities of the 3 functional types significantly differed. They suggested that physiological traits could be employed as indices for distinguishing tree species of different functional types.

The photosynthetic capacity represents the maximum net photosynthetic rate which a plant can reach when exerting its genetic potential under suitable conditions. It is one of the important functional traits of plants. The photosynthetic capacity positively correlates with some other plant functional traits including the growth rate (Ellis et al. 2000, Poorter and Bongers 2006, Janse-Ten Klooster et al. 2007), specific leaf weight (Reich et al. 2003), and drought tolerance (Lusk 2004, Niinemets and Valladares 2006), while it negatively correlates with the leaf lifespan (Givnish 2002, Reich et al. 1999) and successional status (Koike 1988) of a species. Under either high- or low-light conditions, the photosynthetic capacity of shade-intolerant species is always higher than that of shade-tolerant species (Kitajima 1994, Koike 1988, Walters and Reich 1999, Reich et al. 2003, Valladares and Niinemets 2008). Thus, it is plausible to compare the shade-tolerance abilities of species by assessing the photosynthetic capacity of each species. However, no such reports evaluating shade tolerance by the photosynthetic capacity of woody species have been published. The reason is probably not because photosynthetic capacity is not suitable for evaluation, but rather because it is one of the "hard traits" (Cornelissen et al. 2003) not easy to be measured as compared to other functional traits of leaves. If the photosynthetic capacities of many species were measured in a common garden with consistent environmental conditions, this physiological trait should be able to serve as an objective index for classifying tree species into various shade-tolerance levels.

We planted 180 native broadleaf tree species in a common garden at National Pingtung University of Science and Technology (NPUST). The light-saturated photosynthetic rates of all species under similar microenvironmental conditions were measured to represent the photosynthetic capacity of each species. We now faced a problem: how to decide the threshold values of the photosynthetic capacity for each shade-tolerance level? No such reference values are available for subtropical broadleaf tree species. To resolve this problem, a questionnaire was designed and filled out by 6 experts of dendrology who have years of field experience in Taiwan. The questionnaire inquired about the most likely light environment in the field for natural recruits of each tested species. We then determined suitable threshold values for each shade-tolerance level by compiling these experts' opinions. This could ensure that the shade-tolerance level of a species classified by its photosynthetic capacity was more consistent with experts' classification. This research attempted to establish objective criteria for using the photosynthetic capacity to categorize the shade tolerance of broadleaf tree species in Taiwan.

MATERIALS AND METHODS

Species and tested leaves

The 180 tested species are all native species, with 41 of them endemic species, of Taiwan (as noted in Table 1). These trees were 1~5 yr old with 50~300 cm in height, and were planted in a nursery of the Department of Forestry, NPUST. Chosen leaves for measuring the net photosynthetic rates of a species were mostly located at 50~150 cm in height. The tree crown received several hours of direct sunlight, and the outermost newly matured sun-leaves at the leaf positions of 3~5 were chosen for taking measurements.

Measuring the photosynthetic capacity

Our previous study showed that net photosynthetic rates of trees were significantly lower in dry seasons than in rainy seasons (Kuo et al. 2004). Therefore, measurements of the photosynthetic rate were taken during the rainy season (June to October) of 2009~2014. In order to ensure that each species exerted its full photosynthetic potential, measurements were conducted under optimum environmental conditions (including temperature, humidity, soil water, and light intensity) suitable for the physiological activities of each species. The optimum conditions generally occurred in the early morning before the temperature became too high and the relative humidity became too low (Kuo et al. 2004). Therefore, most measurements were taken at 06:30~10:00. A portable photosynthesis system (LI-6400, LI-COR, Lincoln, NE, USA) was employed. When taking measurements, the concentration of CO_2 was set to 400 μl L^{-1}, the relative humidity to 70~80%, and the block temperature to 28℃. Four individuals of each species were chosen, and the light response of photosynthesis of at least 12 leaves was measured. If the tested species was empirically determined to be a shade-intolerant species, then 1200 μmol photon m^{-2} s^{-1} of light intensity was provided for some time before taking any measurements. Once stabilized, the net photosynthetic rate was recorded for every 200-μmol photon m^{-2} s^{-1} increment in light intensity. If the net photosynthesis measured at a certain light intensity did not increase or even decreased compared to that measured at a previous level of light intensity, the measuring procedure for this particular leaf was considered done. If the tested species was empirically determined to be a shade-tolerant species, then 600 μmol photon m^{-2} s^{-1} of light intensity was the starting point. We then multiplied the highest value of net photosynthetic rate by 0.95 (Man and Lieffers 1997), and treated this value as the light-saturated photosynthetic rate of that particular leaf.

Among the acquired values from 12 tested leaves, we chose the 4 highest measurements that had a coefficient of variation (CV) of < 5% and used the mean to represent the photosynthetic capacity of that species.

Questionnaires of experts

Besides one of the authors, we invited another 5 experts who have years of field experience in dendrology to fill out a questionnaire. This questionnaire asked the experts to choose from the following list of light environments where natural recruits or saplings of each species were most likely to appear. Choices (and hence grading) of light environments included (1) open field; (2) partly shaded open field, forest edge, or large forest gap; (3) slightly shaded and forest edge; (4) mildly shaded understory; and (5) closed canopy. The experts could have multiple answers for each species. If multiple answers were selected by an expert, the grading for that particular species was an average value of the answers. For each species, we then averaged all the experts' grading as its mean score. Some species were graded by only 4 or 5 experts, so not all species had 6 grading samples. Furthermore, an expert's grading of a species was treated as an outlier and not adopted in the mean calculation if the grading was at least 2 rankings away from the mean score of all other experts' grading.

RESULTS

Experts' opinions

After calculation, the minimum mean score of experts' opinions was 1.1 and the maximum was 4.5 (Table 1). We needed to redistribute the calculated mean score into 5 discrete shade-tolerance levels. Taking into consideration the ecological characteristics of these species, we subjectively set the threshold mean scores at 1.5, 2.4, 3.3, and 4.1 in this study. In other words, species with mean scores in the range of 1.0~1.5, 1.6~2.4, 2.5~3.3, 3.4~4.1, and 4.2~5.0, were redistributed as shade-tolerance levels of 1, 2, 3, 4, and 5, respectively. Thus, according to the 6 experts' opinions, numbers of species in each shade tolerance level were 21, 52, 63, 40, and 4, respectively (Fig. 1). The level of differences of the light environment of the same species among the 6 experts could be reflected by the CV of the grading. Only 48 of the 180 species showed a CV of ≦ 20%; some species even showed a CV of > 45%, including *Melanolepis multiglandulosa*, *Alnus formosana*, *Deutzia pulchra*, *Quercus variabilis*, *Gordonia axillaris*, and *Gelonium aequoreum* (Table 1). The high CV values indicated a great variation among experts' opinions, which implied that judging the shade-tolerance ability of a species with one's own experience could be very subjective.

Photosynthetic capacity

The photosynthetic capacities (A_{max}) of the 180 species ranged 9.1~35.8 μmol CO_2 m^{-2} s^{-1} (Table 1). Eight species, including *Hibiscus taiwanensis*, *Melia azedarach*, *Mallotus japonicus*, *Hibiscus tiliaceus*, *Broussonetia papyrifera*, *Macaranga tanarius*, *Melanolepis multiglandulosa* and *Acacia confusa*, had an A_{max} of > 30 μmol CO_2 m^{-2} s^{-1}, and 6 species had an A_{max} of < 10 μmol CO_2 m^{-2} s^{-1}. How did we determine the threshold values of A_{max} for each of the 5 shade-tolerance levels? First, all species were sorted by their A_{max} in descending order. Then, we juxtaposed experts' opinions with the A_{max} list of the 180 species. As shown in Table 1, the top 18 species were classified as level 1 by the experts, and then the following 3 species were classified as level 2. Therefore, we set 26.0 μmol CO_2 m^{-2} s^{-1} of A_{max} as a threshold value. Species

Table 1. Shade-tolerance level of 180 subtropical broadleaf tree species in Taiwan

Species	A_{max} [2]	Experts[3]			ST level[4]		Leaf[5]
		n	Mean	CV%	Exp.	A_{max}	l.f.
1. *Hibiscus taiwanensis* (山芙蓉)[1]	35.8	6	1.1	19	1	1	SD
2. *Melia azedarach* (苦楝)	34.6	6	1.1	19	1	1	D
3. *Mallotus japonicus* (野桐)	34.4	6	1.3	22	1	1	E
4. *Hibiscus tiliaceus* (黃槿)	34.2	6	1.1	19	1	1	E
5. *Broussonetia papyrifera* (構樹)	34.1	6	1.3	33	1	1	SD
6. *Macaranga tanarius* (血桐)	31.9	6	1.2	22	1	1	E
7. *Melanolepis multiglandulosa* (蟲屎)	31.0	6	1.5	52	1	1	D
8. *Acacia confusa* (相思樹)	30.9	6	1.3	22	1	1	E
9. *Mallotus paniculatus* (白匏子)	29.4	6	1.3	22	1	1	E
10. *Tournefortia argentea* (白水木)	28.7	5	1.4	30	1	1	E
11. *Pistacia chinensis* (黃連木)	28.1	6	1.5	30	1	1	SD
12. *Trema orientalis* (山黃麻)	27.7	6	1.3	39	1	1	D
13. *Premna serratifolia* (臭娘子)	27.7	5	1.4	31	1	1	E
14. *Firmiana simplex* (梧桐)	27.4	6	1.3	31	1	1	D
15. *Salix warburgii*(水柳)	26.7	6	1.3	31	1	1	D
16. *Vitex negundo* (黃荊)	26.3	6	1.3	31	1	1	E
17. *Rhus javanica* var. *roxburghiana* (山鹽青)	26.0	6	1.3	33	1	1	D
18. *Sapium discolor* (白桕)	26.0	6	1.4	27	1	1	D
19. *Lagerstroemia subcostata* (九芎)	25.7	6	1.8	28	2	2	D
20. *Zelkova serrata* (櫸木)	25.4	6	1.6	31	2	2	D
21. *Gleditsia rolfei* (恆春皂莢)	25.1	6	1.8	37	2	2	D
22. *Alnus formosana* (台灣赤楊)	24.6	6	1.4	57	1	2	D
23. *Thespesia populnea* (繖楊)	24.6	6	1.6	31	2	2	E
24. *Tetradium glabrifolium* (臭辣樹)	24.5	5	2.0	31	2	2	D
25. *Juglans cathayensis* (野核桃)	24.0	6	1.8	33	2	2	D
26. *Ficus microcarpa* (榕樹)	23.9	5	1.6	26	2	2	E
27. *Terminalia catappa* (欖仁)	23.8	5	1.7	39	2	2	D
28. *Ficus septica* (稜果榕)	23.4	6	1.9	34	2	2	E
29. *Ehretia resinosa* (恆春厚殼樹)	23.3	6	2.1	35	2	2	D
30. *Styrax formosana* (烏皮九芎)	23.3	6	2.1	28	2	2	D
31. *Chionanthus retusus* (流蘇)	23.2	5	2.1	26	2	2	D
32. *Diospyros japonica* (山柿)	23.2	6	2.1	28	2	2	D
33. *Albizia procera* (黃豆樹)	23.0	6	1.8	28	2	2	D
34. *Fraxinus griffithii* (白雞油)	23.0	6	1.6	24	2	2	D
35. *Dendrocnide meyeniana* (咬人狗)	23.0	4	1.9	34	2	2	E
36. *Bischofia javanica* (茄苳)	22.7	6	2.2	40	2	2	SD
37. *Kleinhovia hospita* (克蘭樹)	22.6	6	1.6	37	2	2	D
38. *Excoecaria agallocha* (土沉香)	22.6	5	1.8	32	2	2	E
39. *Bridelia tomentosa* (土密樹)	22.3	5	1.7	26	2	2	D
40. *Glochidion zeylanicum* var. *lanceolatum* (披針葉饅頭果)	22.3	6	2.0	42	2	2	E
41. *Ficus superba* var. *japonica* (雀榕)	22.2	5	1.5	24	1	2	D

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42. *Dodonaea viscose* (車桑子)	22.2	6	1.7	45	2	2	E
43. *Guettarda speciosa* (葛塔德木)	22.1	5	1.7	39	2	2	E
44. *Ficus benjamina* (白榕)	22.0	5	1.8	32	2	2	E
45. *Ficus virgata* (白肉榕)	22.0	5	1.9	39	2	2	E
46. *Deutzia pulchra* (大葉溲疏)	21.8	5	1.5	58	1	2	D
47. *Cyclobalanopsis glauca* (青剛櫟)	21.7	6	1.8	45	2	2	E
48. *Idesia polycarpa* (山桐子)	21.5	6	2.0	32	2	2	D
49. *Cinnamomum camphora* (樟樹)	21.4	6	2.1	28	2	2	E
50. *Diospyros oldhamii* (俄氏柿)	21.4	5	2.4	17	2	2	D
51. *Quercus variabilis* (栓皮櫟)	21.4	6	1.8	47	2	2	D
52. *Quercus aliena* (槲櫟)	21.4	6	1.8	32	2	2	D
53. *Quercus dentata* (槲樹)	21.0	5	2.1	31	2	2	D
54. *Glochidion rubrum* (細葉饅頭果)	21.0	6	1.7	24	2	2	E
55. *Morinda citrifolia* (檄樹)	21.0	5	2.0	35	2	2	E
56. *Calophyllum inophyllum* (瓊崖海棠)	20.4	6	2.7	28	3	3	E
57. *Euscaphis japonica* (野鴨椿)	20.4	6	3.0	15	3	3	D
58. *Acer buergerianum* var. *formosanum* (台灣三角楓)	20.4	5	2.2	34	2	3	D
59. *Cerbera manghas* (海檬果)	20.3	6	2.3	23	2	3	E
60. *Pittosporum pentandrum* (台灣海桐)	20.2	5	2.7	28	3	3	E
61. *Elaeagnus oldhamii* (植梧)	20.2	6	2.1	35	2	3	E
62. *Leea guineensis* (火筒樹)	20.1	5	2.7	21	3	3	E
63. *Ehretia dicksonii* (破布烏)	20.0	6	2.2	28	2	3	D
64. *Wendlandia uvariifolia* (水錦樹)	19.8	5	3.0	31	3	3	E
65. *Rhaphiolepis indica* var. *umbellate* (厚葉石斑木)	19.7	6	1.7	45	2	3	E
66. *Machilus zuihoensis* (香楠)	19.7	6	2.6	19	3	3	E
67. *Margaritaria indica* (紫黃)	19.6	5	2.7	17	3	3	D
68. *Celtis formosana* (石朴)	19.6	6	2.5	25	3	3	D
69. *Allophylus timorensis* (止宮樹)	19.5	5	2.1	35	2	3	E
70. *Gordonia axillaris* (大頭茶)	19.4	6	2.3	48	2	3	E
71. *Sapindus mukorossi* (無患子)	19.4	6	1.9	30	2	3	D
72. *Bretschneidera sinensis* (鐘萼木)	19.2	6	2.4	20	2	3	D
73. *Koelreuteria henryi* (台灣欒樹)	19.1	6	1.9	38	2	3	D
74. *Ficus fistulosa* (水同木)	18.9	6	2.8	17	3	3	E
75. *Pyrus taiwanensis* (台灣野梨)	18.8	5	2.2	34	2	3	D
76. *Rhamnus nakaharae* (中原氏鼠李)	18.7	5	2.8	34	3	3	D
77. *Liquidambar formosana* (楓香)	18.6	6	2.0	27	2	3	D
78. *Decaspermum gracilentum* (十子木)	18.5	5	2.4	18	2	3	E
79. *Eriobotrya deflexa* (恆春山枇杷)	18.4	5	2.6	16	3	3	E
80. *Rhaphiolepis indica* var. *shilanensis* (恆春石斑木)	18.1	6	2.4	36	2	3	E
81. *Neonauclea reticulata* (欖仁舅)	18.1	5	2.6	32	3	3	E
82. *Schima superba* var. *kankaoensis* (港口木荷)	18.0	6	2.5	40	3	3	E
83. *Millettia pinnata* (水黃皮)	18.0	6	2.3	32	2	3	D
84. *Viburnum taitoense* (臺東莢迷)	17.9	6	3.0	24	3	3	E
85. *Quercus glandulifera* (思茅櫧櫟)	17.8	6	2.3	23	2	3	E

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86. *Heritiera littoralis* (銀葉樹)	17.7	6	2.5	30	3	3	E
87. *Lindera akoensis* (內苳子)	17.6	6	2.4	16	2	3	E
88. *Maesa perlaria* var. *formosana* (台灣山桂花)	17.6	5	3.3	30	3	3	E
89. *Palaquium formosanum* (大葉山欖)	17.6	6	2.8	34	3	3	E
90. *Prunus campanulata* (山櫻花)	17.6	6	2.5	22	3	3	D
91. *Michelia compressa* (烏心石)	17.5	6	3.1	24	3	3	E
92. *Beilschmiedia tsangii* (廣東瓊楠)	17.5	6	3.1	19	3	3	E
93. *Cyclobalanopsis pachyloma* (捲斗櫟)	17.4	6	2.9	24	3	3	E
94. *Planchonella obovata* (樹青)	17.4	6	2.7	39	3	3	E
95. *Ilex rotunda* (鐵冬青)	17.4	6	2.9	13	3	3	E
96. *Schefflera octophylla* (江某)	17.4	6	3.1	26	3	3	E
97. *Murraya paniculata* (月橘)	17.3	6	2.7	19	3	3	E
98. *Cyclobalanopsis gilva* (赤皮)	17.3	6	2.8	41	3	3	E
99. *Prunus phaeosticta* (墨點櫻桃)	17.2	6	2.8	25	3	3	E
100. *Hernandia nymphiifolia* (蓮葉桐)	16.9	6	2.5	36	3	3	E
101. *Viburnum odoratissimum* (珊瑚樹)	16.8	6	2.8	29	3	3	E
102. *Michelia compressa* var. *lanyuensis* (蘭嶼烏心石)	16.8	6	2.6	26	3	3	E
103. *Myrica adenophora* (青楊梅)	16.7	6	2.4	36	2	3	E
104. *Litsea hypophaea* (小梗木薑子)	16.7	5	3.3	17	3	3	E
105. *Gardenia jasminoides* (山黃梔)	16.5	5	2.9	31	3	3	E
106. *Acer serrulatum* (青楓)	16.5	6	2.7	23	3	3	D
107. *Melicope triphylla* (假三腳鱉)	16.4	5	2.9	19	3	3	D
108. *Melicope semecarpifolia* (山刈葉)	16.3	5	2.9	26	3	3	D
109. *Phoebe formosana* (台灣雅楠)	16.3	6	3.1	19	3	3	E
110. *Cinnamomum kanehirae* (牛樟)	16.2	6	2.8	33	3	3	E
111. *Cinnamomum insulari-montanum* (台灣肉桂)	16.2	6	2.9	33	3	3	E
112. *Archidendron lucidum* (頷垂豆)	16.1	6	2.8	27	3	3	E
113. *Tabernaemontana subglobosa* (蘭嶼山馬茶)	16.1	5	2.8	20	3	3	E
114. *Barringtonia asiatica* (棋盤腳)	16.1	5	2.5	35	3	3	E
115. *Pourthiaea lucida* (台灣石楠)	16.0	6	2.7	15	3	3	D
116. *Machilus obovatifolia* (恆春楨楠)	15.9	6	3.3	21	3	3	E
117. *Barringtonia racemosa* (穗花棋盤腳)	15.8	6	2.5	38	3	3	E
118. *Aglaia formosana* (紅柴)	15.7	6	2.5	38	3	3	E
119. *Elaeocarpus sylvestris* (杜英)	15.6	6	3.0	24	3	3	E
120. *Fagraea ceilanica* (灰莉)	15.5	5	3.1	29	3	3	E
121. *Crateva adansonii* ssp. *formosensis* (魚木)	15.5	6	2.7	33	3	3	D
122. *Neolitsea buisanensis* f. *sutsuoensis* (石厝新木薑子)	15.4	5	3.3	25	3	3	E
123. *Machilus zuihoensis* var. *mushaensis* (霧社楨楠)	15.1	6	3.1	24	3	3	E
124. *Pasania hancei* var. *ternaticupula* (三斗石櫟)	15.1	6	2.9	33	3	3	E
125. *Ardisia sieboldii* (樹杞)	15.0	6	3.3	26	3	3	E
126. *Machilus japonica* var. *kusanoi* (大葉楠)	14.9	6	3.5	18	4	4	E
127. *Pisonia umbellifera* (皮孫木)	14.7	5	3.5	29	4	4	E
128. *Ardisia elliptica* (蘭嶼樹杞)	14.7	5	3.5	14	4	4	E
129. *Syzygium paucivenium* (疏脈赤楠)	14.7	4	4.1	15	4	4	E

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130. *Engelhardia roxburghiana* (黃杞)	14.7	5	3.5	20	4	4	D
131. *Machilus thunbergii* (紅楠)	14.5	6	3.4	22	4	4	E
132. *Daphniphyllum glaucescens* ssp. *oldhamii* (奧氏虎皮楠)	14.5	5	3.7	18	4	4	E
133. *Camellia brevistyla* (短柱山茶)	14.4	6	3.1	24	3	4	E
134. *Diospyros morrisiana* (山紅柿)	14.4	6	3.3	18	3	4	D
135. *Cinnamomum subavenium* (香桂)	14.3	6	3.3	23	3	4	E
136. *Tricalysia dubia* (狗骨仔)	14.2	6	3.8	11	4	4	E
137. *Castanopsis cuspidata* var. *carlesii* (長尾尖葉櫧)	14.1	6	3.0	28	3	4	E
138. *Neolitsea parvigemma* (小芽新木薑子)	14.1	6	3.4	31	4	4	E
139. *Elaeocarpus japonicus* (薯豆)	14.0	6	3.2	30	3	4	E
140. *Cyclobalanopsis longinux* (錐果櫟)	13.9	5	3.6	18	4	4	E
141. *Cinnamomum brevipedunculatum* (小葉樟)	13.7	5	3.4	15	4	4	E
142. *Gelonium aequoreum* (白樹仔)	13.6	5	2.9	46	3	4	E
143. *Beilschmiedia erythrophloia* (瓊楠)	13.5	6	3.3	18	3	4	E
144. *Castanopsis kawakamii* (大葉苦櫧)	13.3	6	3.3	25	3	4	E
145. *Castanopsis formosana* (台灣苦櫧)	13.3	6	3.0	24	3	4	E
146. *Syzygium kusukusense* (高士佛赤楠)	13.3	5	4.0	11	4	4	E
147. *Sloanea formosana* (猴歡喜)	13.3	5	3.6	12	4	4	D
148. *Reevesia formosana* (台灣梭欏木)	13.2	5	3.7	17	4	4	D
149. *Ternstroemia gymnanthera* (厚皮香)	13.2	6	3.7	17	4	4	E
150. *Aglaia elliptifolia* (大葉樹蘭)	13.1	6	3.3	23	3	4	E
151. *Cyclobalanopsis stenophylloides* (狹葉櫟)	13.0	6	3.3	30	3	4	E
152. *Myrsine seguinii* (大明橘)	12.9	6	4.0	19	4	4	E
153. *Cinnamomum osmophloeum* (土肉桂)	12.8	6	3.5	26	4	4	E
154. *Diospyros eriantha* (軟毛柿)	12.7	6	3.8	16	4	4	E
155. *Goniothalamus amuyon* (恆春哥納香)	12.6	5	3.8	24	4	4	E
156. *Osmanthus marginatus* (小葉木犀)	12.6	6	3.4	35	4	4	E
157. *Distylium gracile* (細葉蚊母樹)	12.6	5	3.4	30	4	4	E
158. *Cryptocarya concinna* (土楠)	12.5	5	3.6	18	4	4	E
159. *Turpinia ternate* (三葉山香圓)	12.3	5	4.3	11	5	5	E
160. *Diospyros philippensis* (毛柿)	12.3	5	4.0	18	4	5	E
161. *Diospyros maritima* (黃心柿)	12.2	6	4.5	10	5	5	E
162. *Diospyros kotoensis* (蘭嶼柿)	12.2	5	4.0	13	4	5	E
163. *Turpinia formosana* (山香圓)	12.2	6	4.1	18	4	5	E
164. *Distylium racemosum* (蚊母樹)	12.1	5	3.4	15	4	5	E
165. *Diospyros ferrea* (象牙樹)	12.0	5	4.2	20	5	5	E
166. *Gonocaryum calleryanum* (柿葉茶茱萸)	11.8	5	3.6	27	4	5	E
167. *Liodendron formosanum* (台灣假黃楊)	11.5	5	3.4	41	4	5	E
168. *Myristica ceylanica* var. *cagayanensis* (蘭嶼肉豆蔻)	11.3	4	4.3	12	5	5	E
169. *Calophyllum blancoi* (蘭嶼胡桐)	11.1	5	3.4	34	4	5	E
170. *Euonymus pallidifolia* (淡綠葉衛矛)	11.1	4	4.0	23	4	5	E
171. *Camellia hengchunensis* (恆春山茶)	10.1	6	3.7	32	4	5	E
172. *Illicium arborescens* (台灣八角)	10.0	6	3.8	18	4	5	E
173. *Syzygium formosanum* (台灣赤楠)	10.0	5	4.0	15	4	5	E

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174. *Syzygium euphlebium* (細脈赤楠)🍂	10.0	5	4.0	15	4	5	E
175. *Drypetes littoralis* (鐵色)	9.5	5	3.7	23	4	5	E
176. *Ormosia hengchuniana* (恆春紅豆樹)🍂	9.5	6	3.5	39	4	5	E
177. *Ormosia formosana* (台灣紅豆樹)🍂	9.4	6	3.5	33	4	5	E
178. *Garcinia multiflora* (福木)	9.3	5	3.9	28	4	5	E
179. *Cryptocarya chinensis* (厚殼桂)	9.1	6	4.1	18	4	5	E
180. *Garcinia subelliptica* (菲島福木)	9.1	5	3.5	25	4	5	E

1) 🍂, endemic species of Taiwan.

2) A_{max}, the photosynthetic capacity (μmol CO_2 m^{-2} s^{-1}) of a species.

3) *n*, the number of grading received; CV, coefficient of variation.

4) ST level, shade-tolerance levels; Exp., experts; A_{max}, photosynthetic capacity.

5) Leaf l.f., leaf life-form: D, deciduous; SD, semi-deciduous; E, evergreen.

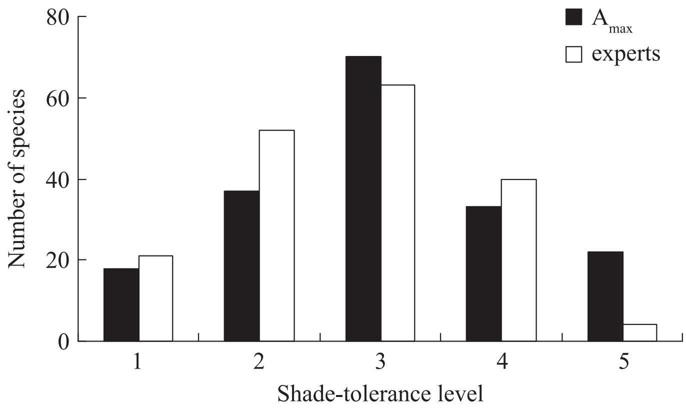

Fig. 1. Numbers of species classified into various shade-tolerance levels according to either the photosynthetic capacity (A_{max}) or experts' opinions for 180 native broadleaf tree species in Taiwan.

having an A_{max} above this value (≧ 26.0 μmol CO_2 m^{-2} s^{-1}) were classified as shade-tolerance level 1. In total, 18 species fit this level. Similarly, we found that after ranking no. 55 of the A_{max} list, experts' opinions began to have species belonging to level 3 (Table 1). Thus, we set this point of A_{max} (21.0 μmol CO_2 m^{-2} s^{-1}) as the second threshold value. Above it, species belonged to level 2. Accordingly, species with an A_{max} in the range of 25.9~21.0 μmol CO_2 m^{-2} s^{-1} were classified as shade-tolerance level 2. In total, 37 species (ranking nos. 19~55) belonged to this level. As classified by the experts, species of shade-tolerance level 3 began from *Calophyllum inophyllum* (ranking no. 56), and level 4 began from *Machilus japonica* var. *kusanoi* (ranking no. 126) (Table 1). Therefore, a corresponding range for level 3 was set at 20.9~15.0 μmol CO_2 m^{-2} s^{-1}. In total, 70 species (ranking nos. 56~125) belonged to this level. However, this range also included 18 species which were classified as level 2 by the experts. Species classified as level 4 by the experts were scattered over ranking nos. 126 to 180. We decided to set the threshold of A_{max} for level 5 at the point where species of level 5 began to appear in the experts' list, which was *Turpinia ternate* (ranking no. 159) (Table 1). Thus, species with an A_{max} in the range of 14.9~12.5 μmol CO_2 m^{-2} s^{-1} were classified as level 4. In total, 33 species (ranking nos. 126~158) belonged to this level. Species with an A_{max} of < 12.5 μmol CO_2 m^{-2} s^{-1} were classified as level 5. In total, 22 species (ranking nos. 159~180) belonged to this level. Conclusively, species with an A_{max} in the ranges of ≧ 26.0, 25.9~21.0, 20.9~15.0, 14.9~12.5, and < 12.5 μmol CO_2 m^{-2} s^{-1} were classified as shade-tolerance levels 1, 2, 3, 4, and 5, which were named very intolerant, intolerant, moderately tolerant, tolerant, and very tolerant, respectively. In this study, there were 18, 37, 70, 33, and 22 species respectively for each shade-tolerance level according to the A_{max} classifications (Fig. 1).

We measured the A_{max} of 180 native broadleaf tree species with same methods under the same environmental conditions in this study. Comparing the results of the A_{max} and mean scores of experts' grading, a significant negative relationship was found (Fig. 2). In addition, there was a positive relationship between shade-tolerance levels classified by the A_{max} and by the experts, with a Pearson correlation coefficient of 0.92. Among the 180 tested species, 131 species (73%) were classified into the same level by the 2 methods while the other 49 species had only a 1-rank difference. Thus, it is reasonable and practical to evaluate the shade-tolerance ability of a species through its A_{max}, a quantified value of important functional traits of plants.

Leaf life-form

The 180 tested species consisted of 124 evergreen, 4 semi-deciduous, and 52 deciduous species. The deciduous species showed an uneven distribution over the 5 shade-tolerance levels. Numbers of deciduous species were 7, 22, and 18 for levels 1, 2, and 3, respectively (Table 1), accounting for 39%, 59%, and 26% of each level. Only 4 deciduous species, *Engelhardia roxburghiana*, *Diospyros morrisiana*, *Sloanea formosana*, and *Reevesia formosana*, were classified as shade-tolerant species (level 4), and none as very tolerant (level 5). This result indicates that shade-tolerant subtropical broadleaf tree species in Taiwan are rarely deciduous.

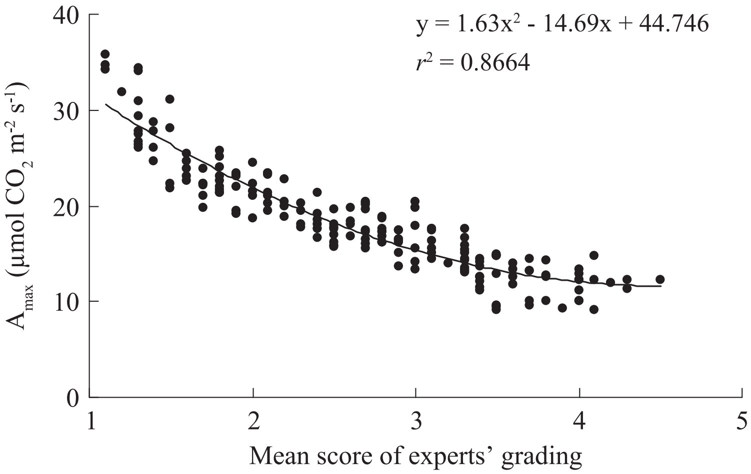

Fig. 2. Relationship between the photosynthetic capacity (A_{max}) of 180 native broadleaf tree species in Taiwan and mean scores of experts' grading for the most likely light environment where natural recruits of a species might appear.

DISCUSSION

The photosynthetic capacity of trees showed a significantly negative relationship with the successional status of the species (Koike 1988, Ellis et al. 2000). A species of an early successional stage had a significantly higher A_{max} than that of the mid or late stages. Shade tolerance of trees also showed a significant relationship with the successional status of the species (Swaine and Whitmore 1989). A species of the late successional stage exhibited higher tolerance to shade, while that of an early stage was shade intolerant. Thus, we can infer from the above relationships that A_{max} is negatively related to the shade tolerance of a species. As confirmed by many studies, shade-intolerant species have higher A_{max} values than shade-tolerant species (Kitajima 1994, Walters and Reich 1999, Valladares and Niinemets 2008). Other studies further indicated that light-saturated photosynthetic rates (or A_{max}) are applicable to determine trees as shade-tolerant or -intolerant species (Ellis et al. 2000, Hallik et al. 2009). These previous studies provided theoretical foundations for employing a quantified physiological trait such as A_{max} to assess the shade tolerance of a species.

However, other literature pointed out that no consistent relationship was found between the A_{max} and shade tolerance of trees (Bassow and Bazzaz 1997, Hallik et al. 2009). Valladares and Niinemets (2008) in their review about shade tolerance stated that the argument of "shade-tolerant species having lower photosynthetic capacity" was challenged. In our opinion, doubts about the relationship between the A_{max} and shade tolerance came mainly from studies of temperate broadleaf species. These species shed their leaves during the winter regardless of whether they are shade-intolerant or -tolerant species. The lifespan of leaves is about 4~6 mo and showed no significant differences among leaves of shade-intolerant, moderately tolerant, and tolerant species (Walters and Reich 1999). Leaves with various shade-tolerant abilities yet with short and similar lifespans, as in the case of temperate broadleaf species, consequently exhibited no significant difference in A_{max} (Walters and Reich 1999, Lusk 2004).

The species tested in this study were subtropical broadleaf tree species. Overall, the major difference between our studied species and the aforementioned temperate broadleaf species lies in the leaf life-form. Our studied species were mainly composed of evergreen species. Among the 180 species, there were 124 (69%) evergreen, 4 semi-deciduous, and only 52 (29%) deciduous species. These deciduous species mostly tended to be shade intolerant (shade-tolerance levels 1, 2, and 3), while shade-tolerant species (shade-tolerance levels 4 and 5) were mostly evergreen. For tropical or subtropical broadleaf tree species, the lifespan of shade-intolerant evergreen or deciduous species (8 mo on average) was proven to be significantly shorter than that of shade-tolerant species (32 mo on average) (Walters and Reich 1999). Studies on plant functional traits of woody species confirmed that leaf lifespan had a significant negative relationship with the photosynthetic capacity (Reich et al. 1999, 2003, Lusk 2004). In the case of tropical or subtropical broadleaf tree species, shade-intolerant species should have higher A_{max} values than shade-tolerant species, since the former have shorter leaf lifespans. The results of our study agreed with this statement. Thus, if temperate deciduous broadleaf species were excluded, a significant negative relationship existed between the A_{max} and shade tolerance of tree species. Using A_{max} of a species to classify the species into different shade-tolerance levels is feasible.

Niinemets and Valladares (2006) assigned shade-tolerance scales (STSs) to 211 woody species of East Asia by means of the reviewing the literature and experts' opinions. They assessed a plant's shade tolerance on a scale from 1 to 5 with higher values being more shade tolerant, the same as in our study. Sixteen species of the 180 tested species in our study were also evaluated in their review. STSs of 10 of the 16 species were consistent with the experts' opinions, as well as the shade-tolerance levels classified by A_{max} in this study. The 10 species were *Mallotus japonicus*, *Pistacia chinensis*, *Rhus javanica* var. *roxburghiana*, *Zelkova serrata*, *Quercus variabilis*, *Quercus dentate*, *Cyclobalanopsis gilva*, *Gardenia jasminoides*, *Ardisia sieboldii*, and *Machilus thunbergii*. Two species, *Acer buergerianum* var. *formosanum* and *Distylium racemosum*, were evaluated to have STSs of 3.0 and 4.25, but were only 2.2 and 3.4 by our experts, which were almost 1 rank difference. However, the shade-tolerance level classified by the A_{max} values of the 2 species in our study agreed with their assessment. On the other hand, another 4 species, including *Alnus formosana*, *Melia azedarach*, *Cyclobalanopsis glauca*, and *Cinnamomum camphora*, had STSs of 2.5, 3.0, 3.25, and 3.5, respectively, in their assessment. And yet these 4 species received gradings of 1.4, 1.1, 1.8, and 2.1 by the experts and shade-tolerance levels 1 or 2 by the A_{max} classification in our study. We suspect that the differences in shade tolerance for these 4 species in the 2 regions may have been a result of different ecotypes, but further investigations are needed.

Few studies have reported tree species showing A_{max} values of > 30 μmol CO_2 m^{-2} s^{-1}, because determining a high A_{max} value would need frequent measurements, plus the physiological characteristics of the species. Ellis et al. (2000) reported 4 pioneer species of a tropical moist forest in Panama, including *Miconia argentea*, *Ochroma pyramidale*, *Cecropia insignis*, and *Trema micrantha*, with high A_{max} values of > 30 μmol CO_2 m^{-2} s^{-1}. Another species, *Ficus insipida*, from the same area also had an A_{max} value of 33 μmol CO_2 m^{-2} s^{-1} (Zotz et al. 1995). In our study, the first 8 species in Table 1 had A_{max} values of > 30 μmol CO_2 m^{-2} s^{-1} with *Hibiscus taiwanensis* reaching as high as 35.8 μmol CO_2 m^{-2} s^{-1}. However, our research was conducted under 400 μl L^{-1} of CO_2 concentration. A_{max} of species in the aforementioned studies were measured under lower concentrations of CO_2 (ambient conditions at that time) and might have higher photosynthetic rates if measured under higher concentrations of CO_2. Our previous research investigated the A_{max} of 30 tree species native to Taiwan. In that report, we classified the 30 species into 3 levels as shade intolerant, moderately tolerant, and tolerant, according to A_{max} value of > 18, 18~12, and < 12 μmol CO_2 m^{-2} s^{-1}, respectively (Kuo et al. 2004). Those measurements were taken under 365 μl L^{-1} of CO_2 concentration, hence lower A_{max} data were acquired and lower threshold values for the 3 shade-tolerance levels were set. If we redistributed the shade tolerance of the 180 species in this study into 3 levels as above, then threshold values of A_{max} could be set to ≧ 21.0, 20.9~15.0, and < 15.0 μmol CO_2 m^{-2} s^{-1}, and with totals of 55, 70, and 55 species in each level. Wright et al. (2003) suggested that only very few species were extremely shade tolerant or extremely light requiring, while most species were moderately shade tolerant. Our results concurred with their opinions.

Net photosynthetic rates of plants are influenced by many environmental factors such as the light intensity, temperature, soil moisture, and relative humidity. In addition, the conductance of stomata affects the supply of CO_2, which indirectly affects net photosynthetic rates of the plant. After years of experience in measuring photosynthesis of trees, we suggest that to acquire higher net photosynthetic rates, measurements should be conducted under higher relative humidity, and that proper sunlight be received by leaves before measuring. After receiving proper sunlight, stomata of leaves will become fully open and enzymes of the photosynthetic systems will be induced. The ideal microclimate condition is to have a rainy day before the measuring day, so that the ambient air and soil are moist. On a sunny measuring day, take the measurement around 06:30~10:00 when the temperature is not > 31℃ and the relative humidity is not < 60%. This study measured A_{max} values of 180 species during the rainy season over 6 consecutive years. We established a database of shade-tolerance levels with objective physiological data for subtropical broadleaf tree species in Taiwan, providing references in forestry and horticulture applications.

CONCLUSIONS

We measured the photosynthetic capacity (A_{max}) of 180 tree species, and set up objective criteria with A_{max} to classify species into various shade-tolerance levels. Species with an A_{max} in the ranges of ≧ 26.0, 25.9~21.0, 20.9~15.0, 14.9~12.5, and < 12.5 μmol CO_2 m^{-2} s^{-1} were classified as shade-tolerance levels 1, 2, 3, 4, and 5, which were named very intolerant, intolerant, moderately tolerant, tolerant, and very tolerant, respectively. Shade-tolerance classifications by means of A_{max} and experts' opinions showed a significantly positive relationship with a Pearson correlation coefficient of 0.92. With these physiological data, we established a database of shade-tolerance levels for 180 native subtropical broadleaf tree species in Taiwan.

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