Research paper

Variations in the Predawn Leaf Water Potential and Photosynthetic Rate during the Dry Season and Drought-Tolerance Mechanisms of Coastal Tree Species

Yau-Lun Kuo,[1,3] Ya-Ping Yang,[1)] Shih-Hsien Peng[2)]

【Summary】

An approximately 6-mon prolonged drought occurs yearly in the Hengchun Peninsula of southern Taiwan. Species capable of establishing themselves in this drought environment should be tolerant to drought either through dehydration postponement or dehydration tolerance. To explore drought adaptations of tree species, we investigated predawn leaf water potentials (PWPs) and values of the net photosynthetic rate (P_n) of 9 native tree species which were established in a secondary forest on the west coast of the Hengchun Peninsula. Results showed that both the PWP and P_n in each species significantly declined during the dry season. The PWP during the dry season was maintained at > -0.9 MPa in *Pittosporum pentandrum*, > -1.5 MPa in *Planchonella obovata*, *Gelonium aequoreum*, and *Melanolepis multiglandulosa*, but < -3.0 MPa in *Aglaia formosana*. The P_n during the dry season was maintained at > 70% of the level during the rainy season in *Hibiscus tiliaceus* and *Pit. pentandrum*, while they were < 50% in *Pla. obovata*, *Gel. aequoreum*, and *Agl. formosana*. A regression analysis was applied to estimate the PWP value of each species when the P_n decreased to 0. It was found that PWP values of *Hib. tiliaceus*, *Allophylus timorensis*, and *Agl. formosana*, were as low as -7.24, -4.57, and -4.40 MPa, respectively, indicating that these 3 species possess high physiological tolerance abilities against drought through dehydration tolerance. During the dry season, few leaves were retained on saplings of *Broussonetia papyrifera*, *All. timorensis*, *Mel. multiglandulosa*, and *Ehretia resinosa*. These species adopted a dehydration-postponement mechanism by shedding most of their leaves. *Pittosporum pentandrum*, *Pla. obovata*, and *Gel. aequoreum*, 3 evergreen species, on the other hand, had extended root systems to enhance soil water absorption, which is also a dehydration-postponement mechanism. The 2 mechanisms are not mutually exclusive, and each species could incorporate various approaches for drought tolerance. *Hibiscus tiliaceus* might also have extended root systems in addition to adopting a dehydration-tolerance mechanism. *Planchonella obovata*, *Bro. papyrifera*, *All. timorensis*, and *Ehr. resinosa* also possessed physiological tolerance abilities in addition to adopting a dehydration-postponement mechanism.

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研究報告

海岸林樹種黎明前葉部水勢及光合作用率在乾季的變化及其耐旱機制

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摘　要

台灣南部恆春半島每年有長達半年的乾季，能在此環境建立的樹種應具備耐旱能力。然而，不同樹種的耐旱機制可能各不相同。林木耐旱機制可分為延遲脫水及忍受脫水兩類，分別可藉由不同方式達成。本研究選取已在恆春西海岸次生林建立的九種原生樹種，測定其黎明前葉部水勢與光合作用率的變化，藉以判斷各樹種可能的耐旱機制。結果發現各樹種在乾季期間，黎明前水勢及光合作用率都顯著較雨季時降低。台灣海桐乾季全期黎明前水勢保持在-0.9 MPa以上，樹青、白樹仔及蟲屎則多在-1.5 MPa以上，但紅柴會降至-3.0 MPa以下。黃槿及台灣海桐在乾季光合作用率可維持雨季時的70%以上，而樹青、白樹仔及紅柴則不到雨季時的一半。藉直線迴歸分析，估算各樹種光合作用率降至零的黎明前水勢。黃槿、止宮樹及紅柴該數值分別低至-7.24、4.57及4.40 MPa，顯示此3樹種有極高的生理耐旱性，具忍受脫水機制。構樹、止宮樹、蟲屎、恒春厚殼樹植株在乾季期間只留存部分葉片，顯示是藉掉落一部分葉片來延遲脫水。常綠樹種台灣海桐、樹青及白樹仔有旺盛的根系，具有延遲脫水機制。此兩類耐旱機制並非互斥，各樹種可兼有不同的耐旱方式。黃槿除了具忍受脫水機制外，可能兼有旺盛的根系。構樹、樹青、止宮樹及恒春厚殼樹除了延遲脫水機制外，另具生理耐旱能力。

關鍵詞：延遲脫水機制、忍受脫水機制、耐旱性、落葉、生理耐性
郭耀綸、楊雅萍、彭世賢。2017。海岸林樹種黎明前葉部水勢及光合作用率在乾季的變化及其耐旱機制。台灣林業科學32(2):131-44。

INTRODUCTION

Drought tolerance is an inherited trait of plants (McDowell et al. 2008). The sensitivity and tolerance for drought greatly vary in different tree species (Niinemets and Valladares 2006, Engelbrecht et al. 2007). As global climate change has become the norm in recent years, the frequency and severity of droughts have also become exacerbated. Some desert short-life herbaceous plants can prevent drought impacts by totally avoiding the dry season in their life cycles (Kozlowski et al. 1991). Perennial woody plants, however, inevitably encounter occasional or recurrent droughts in their lifetimes (Kramer 1983). Mechanisms that plants employ to endure drought can be classified into 2 types:

dehydration postponement and dehydration tolerance (Kramer 1983, Kozlowski et al. 1991), or synonymously desiccation delay and desiccation tolerance (Tyree et al. 2003, Baltzer et al. 2008, Poorter and Markesteijn 2008, Kursar et al. 2009). Dehydration postponement achieves drought tolerance by either increasing water uptake or decreasing water loss. Plants may develop deep and/or extended root systems to increase water uptake, a higher ability for stomatal control, or more water storage organs, or shed leaves to reduce water loss (Kozlowski et al. 1991). For example, *Vitex negundo*, a native species of Hengchun, southern Taiwan, has shallow root systems, but sheds leaves during the dry season to reduce water consumption and grows new leaves soon after the rainy season begins (Kuo 1994). It mainly adopts the mechanism of drought postponement. On the other hand, some plants have a physiological tolerance ability to endure drought or are capable of adjusting the osmotic pressure in leaves to maintain water conductance, gas exchange, and survival of leaf cells under low soil water potentials (Kozlowski et al. 1991, Tyree et al. 2003, Poorter and Markesteijn 2008). Comita and Engelbrecht (2014) reported that the physiological tolerance ability is considered to be the most important trait of drought tolerance. These 2 mechanisms adopted by plants are not mutually exclusive, but rather 1 trait might dominate or groups of traits may cooperate to achieve drought tolerance (Comita and Engelbrecht 2014). For instance, the evergreen tree *Acacia confusa* not only has a deep root system, but also has tough phyllodes which are capable of osmotic adjustment (Kuo 1994), showing traits of both dehydration postponement and dehydration tolerance to endure drought.

To study the drought tolerance of a species, researchers usually monitor the predawn leaf water potential (PWP) of plants. The PWP is a physiological parameter which indicates both the soil water potential around root systems and the leaf water potential at the beginning of daytime (Eamus and Prior 2001, Zhou et al. 2014). As the dry season progresses, soil water is gradually depleted from the surface to lower layers and the PWP of plants decreases in responsive. The net photosynthetic rate (P_n) also declines with a limited availability of soil water. Some species with a physiological tolerance ability, however, can maintain a relatively high P_n (Slot and Poorter 2007). Variations in the P_n with changes in the PWP provide information about the physiological tolerance ability of plants (Zhou et al. 2014).

Most secondary forests on the west coast of the Hengchun Peninsula have been invaded by the exotic species *Leucaena leucocephala*. Even though some native tree species coexist with *Leu. leucocephala* in these forests and have formed mixed stands, *Leu. leucocephala* still dominates these stands. In 2008, an ecological restoration operation was implemented in a coastal forest by cutting *Leu. leucocephala* and planting native tree species to restore the original stand compositions (Chen et al. 2011). However, little was known about the drought-tolerance abilities of these species and the mechanisms adopted to endure a prolonged 6-mon drought in Hengchun every year. Since these native tree species had already established their populations under a drought environment, they must possess some drought tolerance abilities. The objectives of this study were thus to investigate how these species physiologically cope with drought and explore possible drought-tolerance mechanisms adopted by different species. We monitored variations in the PWP and P_n during the dry season of 9 species and compared differences of measurements taken in the dry season and at the beginning of the rainy season for the 2 physiological traits. The justification for the mechanisms each species may adopt was as follows. If a species maintains a high PWP in the dry season, then this species employs the mechanism of dehydration postponement. If the species is an evergreen, then it should have deep and/or extended root systems to obtain sufficient water; if the species is deciduous or semi-deciduous, then it maintains water balance of the entire plant through leaf shedding. On the other hand, if an evergreen without a deep root system shows significant reductions in the PWP during the dry season, it adopts the mechanism of dehydration tolerance to maintain a positive P_n, i.e., it possesses a physiological tolerance ability. Understanding the physiological responses to water stress and the mechanisms of drought tolerance will enhance our ecophysiological knowledge about these species, and provide practical references for ecological restoration of coastal forests.

MATERIALS AND METHODS

Environment of the study site

This study was conducted at Shihchu on the west coast of the Hengchun Peninsula (22°00′08″N, 120°41′48″E) in Kenting National Park, southern Taiwan. The study site is about 60 m from the coastline, adjacent to ecological restoration plots established in 2008 (Chen et al. 2011). It is a coastal area with coral reef landscape. The depth of soil is < 30 cm with a sandy loam to sandy clay loam texture (Wang et al. 2012). According to statistics provided by the Central Weather Bureau, the annual precipitation was 2020 mm and average temperature was 25.1℃ in the Hengchun area from 1981 to 2010. From November to mid-May of the next year is usually the dry season with < 10% of annual rainfall (Fig. 1). Furthermore, a northeasterly monsoon prevails in this area from October to March. Blowing across the Central Mountain Range to the west coast of the Hengchun Pen-

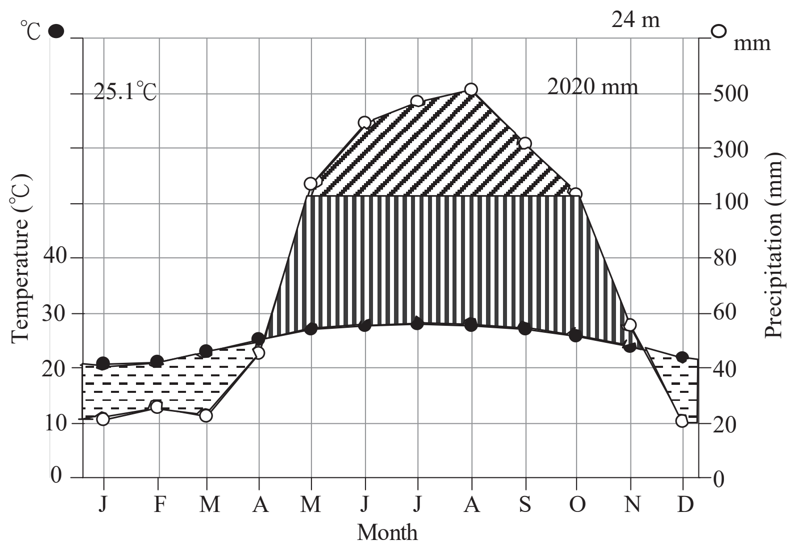

Fig. 1. Climate diagram of Hengchun, southern Taiwan, from 1981 to 2010. It shows an average temperature of 25.1℃ and annual precipitation of 2020 mm in this area. The rainy season runs from May to October each year and the dry season from November to April of the following year.

insula, the monsoon forms a droughty downhill current that dehydrates the air and soil. Moreover, salt stress in seashore areas exerts further adverse effects on coastal plants. Between 14 October 2009 and 22 May 2010, there was 55.8 mm of precipitation. Starting from 23 May 2010, there was 249 mm of precipitation in only 9 d (Fig. 2a), which marked the end of the dry season and the beginning of the rainy season.

Tree species

Nine native tree species are found at the study site, including coastal species *Hibiscus tiliaceus*, *Pittosporum pentandrum*, *Planchonella obovata*, *Allophylus timorensis*, and *Aglaia formosana*, as well as species ubiquitously distributed along the seaside or inland including *Broussonetia papyrifera*, *Melanolepis multiglandulosa*, *Ehretia resinosa*, and *Gelonium aequoreum*. Five individuals of each tested species were sampled. The ground-line diameter of these individuals was within the range of 3~6 cm, and tree heights were mostly 120~300 cm except for larger ones of *Hib. tiliaceus* (Table 1). All sampled individuals were growing in an open environment. The outermost newly matured sun-leaves of each individual were measured for physiological activities. We observed the amount of leaf wilt and estimated the percentage of leaf shedding for each individual tree each measuring day.

Measurements of the PWP

The PWP of each individual was measured periodically from 22 October 2009 (the beginning of the dry season) to July 2010 (rainy season). In total, 19 measuring days were monitored for most tested species except *Hib. tiliaceus* and *Gel. aequoreum*. This was because no sufficient individuals of these 2 species were obtained at the beginning of our experiment, but they were added to our test list in late November 2009 when more individuals were found. These 2 species had only 17 measurements of the PWP. At dawn of each measuring day, a small twig with leaves was cut off from the sampled individual, sealed in a zip lock bag with a damp towel to prevent water loss, and stored in a small fridge prior to measurements. The PWPs of leaves were measured with a pressure chamber (Model 3005, Soilmoisture Equipment Corp., Santa Barbara, CA, USA) within an hour of cutting. For each species, paired t-tests were applied to compare differences between the mean PWP of the dry and rainy seasons for the 5 sampled individuals. An analysis of variance (ANOVA) and Duncan's multiple-range tests were applied to compare interspecific differences for the mean PWPs of the rainy season, dry season, and the 3 lowest measurements, respectively, to examine differences in the water status among tested species.

Measurements of the P_n

Values of the P_n of the 5 sampled individuals of each species were measured periodically from 6 November 2009 to 6 June 2010. In total, 9 measurements were completed for most species except the 2 late enlisted species, *Hib. tiliaceus* and *Gel. aequoreum*, which had only 8 measurements. P_n values were measured between 08:00 and 11:30 on each measuring day with a portable photosynthesis system (LI-6400, LI-COR, Lincoln, NE, USA). When taking a measurement, the CO_2 concentration was set to 400 μl L^{-1}, the relative humidity to 60~80%, the block temperature to 25~30℃, and the light intensity to 800~1700 μmol photon m^{-2} s^{-1} according to the predetermined light saturation points of each species (Yang 2011). For each species, the P_n of the rainy season (represented by the measurement taken on 6 June 2010) and the mean P_n of the dry season for the 5 sampled individuals were compared by paired *t*-tests. Interspecific comparisons were not conducted since the photosynthetic capacities of the 9 tested tree species basically differed (Kuo and Yeh 2015).

RESULTS

Status of leaf shedding

During the dry season, 3 species including *Bro. papyrifera*, *All. timorensis*, and *Ehr. resinosa* showed obvious leaf shedding. The former 2 species shed more than 60% and the latter species about 40% of their leaves before the middle of the dry season. The remaining leaves of *Ehr. resinosa* were mostly infested by insects. Since *All. timorensis* is an evergreen species, leaf shedding induced by water stress could be considered a pseudo-deciduous phenomenon. *Melanolepis multiglandulosa*, a deciduous species, had only about 10 leaves remaining on each individual at the beginning of this experiment and did not further shed during the dry season. *Hibiscus tiliaceus*, *Pit. pentandrum*, *Pla. obovata*, *Gel. aequoreum*, and *Agl. formosana* are evergreen and showed no obvious leaf shedding during the dry season. However, half of the leaves on sampled individuals of the latter 2 species had turned yellow by the middle of the dry season.

PWP

Figure 2 shows the variation patterns of the PWP in each species with reference to the amount of precipitation (Fig. 2a). The PWP of *Pit. pentandrum* fluctuated only in a small range (Fig. 2c), while the PWP of *Agl. formosana* varied the greatest (Fig. 2f). During the dry season, the PWP of many species decreased. This decline was most obvious on 22 January and 5 May (Fig. 2b-j). When rainy events occurred, the PWP of most species increased in responsive but the degree and duration of the increase varied among species. By the beginning of the rainy season in late May 2010, the PWP of all species had risen to a similar level as those at the end of the previous rainy season.

During the rainy season, the mean PWP of each species was between -0.43 and -0.69 MPa. The mean PWP of *Pla. obovata* was significantly higher than those of *Hib. tiliaceus*, *Gel. aequoreum*, and *Agl. formosana* (Table 2). The mean PWP of the entire dry season and the lowest 3 measurements were highest in *Pit. pentandrum* and lowest in *Agl. formosana* (Table 2). Note that the mean PWP of the 3 lowest measurements in *Ehr. resinosa* and *All. timorensis* had decreased to -2.30 MPa and that of *Agl. formosana* had even dropped to as low as -3.39 MPa (Table 2), indicating that these species were suffering severe water stress. For all species, the mean PWP during the rainy season was significantly higher than that during the dry season ($p < 0.001$). *Pittosporum pentandrum* showed the least seasonal difference (0.09 MPa); 5 species had seasonal differences of about 0.5 MPa; *Ehr. resinosa* and *All. timorensis* had seasonal differences of about 1.0 MPa; while *Agl. formosana* had the largest difference of 1.7 MPa (Fig. 3a).

P_n values

The seasonal P_n of all species was low in the dry season and high in the rainy season (Fig. 2b-j). Note that P_n values obtained from each sampled individual were all positive even after a long rainless duration. P_n values of 3 pioneer species, *Hib. tiliaceus*, *Bro. papyrifera*, and *Mel. multiglandulosa*, during the rainy season were all higher than 20.0 µmol CO_2 m^{-2} s^{-1}; those of 5 other species were within the range of 12.0~17.0 µmol CO_2 m^{-2} s^{-1}; and that of *Agl. formosana* was only 6.72 µmol CO_2

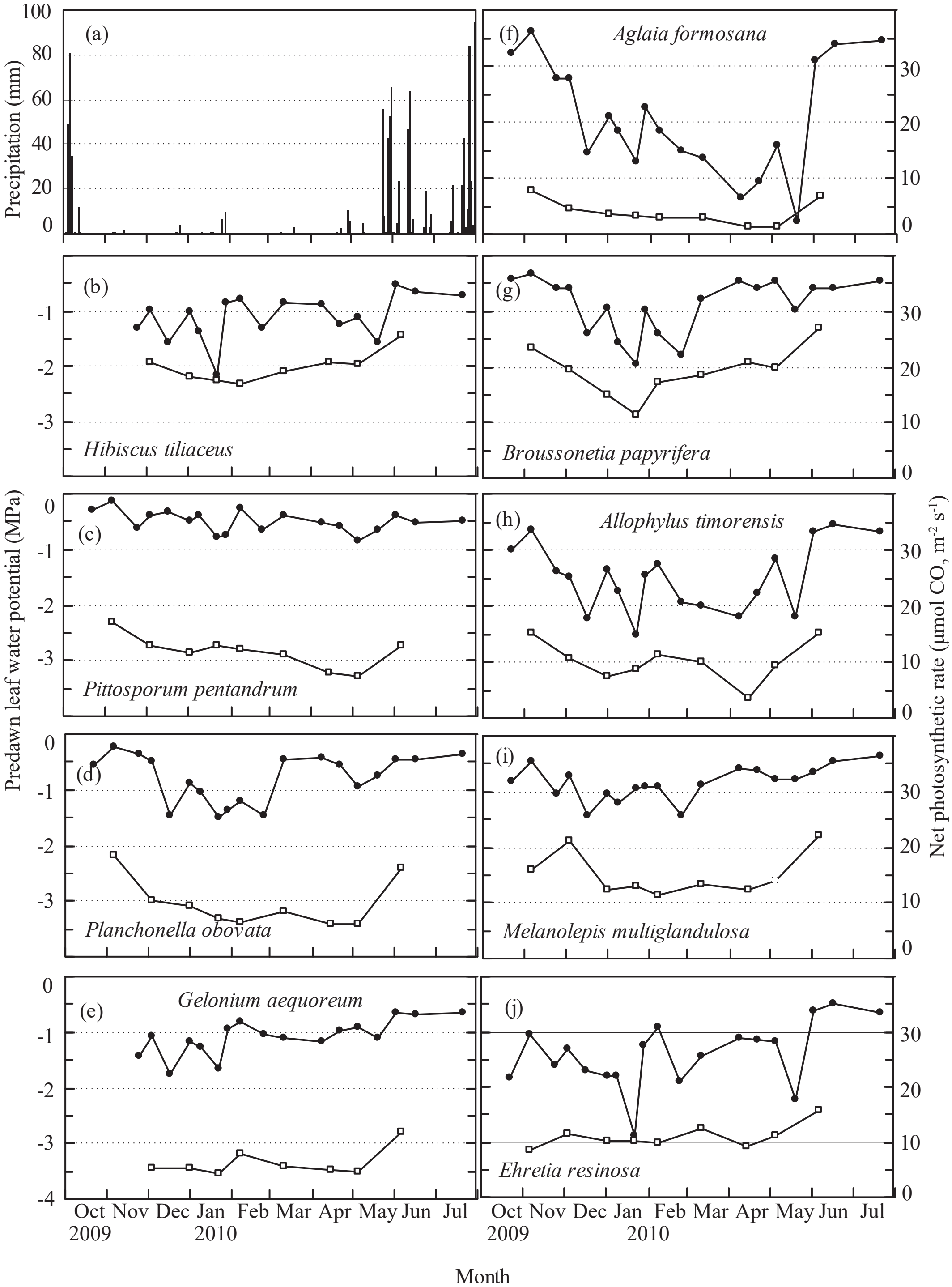

Fig. 2. The amount of precipitation during the experimental period (a) and variations in patterns of the predawn leaf water potential (●) and net photosynthetic rates (□) for 9 tree species (b-j) on the west coast of the Hengchun Peninsula, southern Taiwan.

Table 1. Tree height (HT), ground-line diameter (GLD), crown coverage (Crown), and leaf life form (LLF) of 9 tree species (with abbreviations provided) on the west coast of the Hengchun Peninsula, southern Taiwan (mean±SE, *n* = 5)

Species	Abbr.	HT (cm)	GLD (cm)	Crown (m^2)	LLF
Hibiscus tiliaceus	Ht	356±70	12.4±0.9[1)]	5.23±1.56	E[2)]
Pittosporum pentandrum	Pp	206±15	6.2±1.3	1.48±0.40	E
Planchonella obovata	Po	141±52	3.9±1.6	0.62±0.55	E
Gelonium aequoreum	Ga	258±73	5.9±0.9	1.19±0.40	E
Aglaia formosana	Af	192±13	5.0±0.1	0.84±0.15	E
Broussonetia papyrifera	Bp	148±6	3.4±0.4	0.65±0.25	SD
Allophylus timorensis	At	129±17	4.1±1.1	0.48±0.11	PD
Melanolepis multiglandulosa	Mm	172±41	3.5±1.4	0.57±0.42	D
Ehretia resinosa	Er	273±99	5.4±1 .7	1.08±0.79	D

[1)] Diameter at breast height. [2)] E, evergreen; SD, semi-deciduous; PD, pseudo-deciduous; D, deciduous.

Table 2. Interspecific comparison of the predawn leaf water potential (PWP) in the rainy season, the entire dry season, and the lowest 3 PWP measurements in the dry season (mean±SE, *n* = 3, 14, and 3, respectively)

Species	Rainy season	Entire dry season	Lowest 3
		(MPa)	
Hibiscus tiliaceus	-0.63±0.06 [bc1)]	-1.22±0.10 [bc]	-1.77±0.20 [b]
Pittosporum pentandrum	-0.46±0.03 [ab]	-0.55±0.05 [a]	-0.84±0.03 [a]
Planchonella obovata	-0.43±0.04 [a]	-0.92±0.11 [b]	-1.53±0.07 [b]
Gelonium aequoreum	-0.65±0.01 [bc]	-1.17±0.07 [bc]	-1.62±0.10 [b]
Aglaia formosana	-0.69±0.11 [c]	-2.39±0.20 [d]	-3.39±0.21 [d]
Broussonetia papyrifera	-0.54±0.05 [abc]	-1.03±0.13 [b]	-1.77±0.12 [b]
Allophylus timorensis	-0.63±0.05 [abc]	-1.76±0.11 [c]	-2.30±0.10 [c]
Melanolepis multiglandulosa	-0.48±0.09 [ab]	-0.95±0.07 [b]	-1.37±0.09 [b]
Ehretia resinosa	-0.59±0.05 [abc]	-1.59±0.14 [c]	-2.31±0.31 [c]

[1)] Different letters within a column denote a significant difference at $p < 0.05$.

m^{-2} s^{-1} (Table 3). For all species, the mean P_n was significantly lower during the dry season than during the rainy season (p < 0.001). The seasonal differences in P_n were < 30% in *Pit. pentandrum* and *Hib. tiliaceus*, about 30~45% in *Ehr. resinosa*, *Mel. multiglandulosa*, and *All. timorensis*, and about 55% in *Pla. obovata*, *Gel. aequoreum*, and *Agl. formosana* (Fig. 3b).

Variations in the P_n with changes in the PWP

On the day of taking P_n measurements, we also took PWP measurements in the early morning. Thus, we could observe how the variations in the P_n changed with the PWP using combined data from all individuals of each species (Fig. 4). Some individuals of *Agl. formosana*, *All. timorensis*, and *Ehr. resinosa* maintained a positive P_n even when their PWP values were < -3.0 MPa. With the exception of *Mel. multiglandulosa* and *Ehr. resinosa*, the other 7 species showed significant relationships between the P_n and PWP (Fig. 4).

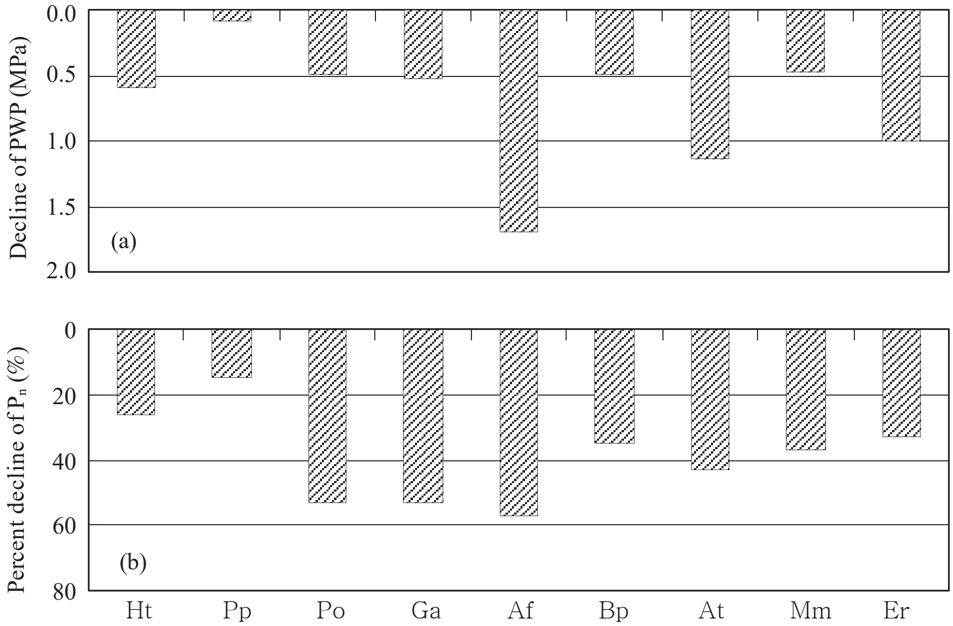

Fig. 3. Differences in the mean predawn leaf water potential (PWP) in the entire dry season compared to that in rainy season (a) and the declining percentage of the net photosynthetic rate (P_n) in the entire dry season compared to that in the rainy season (b). Refer to Table 1 for abbreviations of these species.

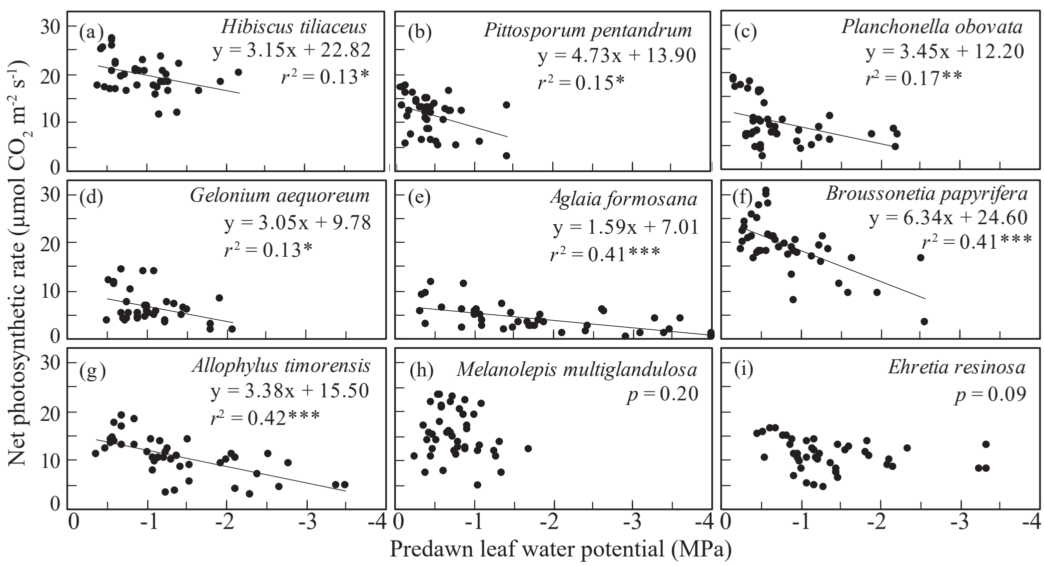

Fig. 4. Variations in the net photosynthetic rate (P_n) with changes in the predawn leaf water potential (PWP) for 9 tree specie on the west coast of the Hengchun Peninsula, southern Taiwan. Each point represents the P_n and PWP values of a sampled individual on a specific measuring day. A linear regression equation is presented if the relationship was significant. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 3. Net photosynthetic rate (P_n) of each species in the rainy season, the entire dry season, and the lowest 3 P_n measurements (mean±SE, *n* = 5)

Species	Rainy season	Entire dry season	Lowest 3
		(μmol CO_2 m^{-2} s^{-1})	
Hibiscus tiliaceus	25.54±0.85	18.91±0.62	17.30±0.44
Pittosporum pentandrum	12.62±0.71	10.67±0.87	8.63±1.21
Planchonella obovata	15.80±0.56	7.44±0.63	6.00±0.12
Gelonium aequoreum	12.04±0.67	5.67±0.42	4.93±0.20
Aglaia formosana	6.72±1.48	2.86±0.45	1.83±0.53
Broussonetia papyrifera	27.12±2.16	17.54±1.25	14.57±1.66
Allophylus timorensis	15.20±1.43	8.70±1.00	6.47±1.53
Melanolepis multiglandulosa	22.14±0.75	13.99±1.24	12.13±0.32
Ehretia resinosa	15.82±0.27	10.60±0.44	9.13±0.38

We assessed PWP values when the P_n had become 0 with a linear regression analysis of the P_n vs. PWP for the 7 species. The estimated PWP was as low as -7.24 MPa for *Hib. tiliaceus*, -4.57 and -4.40 MPa for *All. timorensis* and *Agl. formosana*, -3.88 and -3.54 MPa for *Bro. papyrifera* and *Pla. obovata*, and -3.05 and -2.94 MPa for *Gel. aequoreum* and *Pit. pentandrum*, respectively.

DISCUSSION

The total precipitation from November to April during this research period was only 26% of the 30-yr average in the same period. Obviously, it was a particularly dry season. Under this long water deficit condition, the tested species exhibited their adaptations to a drought environment and differences in their drought-tolerance abilities. The mean PWP of *Pit. pentandrum* during dry season only decreased by 0.09 MPa compared to that in the rainy season, indicating this species did not suffer much water stress. *Hibiscus tiliaceus*, *Pla. obovata*, *Gel. aequoreum*, *Bro. papyrifera*, and *Mel. multiglandulosa* had mean PWP values during the dry season 0.5 MPa less than those in the rainy season, indicating mild or moderate water stress. There are 2 approaches to maintain high levels of leaf water potential during prolonged drought conditions: possessing an extended root system to efficiently absorb soil water, or reducing water loss by shedding leaves (Comita and Engelbrecht 2014, Delzon 2015). Adopting either one of the above approaches to delay severe water stress is so-called dehydration postponement for drought tolerance (Kramer 1983). Among the aforementioned 6 species, *Hib. tiliaceus*, *Pit. pentandrum*, *Pla. obovata*, and *Gel. aequoreum* are evergreen. They do not shed leaves during the dry season; thus these species might possess root systems which are capable of efficiently absorbing soil water. In particular, *Pit. pentandrum* maintained a mean PWP of > -0.9 MPa during severe water deficits. Lin et al. (2014) found that potted 1-yr seedlings of *Pit. pentandrum* allocated more biomass to root systems when experiencing drought stress. Root development is likely an important approach for drought adaptation in *Pit. pentandrum*. However, the soil depth in this coastal study site was only 20~30 cm with coral reef underneath (Wang et al. 2012). Thus, instead of having deep roots, this species might have extended root systems to absorb soil water. The 3 other evergreen species, *Hib. tiliaceus*, *Pla. obo-*

vata and *Gel. aequoreum*, which maintained their PWP values above -1.5 MPa, probably did not have root systems as extensive as *Pit. pentandrum*.

In this study, *Bro. papyrifera*, *Mel. multiglandulosa*, *All. timorensis*, and *Ehr. resinosa* showed different degrees of leaf-shedding. Both *Mel. multiglandulosa* and *Ehr. resinosa* are inherited drought deciduous species. *Broussonetia papyrifera* is considered a drought deciduous species in the karst landscape of southwestern China (Wu et al. 2009, Liu et al. 2011). This species sheds all its leaves of trees that inhabit northern Taiwan, but only 25~50% of leaves for those in southern Taiwan (personal observation), thus it should be a semi-deciduous species. *Allophylus timorensis* is not an inherited deciduous species, but becomes pseudo-deciduous when it encounters severe water stress. This is similar to the leaf behavior observed in *Vit. negundo* (Kuo 1994). The above 4 species showed dehydration postponement through shedding half or most of their leaves to tolerate drought. However, PWP values of *All. timorensis* and *Ehr. resinosa* in the dry season were 1.0 MPa less than those in the rainy season, and some even dropped to < -2.0 MPa, indicating they were experiencing severe water stress. Thus, these 2 species were not as efficient in conserving water as *Bro. papyrifera* and *Mel. multiglandulosa*, which showed a difference of 0.5 MPa between PWP values of the dry and rainy seasons, in maintaining a high water potential by leaf-shedding. Although leaf-shedding is an effective mechanism, it is mostly employed in adult trees and not in young seedlings. Poorter and Markesteijn (2008) suggested that young seedlings have not yet stored enough carbohydrates to cover the expenditure of yearly deciduous costs.

Under a severe water deficiency, some species in this study still maintained a relatively high P_n. *Aglaia formosana* suffered the most severe water deficiency (-3.39 MPa for the mean PWP of the 3 lowest measurements) yet was able to maintain a P_n of > 25% as during the rainy season. Similarly, *All. timorensis* maintained 40% of its P_n, while its mean PWP was -2.30 MPa for the 3 lowest measurements, and *Hib. tiliaceus* maintained 74% of its P_n, while its mean PWP was -1.77 MPa for the 3 lowest measurements. Being capable of maintaining a relatively high P_n even under extremely low PWPs suggests that these 3 species might possess physiological tolerance ability (Ni and Pallardy 1991, Comita and Engelbrecht 2014). They probably adopted a mechanism of dehydration tolerance to endure the prolonged drought. Kursar et al. (2009) found that drought tolerance in seedlings of tropical tree species was mainly determined by their physiological traits. As soil water availability decreased, both the PWP and P_n of plants would decrease accordingly. But for those plants with a higher physiological tolerance ability, the PWP would need to be substantially low in order to have the P_n become 0 (Zhou et al. 2014). Zhou et al. (2014) found that the Ψ_0 (PWP when P_n is 0) of the evergreen *Eucalyptus striaticalyx* growing in a xeric environment of Australia was -5.88 MPa, and 2 other species of eucalyptus had Ψ_0 values of -3.23 and -3.05 MPa. In this study, estimated Ψ_0 values of *Hib. tiliaceus*, *All. timorensis* and *Agl. formosana* were -7.24, -4.57, and -4.40 MPa, respectively, indicating that these 3 species had a very high physiological tolerance to drought. For *Bro. papyrifera* and *Pla. obovata*, estimated Ψ_0 values were -3.88 and -3.54 MPa, respectively. All of the above 5 species likely adopted a mechanism of dehydration tolerance to endure drought. Although the regression analysis of P_n vs. PWP was not statistically significant, *Ehr. resinosa* still had a positive P_n when the PWP was < -3.00 MPa. We considered this species to have physiological tolerance as well.

Maintaining high biodiversity is one of the most effective methods to prevent the invasion of exotic species (Kennedy et al. 2002). However, in stands already invaded by the exotic tree species *Leu. leucocephala*, ecological restoration practices were implemented by cutting *Leu. leucocephala* and replacing it with various native species to restore the stand compositions (Walton 2003, Wang et al. 2009, Chen et al. 2011). Because *Leu. leucocephala* can only grow rapidly under high light conditions, its growing potential is suppressed when shaded. Therefore, when choosing species for restoration practices, the species should include fast-growing pioneers in order to compete with *Leu. leucocephala*, and shade-tolerant species to increase biodiversity and ecological functions of the stands. In this study, *Hib. tiliaceus* and *Bro. papyrifera* were fast-growing pioneers. Their photosynthetic capacity can exceed 34.0 μmol CO_2 m^{-2} s^{-1} under suitable conditions (Kuo and Yeh 2015). *Hibiscus tiliaceus* is an evergreen with a wide spanning canopy which can overcast the new stump sprouts of *Leu. leucocephala*. *Hibiscus tiliaceus* has been planted in southern Taiwan (Wang et al. 2009), northern Taiwan (Kan and Hu 1987), and open coastal areas of Penghu (Lee et al. 1993, Lin et al. 2009) with excellent survival rates and growth performances. *Broussonetia papyrifera* can propagate numerous new stems from root sprouts, grows fast, and possesses good physiological tolerance ability, making it suitable for planting in coastal open sites to inhibit *Leu. leucocephala*. *Pittosporum pentandrum* has high survival rates and good growth performances in coastal areas (Lee et al. 1993, Chen et al. 2011). In this study, we judged that it has extended root systems to facilitate its adaptation to drought conditions in coastal environments, thus it is also an excellent choice for ecological restoration. In addition to the above 3 species, planting the other 6 species can increase species diversity and ecological functions of the restored stands. In addition, *Pit. pentandrum*, *Ehr. resinosa*, and *All. timorensis* can prolifically produce seeds during their juvenile stage, attracting birds and other animals to disperse seeds for natural regeneration (Lee et al. 1993), which is very beneficial for the success of ecological restoration (Tucker et al. 1997).

CONCLUSIONS

The 9 tested species had different approaches of drought-tolerance mechanisms. We determined that *Pit. pentandrum*, *Pla. obovata*, and *Gel. aequoreum* had extended root systems and adopted dehydration postponement as their main mechanism. *Broussonetia papyrifera*, *All. timorensis*, *Mel. multiglandulosa* and *Ehr. resinosa* shed their leaves to achieve dehydration postponement. The other 2 evergreen species, *Hib. tiliaceus* and *Agl. formosana*, had high physiological tolerance abilities with a dehydration-tolerance mechanism. However, some species probably adopted both mechanisms to enhance drought tolerance. For example, *Hib. tiliaceus* might have extended root systems as well; and *Bro. papyrifera*, *Pla. obovata*, *All. timorensis* and *Ehr. resinosa* also possessed traits of physiological tolerance. For ecological restoration operations, *Hib. tiliaceus* and *Bro. papyrifera* can be planted to compete with stump sprouts of *Leu. leucocephala*, while the other species can increase biodiversity and ecological functions of stands.

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