Research paper

# Physiological Drought Tolerance of Tree Species Inhabiting the Ridge of the Kenting Karst Forest

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【Summary】

The topography and tree species compositions significantly differ between the ridge and valley habitats of the Kenting karst forest, southern Taiwan. The objective of this research was to explore how tree species inhabiting the ridge habitat have adapted to the drought environment in terms of physiological traits and leaf morphology. *Drypetes littoralis* and *Aglaia formosana*, 2 species inhabiting the ridge, were investigated for this purpose. As a comparison, *Pisonia umbellifera* and *Melanolepis multiglandulosa*, 2 species inhabiting the valley, as well as *Diospyros maritima* which is distributed in both habitats, were also studied. Results showed that ridge species had a significantly higher leaf mass per area than did valley species. The predawn leaf water potential (PWP) during the dry season was significantly lower than that during the rainy season for each of the 5 species. The net photosynthetic rate ($P_n$) during the dry season was also significantly lower than that during the rainy season for 4 species, with the exception of *P. umbellifera*. During the dry season, the PWP of ridge species *Dry. littoralis* and *A. formosana* decreased to -3.40 and -3.69 MPa, respectively, indicating that these 2 species were suffering severe water stress, while the valley species were experiencing only mild water stress. Yet, these 2 ridge species still maintained positive $P_n$ values at about 46 and 25%, respectively, of the $P_n$ during the rainy season. Individuals of *Dio. maritima* growing in the ridge habitat showed a slightly lower PWP than that of the same species growing in the valley habitat (-1.88 vs. -1.29 MPa) during the dry season, but maintained the $P_n$ at 62% of the $P_n$ during the rainy season. To have their $P_n$ values decline to 0, the PWPs of ridge species *Dry. littoralis*, *A. formosana*, and *Dio. maritima* would need to be as low as -5.89, -4.84, and -5.03 MPa, respectively. The results indicated that these 3 ridge species possessed a high physiological tolerance ability and could adapt to the stressful conditions of strong winds and water deficits in the ridge habitat during the dry season. Individuals of *Dio. maritima* growing in the ridge habitat showed both physiological and morphological acclimation to the drought environment.
**Key words:** drought environment, karst forest, net photosynthetic rate, physiological drought tolerance, predawn leaf water potential.

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研究報告

# 墾丁喀斯特森林礁頂樹種的生理耐旱性

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## 摘　要

墾丁喀斯特森林礁頂及峽谷兩生育地，在地形及樹種組成上有明顯差異。本研究探討長在礁頂的樹種，生理性狀及葉形態如何適應乾燥環境。供試樹種為長在礁頂的鐵色及紅柴，並以長在峽谷的皮孫木及蟲屎，以及兩處均有的黃心柿做比較。結果發現礁頂樹種的比葉重顯著高於峽谷的樹種。供試5樹種乾季的黎明前葉部水勢都顯著低於雨季。除了皮孫木，另4樹種乾季的淨光合作用率也都顯著低於雨季。乾季時鐵色及紅柴的黎明前葉部水勢分別低至-3.40及-3.69 MPa，顯示遭嚴重水逆境，而峽谷樹種僅遭輕微水逆境。乾季時鐵色及紅柴淨光合作用率均仍為正值，分別可維持雨季時的46及25％。長在礁頂的黃心柿，黎明前水勢僅稍低於峽谷的同種植株(-1.88 vs. -1.29 MPa)，淨光合作用率則可維持雨季時的62％。礁頂的鐵色、紅柴及黃心柿，黎明前水勢分別要低至-5.89, -4.84, -5.03 MPa時，淨光合作用率才會降至零。結果顯示此三樹種生理耐旱性強，能適應礁頂生育地乾季時強風且缺水的逆境。此外，礁頂黃心柿植株的生理活動及葉形態兩方面都有馴化乾燥環境的表現。

關鍵詞：乾燥環境、喀斯特森林、淨光合作用率、生理耐旱性、黎明前葉部水勢。

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## INTRODUCTION

At a local scale, topography and micro-habitat gradients of soil water availability are strongly linked, i.e., the lower slope or valley has a higher soil water availability, while the higher slope or ridge top is drier (Daws et al. 2002, Comita and Engelbrecht 2009). This type of variation in soil water availability due to topography would normally cause niche specialization in tropical tree species, and influence the composition of species associations (Tyree et al. 2003, Engelbrecht et al. 2007, Zhang et al. 2010, Liu et al. 2014). Karst forests are a unique ecosystem characterized with thin soil layers and bedrock with high water permeability. Soils have very limited ability to retain water, so that species growing in karst forests frequently suffer severe water stress during the dry season (Fu et al. 2012, Wang et al. 2014, Guo et al. 2017).

Researchers speculated that those species inhabiting the dry and high-light ridge of a karst landscape should possess a higher drought-tolerance ability (Zhang et al. 2010, Wang et al. 2014, Geekiyanage 2017, Guo et al. 2017). However, only a few studies have compared the physiological drought-tolerance abilities or the drought-tolerance mechanisms of species inhabiting different habitats of karst forests (Liu et al. 2011, Fu et al. 2012).

The Kenting Uplifted Coral Reef Nature Reserve, located at the southern tip of Taiwan, has the only karst landscape in Taiwan and forms a unique karst forest (Wang et al. 2004, Wu et al. 2011). After years of leaching, the uplifted coral reefs have become complex habitat mosaics of steep rocky ridges, flat hills, valleys, and depressions. Species associations in the ridge habitat differ greatly from

those in the flat hill and valley habitats (Wang et al. 2004). In this karst forest, trees growing in various habitats receive sufficient water resources during the rainy season. Yet, during the dry season, which normally lasts from November to mid-May of the following year, little precipitation only supplies a minimum amount of water resources. Coupled with the prevailing northeasterly monsoon during this period, the strong, dry wind escalates water loss of plants and the soil surface. As a consequence, water availability in the ridge habitat is gradually depleted during the dry season, exerting severe water stress on plants in the habitat. Do the tree species growing in the ridge habitat possess a high drought-tolerance ability? What kind of drought-tolerance mechanisms do these species adopt to cope with the 6-mo-long water stress? So far, no research has yet answered these questions.

Drought tolerance is a genetic trait of plants and varies in different species (Kozlowski and Pallardy 2002, Lenz et al. 2006, Niinemets and Valladares 2006, Engelbrecht et al. 2007). Drought tolerance of woody species can be achieved by morphological and/or physiological approaches, mainly including 2 mechanisms: dehydration postponement and dehydration tolerance (Kramer 1983, Kolzowski et al. 1991). These 2 mechanisms are not mutually exclusive, but rather 1 trait may dominate or groups of traits may cooperate to achieve drought tolerance (McDowell et al. 2008, Comita and Engelbrecht 2014, Kuo et al. 2017). For example, some species morphologically have deep root systems or a good water-storage ability, or their stomata physiologically have a good controlling ability to reduce transpirational loss of water, or they are deciduous. The above 3 traits are categorized into the mechanism of dehydration postponement (Kramor 1983, Kolzowski et al. 1991). As for the mechanism of dehydra-

tion tolerance, several traits have been discussed as follows. Some species, compared to others, can maintain positive turgor pressure in leaves and perform normal physiological activities under lower water potentials (Kolzowski et al. 1991, Baltzer et al. 2008). The leaf water potential at the turgor loss point ($\pi_{tlp}$) has thus been adopted to quantify the drought-tolerance ability of tree species (Lenz et al. 2006, Blackman et al. 2010, Bartlett et al. 2012). Other research used the lethal leaf water potential as a holistic indicator to determine the dehydration-tolerance ability of tree species (Tyree et al. 2003, Baltzer et al. 2008, Kursar et al. 2009, Comita and Engelbrecht 2014). However, drought tolerance is defined as a plant's ability to maintain positive photosynthesis under conditions of a diminishing water potential (DeLucia and Schlensibger 1991). The water potential which a plant can endure and maintain gas exchange is lower than the $\pi_{tlp}$ (Bartlett et al. 2016). Adopting the leaf water potential (or soil water potential) at which a plant loses its gas exchange ability as an indicator of physiological drought-tolerance ability should be of more significance to the aspect of ecological physiology. Thus in some research, the predawn leaf water potential (PWP) at which the net photosynthesis decreased to 0 ($\Psi_0$) was used to compare the physiological drought-tolerance ability of species (Zhou et al. 2014, Kuo et al. 2017). A lower value of $\Psi_0$ suggests a higher drought-tolerance ability of a species. In the xeric environment of southwest Australia, $\Psi_0$ of the evergreen species *Eucalyptus striaticalyx* was -5.88 MPa, indicating that the species was extremely drought tolerant (Zhou et al. 2014). In the mesic environment of Europe, $\Psi_0$ of 5 evergreen oak tree species were in the range of -1.0 to -1.8 MPa, and that of deciduous species was > -1.0 MPa (Zhou et al. 2014). In coastal forests of Hengchun, southern

Taiwan, $\Psi_0$ values of *Hibiscus tiliaceus*, *Allophylus timorensis*, and *Aglaia formosana* were -7.24, -4.57, and -4.40 MPa, respectively, all showing high physiological drought-tolerance abilities (Kuo et al. 2017). In this study, we used $\Psi_0$ to compare the drought-tolerance ability of the investigated species as well. Comita and Engelbrecht (2014) pointed out that the most important mechanism in determining the drought-tolerance ability of a tropical tree species would be the dehydration tolerance and not the dehydration postponement mechanism, since a drought-tolerant tropical species could tolerate a low water potential, while those species sensitive to drought would have died at a relatively higher water potential.

In the Kenting karst forest, *Drypetes littoralis* and *Aglaia formosana* are 2 dominant species in the ridge habitat; *Pisonia umbellifera* and *Melanolepis multiglandulosa* are 2 dominant species in the valley habitat; and the most abundant species in this forest is *Diospyros maritima*, which is distributed in both habitats (Wang et al. 2004, Wu et al. 2011). The objective of this study was to investigate how tree species growing in the ridge habitat adapted to the microenvironment of strong winds and water deficits during the dry season. We asked 3 questions: (1) Do the species growing in the ridge habitat, including *Dry. littoralis*, *A. formosana*, and *Dio. maritima*, adopt the mechanism of dehydration postponement or dehydration tolerance to endure the drought? (2) Is the drought-tolerance ability of ridge species, i.e., *Dry. littoralis* and *A. formosana*, better than that of valley species, i.e., *P. umbellifera* and *M. multiglandulosa*? (3) Do individuals of *Dio. maritima* growing in the ridge habitat exhibit drought-acclimation performances? And do they have a higher drought-tolerance ability than those of the same species growing in

the valley habitat? For the above questions, we proposed the following hypothesis: (1) Since *Dry. littoralis*, *A. formosana*, and *Dio. maritima* do not shed leaves during the dry season and cannot retrieve soil water through deep root systems from the bottom of the reefs, these species should have adopted the mechanism of dehydration tolerance to cope with the drought environment on the ridge. (2) Since *Dry. littoralis* and *A. formosana* inhabit the drought environment on the ridge, these ridge species should possess better drought-tolerance abilities than valley species which experience much less water stress. (3) Individuals of *Dio. maritima* growing in the ridge habitat should reveal some morphological or physiological acclimation performances to drought, and have a higher drought-tolerance ability than individuals of the same species growing in the valley habitat.

## MATERIALS AND METHODS

### Study site

The study site was located at the Kenting karst forest dynamics plot (120°49'E, 21°57'N) in the Kenting Uplifted Coral Reef Nature Reserve, southern Taiwan. The geology of this area belongs to limestone of Pleistocene age, and is composed of coral, foraminifers, calcareous algae, and shells. According to radiocarbon dating, the Hengchun Peninsula rises at about 2.5 mm $yr^{-1}$ and has become this uplifted reef terrain nowadays after 500,000 yr of formation (Shi et al. 1988). Soil in this area is neutral or slightly acidic sandy loam and light clay of a limey nature (Hseu et al. 2004). The average temperature was 25.1℃ and the annual precipitation was 2020 mm in the Hengchun area from 1981 to 2010, according to statistics provided by the Central Weather Bureau of Taiwan. The Kenting area has distinct dry and rainy seasons.

From mid-May to October is the rainy season, while November to mid-May of the following year is the dry season with < 10% of annual rainfall. Furthermore, a northeasterly monsoon prevails in this area from October to March every year. Flora in the forest dynamics plot is the only intactly preserved natural forest of karst terrain in Taiwan. In total, 95 tree species, with *Dio. maritima* being the most abundant species, were identified by the first re-census of this forest in 2008 (Wu et al. 2011).

**Temperature and wind speed**

An auto-recording anemometer (wind speed/direction smart sensor, S-WCA-M003, Onset Computer, Bourne, MA, USA) and a thermometer (HOBO-Pro series, Onset Computer) were set up in both the ridge and valley habitats to monitor variations in temperature and wind speed at the canopy. In the ridge habitat, the anemometer and thermometer were anchored directly on a rock of similar height as the canopy of ridge species. In the valley habitat, the anemometer and thermometer were securely fastened to the tip of a steel pole of similar height as the canopy of valley species. Average temperature was recorded every 30 min and average wind speed every 10 s from 18 December 2009 to 5 July 2010.

**Tree species**

In total, 5 species were investigated, including *Dry. littoralis* and *A. formosana*, 2 dominant species on the ridge, *P. umbellifera* and *M. multiglandulosa*, 2 dominant species in the valley, as well as *Dio. maritima*, a species that thrives in both habitats. For *Dry. littoralis*, *A. formosana*, and *Dio. maritima* growing in the ridge habitat, 7 individuals each of 5~8 m in height and 12~18 cm in diameter at breast height (DBH) were sampled. The ridge top was about 18~24

m above the ground. For *P. umbellifera*, *M. multiglandulosa* and *Dio. maritima* growing in the valley habitat, 7 individuals each were sampled as well. Individuals of *P. umbellifera* were 11~14 m in height and 27~37 cm in DBH, individuals of *M. multiglandulosa* were 9~12 m in height and 22~29 cm in DBH, and individuals of *Dio. maritima* in the valley were 9~12 m in height but smaller at only 11~17 cm in DBH. All sampled individuals could receive direct sunlight at the canopy level.

**Measurement of leaf traits**

For each sampled individual, 3 mature sun-leaves at the top of the canopy were selected to measure leaf traits. The selected leaves were picked in the morning, sealed in a bag with a damp paper towel, and stored in an ice bucket for later measurement in the afternoon. The leaf fresh weight was measured after the petiole was removed. To calculate the leaf area, we used a micrometer to measure the leaf thickness on both sides of the midrib, digitalized the leaf image using a scanner (GT-2500, Epson, Long Barch, CA, USA) and computed the leaf area with the software "Image processing and analysis in Java, Image J." The sampled leaf was subsequently placed in an oven at 60℃ for drying out, and then the leaf dry weight was measured. The leaf mass per area was calculated by dividing the leaf dry weight by the leaf area. The water content of the leaf was calculated by deducting the leaf dry weight from the leaf fresh weight and then dividing by the leaf dry weight.

**Measurement of the predawn leaf water potential (PWP)**

The PWP of a species represents the water status and soil water potential around root systems of that species on the measuring day,

indicating the level of water stress experienced by that species (Eamus and Prior 2001, Zhou et al. 2014, Kuo et al. 2017). During the dry season, measurements of PWP were taken on 10 and 28 April and 13 May 2010; during the rainy season, measurements of PWP were taken once in each month of July, August, and October. At 05:00~07:00 each measuring day, the research teams (with 1 team on the ridge and 1 team in the valley) cut 2 branches out of the tree crown of each sampled individual. One mature healthy leaf at the tip of each branch was picked, placed into a sealed bag with a damp paper towel, and stored in an ice bucket to decelerate dehydration. PWP values of the 2 leaves were subsequently measured in the field with a pressure chamber (Model 3005, Soilmoisture Equipment, Santa Barbara, CA, USA). The 2 PWP values were then averaged to represent the water status of the sampled individual on that measuring day.

## Measurement of the net photosynthetic rate ($P_n$)

The $P_n$ of each sampled individual was measured at 08:00~11:00 on the same day that the PWP was measured. Due to the height of sampled individuals, we were unable to take direct measurements in the tree crown. As an alternative, a branch from the tree crown was cut and inserted in a water vase; then 1 mature healthy leaf from the branch was selected to measure the $P_n$. This procedure was repeated with another branch of the same individual. A portable photosynthesis system (LI-6400, LI-COR, Lincoln, NE, USA) was employed to measure the $P_n$. When taking the measurements, the light intensity was set to 1200 μmol photon $m^{-2} s^{-1}$, $CO_2$ to 400 μl $L^{-1}$, temperature to 22~25℃ (according to the season), and relative humidity to 60~80%. The 2 $P_n$ values were then averaged to represent the

photosynthetic rate of the sampled individual on that measuring day.

## Statistical analysis

Differences in the monthly mean temperature, monthly mean maximum temperature, monthly mean minimum temperature, daily mean wind speed, and daily maximum wind speed were compared between the ridge and valley habitats with a *t*-test at a significance level of 0.05. Differences in the PWP and $P_n$ of each species between the dry and rainy seasons were also compared with a *t*-test at a significance level of 0.05. With respect to the dry and rainy seasons, an analysis of variance (ANOVA) was applied to compare the PWP, $P_n$, leaf thickness, and leaf mass per area among the species. If the result of the ANOVA was significant, then Duncan's multiple-range tests were further applied to specify the difference among species.

## RESULTS

### Wind speed and temperature

The northeasterly monsoon directly blows upon the ridge. Thus, wind speed in the ridge habitat was clearly higher than that in the valley habitat which is surrounded by outcrops of reefs. From December 2009 to June of the following year, the daily mean wind speed and daily maximum wind speed in the ridge habitat were both significantly higher than those in the valley habitat (Fig. 1). The highest monthly mean wind speed (2.94 m $s^{-1}$) and the highest monthly mean maximum wind speed (11.13 m $s^{-1}$) in the ridge habitat were recorded in January with the highest wind speed reaching 16.8 m $s^{-1}$ on 25 January 2010. As to temperature, no significant differences in the monthly mean temperature each month or the monthly mean minimum temperature were observed between the 2 habi-
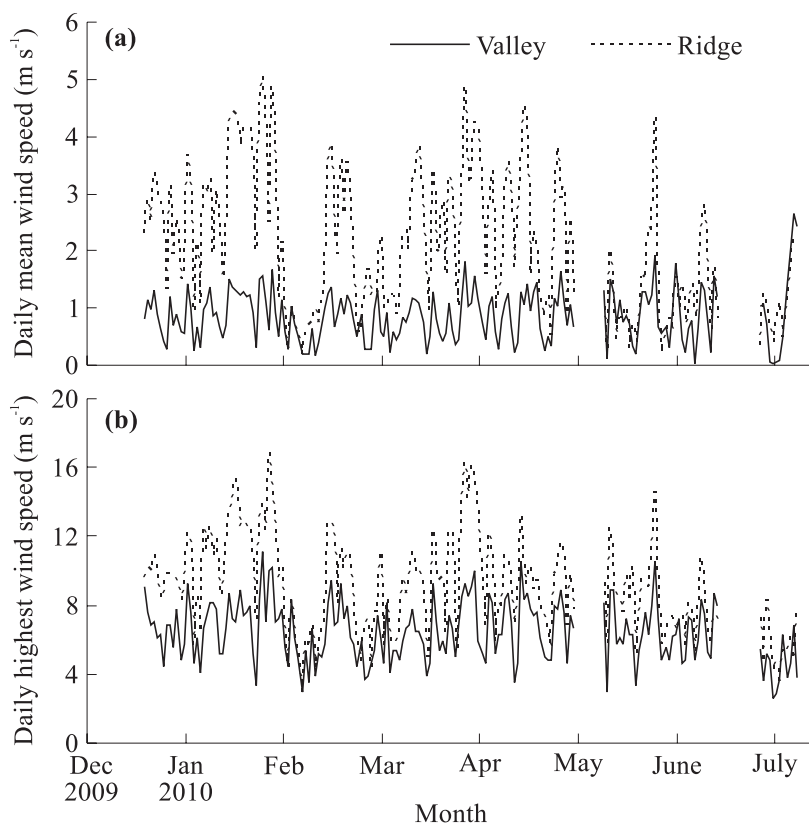
**Fig. 1. Daily mean (a) and daily maximum (b) wind speed in the ridge and valley habitats of the Kenting karst forest.**

tats from January to April 2010. However, the ridge habitat did show significantly higher monthly mean maximum temperatures than the valley habitat (Table 1).

**Leaf traits**

For leaf thickness, *Dry. littoralis* had the thickest leaf, followed by *Dio. maritima* in the ridge habitat, and *M. multiglandulosa* had the thinnest (Table 2). Values of the leaf mass per area of *Dry. littoralis*, *A. formosana*, and *Dio. maritima* in the ridge habitat were 14.99, 14.50, and 14.31 mg cm$^{-2}$, respectively, which were significantly higher than those of *P. umbellifera*, *M. multiglandulosa*, and *Dio. maritima* in the valley habitat (all < 10.0 mg cm$^{-2}$) (Table 2).

**PWP values**

During the most severe drought months of April and May, PWP values of the ridge species *Dry. littoralis* and *A. formosana* were all < -3.0 MPa with mean PWP values of -3.40 and -3.69 MPa, respectively (Table 3). The PWP of *Dio. maritima* growing in the ridge habitat was significantly higher than that of *Dry. littoralis* and *A. formosana*, but significantly lower than that of the same species growing in the valley habitat (-1.88 vs. -1.29 MPa) (Table 3). PWP values of the valley species *P. umbellifera* and *M. multiglandulosa* reached -0.69 and -0.91 MPa, respectively, and were significantly higher than those of the other 3 species (Table 3). During the rainy season, PWP values of each species increased

**Table 1. Comparisons of the monthly mean temperature ($T_{mean}$), monthly mean maximum temperature ($T_{max}$) and minimum temperature ($T_{min}$) of the dry season, 2010, between the ridge and valley habitats in the Kenting karst forest (mean ± SD)**

| Month | $T_{mean}$ (℃) | | $T_{max}$ (℃) | | $T_{min}$ (℃) | |
|---|---|---|---|---|---|---|
| | Ridge | Valley | Ridge | Valley | Ridge | Valley |
| Jan. | 18.8±1.91 | 18.5±1.74 | 22.7±2.50 | 21.6±2.35 | 16.5±1.71 | 16.6±1.54 |
| Feb. | 20.8±2.25 | 20.5±2.34 | 25.0±2.84 | 24.3±2.90 | 18.2±2.37 | 18.3±2.33 |
| Mar. | 21.2±2.78 | 21.1±2.81 | 25.2±3.61 | 24.9±3.57 | 18.5±2.80 | 18.6±2.75 |
| Apr. | 21.4±1.89 | 21.2±1.93 | 25.0±3.20 | 24.9±3.27 | 18.7±1.26 | 18.8±1.30 |
| Mean | 20.6±0.6[a1)] | 20.3±0.6[a] | 24.5±0.6[a] | 23.9±0.8[b] | 18.0±0.5[a] | 18.1±0.5[a] |

[1)] Different letters between ridge and valley habitats denote a significant difference by the *t*-test at $p <$ 0.05.

**Table 2. Interspecific comparisons of the leaf thickness, leaf mass per area (LMA), leaf area (LA), and leaf water content (WC) of tree species growing in the ridge or valley habitats of the Kenting karst forest (mean ± SD, *n* = 6)**

| Leaf trait | Ridge habitat | | | Valley habitat | | |
|---|---|---|---|---|---|---|
| | Dl[1)] | Af | Dm | Pu | Mm | Dm |
| Thickness (mm) | 0.45±0.06[a2)] | 0.27±0.06[c] | 0.39±0.08[b] | 0.33±0.08[c] | 0.10±0.02[d] | 0.26±0.10[c] |
| LMA (mg cm$^{-2}$) | 14.99±3.9[a] | 14.50±1.3[a] | 14.31±2.3[a] | 8.32±1.9[c] | 6.00±1.5[d] | 9.64±0.4[b] |
| LA (cm$^2$) | 16.0±5.2[d] | 26.6±8.8[c] | 26.8±4.7[c] | 109.7±27.3[b] | 142.8±54.6[a] | 22.3±5.6[c] |
| WC (%) | 58±5 | 55±2 | 56±2 | 80±3 | 66±7 | 59±2 |

[1)] Abbreviations for each species: Dl, *Drypetes littoralis*; Af, *Aglaia formosana*; Dm, *Diospyros maritima*; Pu, *Pisonia umbellifera*; Mm, *Melanolepis multiglandulosa*.

[2)] Different letters in each trait among the species denote a significant difference by Duncan's test at *p* < 0.05.

to -0.24 to -0.56 MPa and showed no significant differences among the 5 species. However, PWP values during the rainy season were all significantly higher than those during the dry season in each of the 5 respective species (Table 3). Compared to PWP values during the rainy season, PWP values during the dry season of the ridge species *Dry. littoralis* and *A. formosana* decreased 2.76 and 3.13 MPa, respectively, and that of *Dio. maritima* growing in the ridge habitat decreased 1.33 MPa; while PWP values only decreased 0.45, 0.42, and 0.86 MPa, respectively, for *P. umbellifera*, *M. multiglandulosa*, and *Dio. maritima* growing in the valley habitat (Fig. 2a). The results indicated that during the dry season,

species growing in the ridge environment suffered more-severe water stress than did species growing in the valley. As demonstrated by the same species of *Dio. maritima*, individuals on the ridge experienced more-severe water stress than those in the valley during the dry season.

**$P_n$ values**

$P_n$ values during the dry season of *Dry. littoralis*, *A. formosana*, and *Dio. maritima* growing in the ridge habitat were all significantly lower than those during the rainy season (Table 4). $P_n$ values during the dry season of *M. multiglandulosa* and *Dio. maritima* growing in the valley habitat were

**Table 3. Interspecific comparisons of the predawn leaf water potential (MPa) of tree species growing in the ridge or valley habitats of the Kenting karst forest during the dry and rainy seasons of 2010 (mean±SD, $n$ = 7)**

| | Ridge habitat | | | Valley habitat | | |
|---|---|---|---|---|---|---|
| | Dl[1] | Af | Dm | Pu | Mm | Dm |
| Dry season | | | | | | |
| Apr 10 | -3.14±0.69 | -3.41±0.47 | -1.88±0.31 | -0.77±0.26 | -0.94±0.22 | -1.42±0.43 |
| Apr 28 | -3.35±0.52 | -3.68±0.33 | -1.93±0.44 | -0.71±0.25 | -0.82±0.15 | -1.27±0.38 |
| May 13 | -3.70±0.24 | -3.98±0.01 | -1.83±0.54 | -0.59±0.22 | -0.99±0.19 | -1.17±0.25 |
| Mean | -3.40±0.28[d2] | -3.69±0.28[d] | -1.88±0.05[c] | -0.69±0.09[a] | -0.91±0.08[a] | -1.29±0.12[b] |
| Rainy season | | | | | | |
| July 19 | -0.35±0.54 | -0.38±0.45 | -0.27±0.10 | -0.25±0.05 | -0.32±0.07 | -0.38±0.06 |
| Aug 4 | -0.89±0.07 | -0.71±0.16 | -0.77±0.14 | -0.38±0.05 | -0.47±0.08 | -0.40±0.07 |
| Oct 1 | -0.60±0.15 | -0.59±0.10 | -0.60±0.08 | -0.10±0.07 | -0.69±0.05 | -0.51±0.11 |
| Mean | -0.64±0.25[a] | -0.56±0.16[a] | -0.55±0.25[a] | -0.24±0.14[a] | -0.49±0.18[a] | -0.43±0.07[a] |
| Seasonal comparison | ***[3] | *** | ** | ** | * | *** |

[1] Refer to Table 2 for the abbreviation of each species.

[2] Different letters among the species within the same season denote a significant difference by Duncan's test at $p < 0.05$.

[3] Significant level for comparing a same species in different season by the $t$-test, *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.
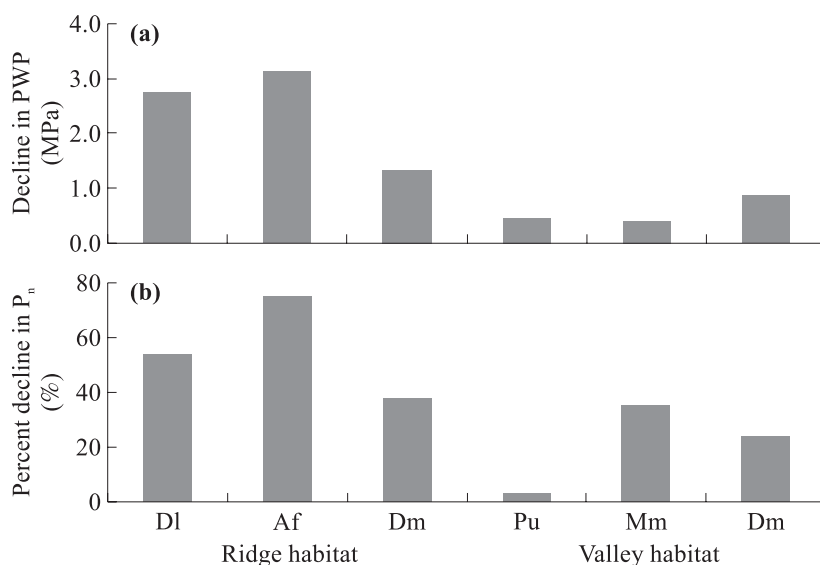


**Fig. 2. Differences in the mean predawn leaf water potential (PWP) during the dry season compared to that during the rainy season (a) and the declining percentage of the net photosynthetic rate ($P_n$) during the dry season compared to that during the rainy season (b) of species in the ridge and the valley habitats of Kenting karst forest. Refer to Table 2 for the abbreviation of each species.**

**Table 4. Interspecific comparisons of the net photosynthetic rate (µmol $CO_2$ m$^{-2}$ s$^{-1}$) of tree species growing in the ridge or valley habitats of the Kenting karst forest during the dry and rainy seasons of 2010 (mean±SD, $n$ = 7)**

| | Ridge habitat | | | Valley habitat | | |
|---|---|---|---|---|---|---|
| | Dl[1] | Af | Dm | Pu | Mm | Dm |
| **Dry season** | | | | | | |
| Apr 10 | 3.41±1.63 | 2.43±0.99 | 5.69±1.54 | 9.60±3.74 | 11.87±3.06 | 9.26±1.33 |
| Apr 28 | 2.98±1.12 | 1.37±0.50 | 5.15±1.17 | 9.48±1.50 | 12.37±2.71 | 7.17±0.87 |
| May 13 | 3.28±1.64 | 2.63±0.69 | 5.92±1.35 | 11.72±2.42 | 7.87±4.06 | 8.01±1.99 |
| Mean | 3.22±0.42[d2] | 2.14±0.67[d] | 5.58±0.39[c] | 10.27±1.25[ab] | 10.70±2.46[a] | 8.14±1.05[b] |
| **Rainy season** | | | | | | |
| July 19 | 6.69±0.94 | 8.49±1.08 | 7.80±0.86 | 10.03±2.19 | 15.54±3.25 | 10.66±0.80 |
| Aug 4 | 7.57±0.50 | 8.86±0.78 | 8.99±0.91 | 12.39±3.09 | 13.13±1.62 | 10.60±1.47 |
| Oct 1 | 6.74±0.51 | 8.18±0.83 | 10.10±1.25 | 9.45±1.31 | 20.71±2.64 | 10.93±1.38 |
| Mean | 6.99±0.49[c] | 8.59±0.34[bc] | 8.96±1.15[bc] | 10.62±1.55[b] | 16.48±3.87[a] | 10.73±0.17[b] |
| Seasonal comparison | ***[3] | *** | * | NS | * | * |

[1] Refer to Table 2 for the abbreviation of each species.

[2] Different letters among the species within the same season denote a significant difference by Duncan's test at $p < 0.05$.

[3] Significant level for comparing the same species in different seasons by the $t$-test, *** $p < 0.001$; * $p < 0.05$.

also significantly lower than those during the rainy season. However, no significant difference between $P_n$ values in the 2 seasons was found for *P. umbellifera* (Table 4), a different result from the other 4 species. During the dry season, $P_n$ values of *Dry. littoralis* and *A. formosana* were maintained at very low levels of mean $P_n$ of 3.22 and 2.14 µmol $CO_2$ m$^{-2}$ s$^{-1}$, respectively, which were significantly lower than the $P_n$ of *Dio. maritima* growing in the ridge habitat and even much lower than $P_n$ values of valley species (Table 4). Comparing within the same species of *Dio. maritima*, the $P_n$ of individuals growing in the ridge habitat was significantly lower than that of plants growing in the valley habitat during the dry season (5.58 vs. 8.14 µmol $CO_2$ m$^{-2}$ s$^{-1}$); yet, no significant difference was observed during the rainy season (Table 4).

Comparing $P_n$ values during the dry and rainy seasons, the ridge species exhibited distinct differences, while the valley species showed relatively smaller differences. $P_n$ values during the dry season of *Dry. littoralis* and *A. formosana* declined 54 and 75%, respectively, of $P_n$ values during the rainy season; yet, the decreased amounts were only 3 and 35%, respectively, for *P. umbellifera* and *M. multiglandulosa* (Fig. 2b). For the same species of *Dio. maritima*, $P_n$ values during the dry season of individuals in the ridge and valley habitats respectively decreased 48 and 24% compared to the rainy season (Fig. 2b). These results indicated that during the dry season, ridge species suffered more-severe water stress than did valley species and consequently had a larger degree of decrease in the $P_n$.

**Variations in the $P_n$ with changes in the PWP**

At the dawn of the day when we measured the $P_n$ of a sampled individual, we

also monitored the PWP of that individual. Combining the $P_n$ and PWP data obtained for the 7 sampled individuals of each species on every measurement day, we acquired variations in the $P_n$ with changes in the PWP for each species (Fig. 3). Results showed that $P_n$ values of *Dry. littoralis* and *A. formosana* still remained positive even under the condition of a PWP of < -3.00 MPa. With the exception of *P. umbellifera*, significant or extremely significant relationships between $P_n$ and PWP were found in the other 4 species (Fig. 3). Estimated by a linear regression of the PWP vs. $P_n$, PWP values when $P_n = 0$ ($\Psi_0$) were as low as -5.89 and -4.84 MPa, respectively, for *Dry. littoralis* and *A. formosana*, -2.74 MPa for *M. multiglandulosa*, and -5.03 and -4.22 MPa, respectively, for *Dio. maritima* growing in the ridge and valley habitats. The above results indicated that ridge species had higher physiological drought-tolerance abilities than did valley species. Individuals of *Dio. maritima* growing in the ridge habitat exhibited accli-

mation performances to the drought environment in the aspect of physiological drought tolerance.

## DISCUSSION

In karst forests, the effect of soil depth on water availability can determine not only seedling persistence (Lin et al. 2016) but also species-habitat associations of tree species (Guo et al. 2017). A deeper soil profile can accumulate a larger amount of soil water, thus providing more sufficient water resources for plants. In this study, the soil depth in the valley habitat was substantially deeper than that in the ridge habitat. The A horizon of the soil profile was 14 cm and the B horizon reached 150~200 cm below the soil surface in the valley habitat, while in the ridge habitat the A horizon was only 5 cm and B horizon only 40~60 cm at a sampling site with deeper soil (Hseu et al. 2004). The valley habitat might be able to retain soil water at a
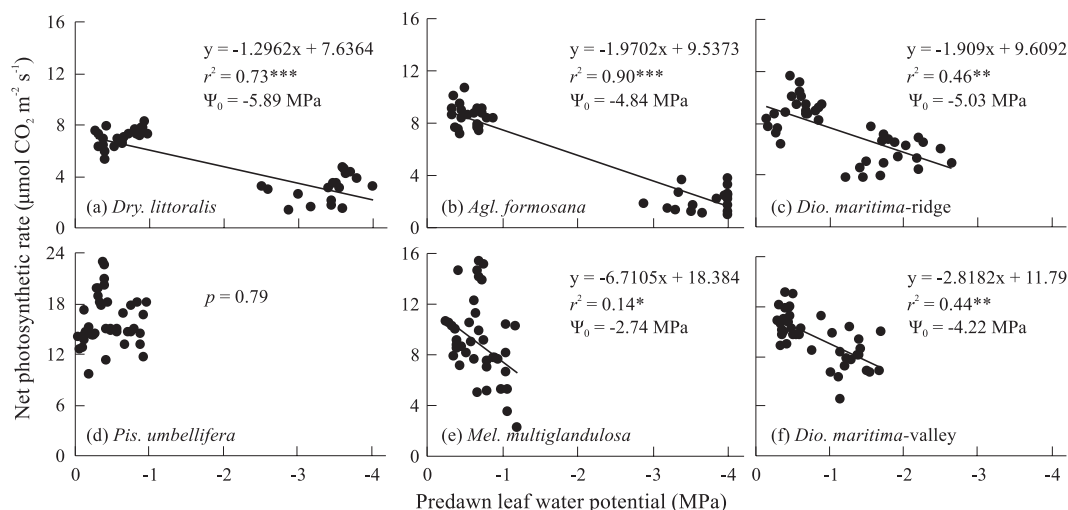


Fig. 3. Variations in the net photosynthetic rate ($P_n$) with changes in the predawn leaf water potential (PWP) of tested species in the Kenting karst forest. Each point represents the $P_n$ and PWP values of the same individual on a specific measuring day. A linear regression equation is presented if the relationship was significant. *Dry.*, *Drypetes*; *Agl.*, *Aglaia*; *Dio.*, *Diospyros*; *Pis.*, *Pisonia*; *Mel.*, *Melanolepis*. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

relatively higher level during the dry season than the ridge habitat, so that the valley species *P. umbellifera* and *M. multiglandulosa* could maintain mean PWP values at high levels of -0.69 and -0.91 MPa, respectively, which indicated that these species were experiencing only mild water stress. However, individuals of *Dio. maritima* growing in the valley habitat showed a significantly lower mean PWP (-1.29 MPa) than the above 2 valley species (Table 3). Growing in the same habitat with deep soil, why was the PWP of *Dio. maritima* significantly lower than that of the other 2 species? Plausible causes include that individuals of *Dio. maritima* were much smaller in size (11~17 cm in DBH) compared to individuals of *P. umbellifera* and *M. multiglandulosa* (32.2 and 25.5 cm, respectively, in mean DBH). Larger plants have deeper and/or more-expanded root systems to acquire sufficient water resources (Prior and Eanus 1999). Furthermore, the leaf texture of *P. umbellifera* is of the succulent type, which had an 80% water content. Sap can seep out if the bark is damaged (personal observation). This phenomenon suggested that *P. umbellifera* was capable of preserving water in its leaves and trunks so as to maintain a higher water potential. As for the deciduous species *M. multiglandulosa*, not all the leaves were defoliated, but it retained about 30% of the leaf area in the canopy during the dry season (personal observation). Decreasing leaf areas by shedding leaves during the dry season is a mechanism of dehydration postponement for drought tolerance (Kramer 1983, Kuo et al. 2017). Thus, due to a larger size and being deciduous, *M. multiglandulosa* could possess a significantly higher PWP than *Dio. maritima* during the dry season.

In contrast to the flat terrain, shielded light, low wind, deep soil, and sufficient water in the valley environment, the ridge environment has coral reef outcrops, direct sunlight, strong wind, shallow soil, and little moisture in both the air and soil during the dry season. Plants cannot establish themselves on the rocky outcrops of the coral reefs, but can only develop their roots in the organic substrates accumulated in the depressions among the reefs. Because the soil depth in the depressions varies greatly but is basically shallow, plus the coral reefs are porous such that water in the reefs easily leaks out, the amount of soil water retained in the ridge habitat is thus very limited, especially during the dry season. In addition, the northeasterly monsoon prevails in this area from October to March every year. Under conditions of strong winds and direct sunlight, moisture in the air and soil greatly decreases. Most trees growing in this ridge environment suffer severe water stress. During the rainy season when water resources are sufficient, values of the PWP of *Dry. littoralis*, *A. formosana*, and *Dio. maritima* growing in the ridge habitat had no significant differences with those of the valley species; but during the dry season when water availability is very limited, values of the PWP of ridge species were significantly lower than those of valley species. PWP values of *Dry. littoralis* and *A. formosana* decreased to -3.4 and -3.69 MPa, indicating that these species were experiencing severe water stress. Yet, the PWP of *Dio. maritima* growing in the ridge habitat was -1.88 MPa, which suggests a level of moderate water stress. Why could *Dio. maritima* retain relatively more water and thus have a higher PWP than *Dry. littoralis* and *A. formosana*? These 3 species did not show significant differences in tree height or DBH, which excluded the factor of deeper and more-extended root systems due to a larger size of trees. In this karst forest dynamics plot, *Dio. maritima* is the absolute dominant species (Wang et al. 2004, Wu et al.

2011). There are a large amount of seedlings, saplings, and adult trees of this species both in the valley and ridge habitats. It has apparently adapted to the diversified terrain and microenvironments of this area. A study reported that some tree species in the dry karst forests of southwestern China can maintain a higher water potential due to having higher stem hydraulic conductance (Fu et al. 2012). *Diospyros maritima* might also possess higher stem hydraulic efficiency than the other 2 ridge species, which is yet to be studied.

After a long rainless period, although *Dry. littoralis* and *A. formosana* in the ridge habitat suffered severe water stress (PWP < -3.0 MPa), their $P_n$ values remained positive and were maintained at 46 and 25%, respectively, of $P_n$ values during the rainy season (Table 4). This phenomenon indicated that their photosynthetic functions were not severely inhibited even under such a water-deficient situation. Many evergreen species commonly employ osmotic adjustment to maintain positive turgor pressure, so that they can have relatively high photosynthetic efficiency (Kuo 1994, Eamus 1999, Slot and Poorter 2007). Shrubs growing on the open hill slopes of karst forests in southwestern China were found to have higher capacities of osmotic adjustment and antioxidant protection, hence higher drought tolerance abilities (Liu et al. 2011). Fu et al. (2012) found that evergreen species in dry karst forests have extremely high physiological drought tolerance abilities due to the greater xylem-cavitation resistance and lower leaf turgor-loss point water potential in those species. Since both *Dry. littoralis* and *A. formosana* are evergreen species, they might exploit xylem-cavitation resistance and osmotic adjustment to enhance the ability for physiological drought tolerance. We further estimated the PWP value when $P_n$ decreased to 0 ($\Psi_0$) with a linear re-

gression of $P_n$ vs. PWP, and found that values of $\Psi_0$ of *Dry. littoralis* and *A. formosana* were -5.89 and -4.84 MPa, respectively (Fig. 3). These results indicated that these 2 species possessed high physiological drought-tolerance abilities. In addition, since the $\Psi_0$ of *Dry. littoralis* was lower (more negative) than that of *A. formosana*, *Dry. littoralis* had a higher physiological drought-tolerance ability than *A. formosana*. Differences in the $\Psi_0$ of *Dry. littoralis* and *A. formosana* can also explain why *Dry. littoralis* was capable of maintaining 46% of the $P_n$ of the rainy season when its PWP was as low as -3.40 MPa, yet *A. formosana* could only maintain 25% of the $P_n$ of the rainy season when its PWP was -3.69 MPa, during the dry season. Concurrently, other research measuring the physiological activities of 9 coastal tree species (including *A. formosana*) on the west coast of Hengchun was conducted. That research found that *A. formosana* on the coast could maintain 24% of the $P_n$ of the rainy season when its PWP was -3.39 MPa and had a $\Psi_0$ value of -4.40 MPa during the dry season of April and May 2010 (Kuo et al. 2017). Comparing the $P_n$ and $\Psi_0$ values of *A. formosana* growing on the ridge or on the coast, the results were quite similar. Both studies indicated that *A. formosana* possesses a good physiological drought-tolerance ability and adopts the mechanism of dehydration tolerance to cope with severe water stress during the dry season. *Drypetes littoralis* maintained an even higher $P_n$ and a much lower $\Psi_0$ value than *A. formosana* did during the dry season, indicating that this species also possesses a good physiological drought-tolerance ability and adopts the mechanism of dehydration tolerance to endure drought periods. As for *Dio. maritima* growing in the ridge habitat, it showed a lower level of decrease in the PWP during the dry season than *Dry. littoralis* and *A. formosana*. We inferred

that *Dio. maritima* had a better ability to obtain and/or transport water than the above 2 species and might adopt the mechanism of dehydration postponement. However, this research is yet to study the specific methods *Dio. maritima* uses to delay the dehydration affect. Furthermore, the $\Psi_0$ of *Dio. maritima* at the ridge was -5.03 MPa which was lower than the $\Psi_0$ of *A. formosana*, while the $\Psi_0$ of *Dio. maritima* in the valley was -4.22 MPa, which was slightly higher than the $\Psi_0$ of *A. formosana*. This result implies that individuals of *Dio. maritima* growing on the ridge have a good physiological drought-tolerance ability as well. They adopt both dehydration postponement and dehydration-tolerance mechanisms for adapting to a water-deficient environment.

Comparing the performance of the $P_n$ during the rainy and dry seasons for the 5 tested species, *M. multiglandulosa* had the highest value during the rainy season (Table 4). Although this result implies that *M. multiglandulosa* has the highest photosynthesis among the 5 species, the photosynthetic potential ($A_{max}$) of each species should be taken into consideration when assessing the photosynthetic productivity of a species. $A_{max}$ in essence is genetically different for each species (Kuo and Yeh 2015), thus evaluating the $P_n$ with reference to $A_{max}$ of each species would provide greater ecophysiological significance.

For this purpose, we calculated the ratio of the mean $P_n$ during the rainy and dry seasons over $A_{max}$ for each species (Table 5). Comparing the ratio of the mean $P_n$ during the rainy season over $A_{max}$ of each species, the highest was for *Dio. maritima* in the valley habitat (88%), and the lowest values were for *A. formosana* (55%) and *M. multiglandulosa* (53%); comparing the ratio of the mean $P_n$ during the dry season over $A_{max}$ of each species, the highest values were for *P. umbellifera* (70%) and *Dio. maritima* in the valley (67%), and the lowest was for *A. formosana* (14%) (Table 5). Notice that the ratio of the mean $P_n$ during the dry season over $A_{max}$ of *M. multiglandulosa* was only 35%. *Diospyros maritima* in the valley had a higher $P_n/A_{max}$ ratio than *M. multiglandulosa* during both the rainy and dry seasons. In the ridge habitat, *A. formosana* had a higher $A_{max}$ than *Dry. littoralis* and *Dio. maritima*, but showed the lowest $P_n/A_{max}$ ratio during both the dry and rainy seasons. Although *Dio. maritima* had a lower $A_{max}$ than *A. formosana* and no significant difference in the $P_n$ with *A. formosana* during the rainy season, *Dio. maritima* in the ridge habitat exhibited a significantly higher $P_n$ than *A. formosana* during the dry season (Table 4), indicating that *Dio. maritima* in the ridge habitat possesses better competitiveness than *A. formosana*.

The texture of leaves of trees growing in a windy environment tends to be tough with

**Table 5. Photosynthetic capacity ($A_{max}$), ratio of the mean photosynthetic rate during the rainy season over $A_{max}$ ($P_{n-rainy}/A_{max}$), and ratio of mean photosynthetic rate during the dry season over $A_{max}$ ($P_{n-dry}/A_{max}$) of each species**

| | Ridge habitat | | | Valley habitat | | |
|---|---|---|---|---|---|---|
| | Dl[1] | Af | Dm | Pu | Mm | Dm |
| $A_{max}$ (µmol m$^{-2}$ s$^{-1}$)[2] | 9.5 | 15.7 | 12.2 | 14.7 | 31.0 | 12.2 |
| ($P_{n-rainy}/A_{max}$) (%) | 74 | 55 | 73 | 72 | 53 | 88 |
| ($P_{n-dry}/A_{max}$) (%) | 34 | 14 | 46 | 70 | 35 | 67 |

[1] Refer to Table 2 for the abbreviation of each species.
[2] Data refer to Kuo and Yeh (2015).

a higher leaf mass per area to withstand the mechanical damage due to wind disturbance (Su 1993, Kuo and Lee 2003, Wu and Kuo 2011). Sclerophyllous leaves with high leaf mass per area (LMA) are normally composed of a higher carbon content (Bussotti et al. 2000), and exhibit higher strength, stiffness, and toughness in terms of the mechanical quality (Edwards et al. 2000). The LMA of tree species growing in the karst forest hilltop of southwestern China can reach 23 mg cm$^{-2}$ (Geekiyanage 2017), while values of those growing on a windward slope of the Nanjenshan forest in southern Taiwan were in the range of 14~24 mg cm$^{-2}$ (Kuo and Lee 2003). In this study, leaves of *Dry. littoralis*, *A. formosana*, and *Dio. maritima* in the ridge habitat all had LMA values of > 14 mg cm$^{-2}$ and showed characteristics of sclerophyll.

Past research found that seedlings of *Dio. maritima* showed no obvious acclimation in terms of photosynthetic traits to various light regimes, yet exhibited high morphological plasticity under different light environments (Kuo and Wu 1997). In this study, in response to decreased water availability, the leaf thickness and LMA of *Dio. maritima* showed significant increases of 50 and 48%, respectively, when comparing individuals of *Dio. maritima* growing on the ridge versus those growing in the valley habitat. This result indicates an explicit acclimation of *Dio. maritima* in leaf morphology. LMA values of trees growing in high-light environments or water-deficient habitats would usually be elevated (Poorter et al. 2009). However, the sampled leaves of *Dio. maritima* in both habitats of this study were all collected from the canopy top where direct sunlight was available. Thus, the difference in LMA did not result from differences in light environments but more likely from acclimation to a drought environment. In the aspect of acclimation in physiological

traits, the $\Psi_0$ of individuals of *Dio. maritima* growing on the ridge was 0.81 MPa lower than those growing in the valley, which might have due to the osmotic adjustment in ridge individuals. The osmotic potential of tree species can decrease by around -0.2 to -1.0 MPa in drought environments (Kolzowski et al. 1991, Eamus and Prior 2001). In this study, individuals of *Dio. maritima* growing on the ridge showed a corresponding decrease in the $\Psi_0$, indicating that there was evidence of physiological acclimation to drought in this species.

## CONCLUSIONS

During the dry season, values of the PWP of *Dry. littoralis* and *A. formosana* growing on the ridge of the Kenting karst forest were as low as -3.40 and -3.69 MPa, respectively, indicating that water availability is limited in this habitat. However, these 2 species still maintained positive $P_n$ values at 46 and 25%, respectively, of the $P_n$ during the rainy season. The physiological activities of these 2 species were not severely inhibited. To have $P_n$ values decline to 0, the PWP of *Dry. littoralis* and *A. formosana* would need to decrease to -5.89 and -4.84 MPa, respectively. Evidently, these 2 species possess high physiological drought-tolerance abilities. They adopted the mechanism of dehydration tolerance to endure a water-deficient environment in the ridge habitat during the dry season. Individuals of *Dio. maritima* growing in the ridge habitat had a significantly higher PWP than did *Dry. littoralis* and *A. formosana*, and slightly higher physiological drought-tolerance ability than *A. formosana*. *Diospyros maritima* growing in the ridge habitat adopted both the dehydration postponement and dehydration tolerance mechanisms. Compared to those of the same species growing in the valley, *Dio. maritima*

growing in the ridge habitat had a higher leaf mass per area and physiological drought tolerance, revealing acclimation performance in leaf morphology and physiological activities to a drought environment. The valley species *P. umbellifera* and *M. multiglandulosa* experienced only mild water stress during the dry season. The drought-tolerance abilities of valley species were lower than those of ridge species.

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