

Research paper

Wind Effects on Stomatal Conductance and Leaf Temperature of Tree Seedlings Distributed in Various Habitats of the Nanjenshan Forest, Southern Taiwan

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【 Summary 】

Forests of Nanjenshan, located in southern Taiwan, are chronically disturbed by strong winds of the northeasterly monsoon for as long as 6 mo each year. However, not much is known about the effects of wind on stomatal activities of trees that are found there. This research chose seedlings of 18 species representing tree species either growing specifically at a windward site, a leeward site, or ubiquitously at both sites. We measured variations in stomatal conductance of these species in a walk-in growth chamber, where the wind speeds were adjusted to 1~4 m s⁻¹. Results showed that at wind speeds of 1 and 2 m s⁻¹, 9 and 17 species, respectively, of the 18 tested species showed significantly lower stomatal conductance than that of the control. Under wind speeds of 3 and 4 m s⁻¹, reductions in the stomatal conductance of windward species were significantly less than those of species from the other 2 habitat types. At a wind speed of 4 m s⁻¹, stomatal conductance of leeward species and ubiquitous species had decreased 43 and 34%, respectively, but had only decreased by 27% in windward species. The slope obtained from a linear regression analysis of variation in the percentages of stomatal conductance vs. increasing wind speeds of each species was also significantly steeper in leeward species than in windward species. In another experiment, we exposed seedlings of all 18 tested species to a wind speed of 6 m s⁻¹ for 10 min and monitored variations in leaf temperatures. The leaf temperature of windward species decreased 3.4°C on average, while it decreased 4.8°C (significantly differing from the former) in leeward species. Species with a larger leaf mass per unit area or smaller leaf area were less affected by wind, in terms of both lowered leaf temperatures and decreased stomatal conductance. Windward species of the Nanjenshan forest, in contrast to leeward species, had larger leaf masses per unit area and smaller leaf areas; they did not exhibit substantial reductions in stomatal conductance or leaf temperatures under windy conditions. Possessing the aforementioned morphological and physiological characteristics, the

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windward species of the Nanjenshan forest clearly have adapted to the chronic wind stress of the northeasterly monsoon.

Key words: leaf area, leeward species, northeasterly monsoon, wind speed, windward species.

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研究報告

風對南仁山森林不同生育地分布型樹種苗木氣孔導度 與葉溫的影響

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摘要

台灣南部的南仁山森林，每年遭受東北季風的擾動長達半年，但風的作用對當地林木葉片的氣孔活動有何影響，目前所知仍少。本研究選定南仁山森林迎風坡樹種、背風坡樹種，以及兩處共有的廣泛分布樹種共18種的樹苗，於進入式生長箱內在風速1~4 m s⁻¹的處理下，測定各樹種葉片氣孔導度的變化。結果發現在風速1及2 m s⁻¹的處理下，18樹種的氣孔導度即分別有9及17樹種顯著低於未吹風時。在3及4 m s⁻¹風速處理下，迎風坡樹種氣孔導度降低程度均顯著小於另二類樹種，背風坡樹種在風速4 m s⁻¹時，氣孔導度的下降率平均達43%，廣泛分布樹種為34%，而迎風坡樹種僅27%。背風坡樹種氣孔導度下降率與風速直線迴歸的斜率，也顯著較迎風坡樹種陡。另將各供試樹苗在風速6 m s⁻¹下處理10分鐘，發現迎風坡樹種葉溫平均下降3.4°C，而背風坡樹種葉溫下降達4.8°C，二者具顯著差異。本研究也發現比葉重較大或單葉面積較小的樹種，因風吹致葉溫及氣孔導度下降的程度均較小。迎風坡樹種相較於背風坡樹種，兼有較小的葉面積與較大的比葉重，在吹風條件下氣孔導度與葉溫並不會大幅度減小。迎風樹種葉片具備上述形態與生理性狀，顯示已適應南仁山森林長期慢性的東北季風逆境。

關鍵詞：葉面積、背風樹種、風速、東北季風、迎風樹種。

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INTRODUCTION

Wind, a commonly existing climatic factor, exerts differential effects on plants. It varies in frequency, intensity, direction, and duration among different types of habitats, especially in coastal and mountainous areas where its effects are most significant (Telewski 1995, Retuerto et al. 1996). On one hand, it is beneficial to plants in aiding the dispersal

of pollen, spores, seeds and other propagules; but on the other hand, strong winds can break twigs and trunks, damage leaves, and inhibit plant growth. In Taiwan, typhoons which prevail in summer commonly cause severe wind damage to forested ecosystems within a few days (Lin et al. 2003, Kuo et al. 2007). The northeasterly monsoon which occurs in

winter, however, exerts long-term, chronic effects on coastal and mountainous windward forests.

The effects of wind on the morphology or physiology of a plant can act in two ways. One is direct mechanical damage to leaves, and the other is via influencing the humidity, heat, and CO₂ concentrations around the leaf surface, leading to changes in stomatal activities of leaves (Telewski 1995). As wind passes by leaves, vapor and heat on the leaf surface are carried away by convection, resulting in a vapor deficit at the leaf surface and a reduction in leaf temperature. The thickness of the boundary layer between the leaf surface and the surrounding ambient air is also reduced such that boundary layer conductance increases, which is beneficial for the transfer of water vapor and other gases (Nobel 1981, Van Gardingen and Grace 1991). Thus wind can have a significant influence on transpiration. Besides the aforementioned physical factors, transpiration of a plant is also controlled by the biological factor of the stomatal apparatus. Under conditions of lower light, lower humidity, lower temperature, lower leaf water potential, and higher CO₂ concentrations, plants usually have lower stomatal conductance (Lambers et al. 1998). In a windy situation, the microclimate at the leaf surface, including humidity, heat, and CO₂ concentrations, all change. The stomatal response to wind is usually a reduction in openness (Dixon and Grace 1984, Kozlowski et al. 1991, Van Gardingen and Grace 1991, Meinzer et al. 1996).

Forests in coastal areas of northeastern and southeastern Taiwan are significantly affected by the northeasterly monsoon prevailing in winter. The physiognomy of windward forests of these areas exhibits lower tree heights, less stratification of the tree crown, smaller tree diameters, and higher stem densi-

ties (Su and Su 1988, Chen 2000, Fan et al. 2005). Every year from late October to March of the following year (almost 6 mo), the northeasterly monsoon prevails in the Nanjenshan forest of southern Taiwan. The average wind speed during the monsoon season (October to March) is 5.2 m s⁻¹ at windward sites of the Nanjenshan forest, while it is only 1.6 m s⁻¹ at leeward sites (Fan 2005). To adapt to this prolonged and chronic wind stress, trees at windward sites may have developed some special morphological or physiological traits. In terms of leaf functional traits, previous ecophysiological research found that trees growing at windward sites of the Nanjenshan forest, in contrast to those at leeward sites, possess sclerophyllous structures with a higher leaf mass per unit area (LMA; Su 1993, Kuo and Lee 2003) and better tolerance to dehydration stress (Kuo and Lee 2003, Wu 2005). Wind-caused mechanical damage to leaves of tree seedlings at windward sites is less severe (Wu 2005), and the growth, development, and biomass of the seedlings are not significantly inhibited by wind stress (Fan 2005). Photosynthetic rates of species at windward sites are higher during the monsoon season than during the non-monsoon season (April to September) (Hong 2003). Although the optimal temperature for photosynthesis does not significantly differ from that of species growing at leeward sites, species growing at windward sites can maintain a higher photosynthetic potential in conditions of relatively lower temperature such as 15°C (Chen and Kuo 2008).

Clearly, trees growing at windward sites of the Nanjenshan forest have adapted to the prolonged and chronic wind stress of the northeasterly monsoon in terms of morphological and physiological aspects. But, do their stomatal activities show similar adaptations? During windy conditions, can

species growing at windward sites maintain their stomatal conductance at the same level as under no wind conditions? If disturbed by strong winds, are the decreased levels of stomatal activities of these species less than those of species growing at leeward sites? So far no such data are available for comparison. Therefore, we set up a man-made wind experiment in a walk-in growth chamber, where the environmental conditions were controllable, to investigate wind effects on the stomatal activities of tree seedlings distributed in habitats receiving different levels of wind effects in the Nanjenshan forest. According to a study by Fan (1999) of the species composition in the Nanjenshan forest, tree species were classified into 3 habitat types: either growing specifically at a windward site (windward species), a leeward site (leeward species), or ubiquitous at both sites (ubiquitous species). Our question was: when exposed to various wind speeds, are there significant differences among the magnitudes of variations in stomatal conductance of trees in the 3 habitat types? Our hypothesis to this question was that windward species had already adapted to windy environments, and their stomatal activities would be less affected by wind stress. Especially when treated with high wind speeds, the windward species should show significantly smaller magnitudes of decrease in stomatal conductance than would leeward species. Ubiquitous species should have decreasing magnitudes in between those of species of the other 2 habitat types. In addition, we also compared variations in leaf temperatures of the 3 habitat types under a high wind speed. We hypothesized that since the leaf areas of the windward species are smaller, the convective heat loss in their leaves would be less, and hence decreases in leaf temperature of windward species would be less than species of the other 2 habitat types.

MATERIALS AND METHODS

Materials

According to species compositions in the 3 habitat types proposed by Fan (1999), we chose 6 windward species, 7 leeward species, and 5 ubiquitous species, a total of 18 species, as our tested tree species. Windward species included *Gordonia axillaris*, *Lindera akoensis*, *Machilus (Mch.) obovatifolia*, *Myrica (Myr.) adenophora*, *Nageia nagi*, and *Rhaphiolepis indica*; leeward species included *Bischofia (Bis.) javanica*, *Elaeocarpus sylvestris*, *Ficus septica*, *Macaranga (Mca.) tanarius*, *Mch. japonica*, *Mch. zuihoensis*, and *Melanolepis (Mel.) multiglandulosa*; and ubiquitous species included *Ardisia sieboldii*, *Beilschmiedia (Bei.) tsangii*, *Daphniphyllum glaucescens*, *Illicium arborescens*, and *Schefflera octophylla*. Seedlings of these 18 species were either purchased from nurseries at Manchou, Pingtung County or cultivated ourselves from seeds collected in the field. They were planted in plastic pots of 18 cm in diameter, placed under 40% full sunlight, watered regularly, and supplied sufficient organic fertilizer in the nursery of National Pingtung University of Science and Technology (NPUST). At the beginning of our experiment, seedlings were mostly 1~2 yr old with heights of around 20~30 cm.

Influence of various wind speeds on stomatal conductance

Experiments were conducted in a walk-in growth chamber located at the Department of Forestry, NPUST, from August to October 2004. This growth chamber is 350 cm long, 260 cm wide, and 240 cm high. Its temperature is controllable; the relative humidity (RH) is adjustable by humidifier and dehumidifier devices; the photosynthetic photon flux density (PPFD) received by leaves was modified

by arranging the position of high-pressure mercury lamps; and wind speeds were manufactured by a 50-cm (in diameter) fan. By adjusting the fan speed and distance to the plants, we could simulate wind speeds of 1, 2, 3, and 4 m s⁻¹, which were measured by an anemometer (Testo 425, Testo, Lenzkirch, Germany). Stomatal resistance was measured by a steady-state porometer (LI-1600, LI-COR, Lincoln, NE, USA). In fact, this equipment measures leaf resistance which combines both the stomatal resistance and boundary layer resistance. However, since the boundary layer resistance of this equipment was set to 0.15 s cm⁻¹, any changes in the leaf resistance must have been due to changes in the stomatal resistance. Thus, we used stomatal resistance to represent leaf resistance in this article. Stomatal resistance (s cm⁻¹) was then converted into a more commonly adopted term of stomatal conductance (g_s, mmol m⁻² s⁻¹) (Nobel 1983). One day before the experiment, 4 seedlings each of 3 species were chosen and moved from the nursery into the growth chamber. The temperature was set to 26°C and RH to 80%. At 07:30 the next morning, the mercury lamps were turned on to provide 700 μmol m⁻² s⁻¹ of PPFD to the seedlings. Levels of openness of the stomata were constantly monitored by the steady-state porometer. Not until stomatal conductance exceeded 100 mmol m⁻² s⁻¹ (this procedure normally required 30~60 min of lighting, depending on the tree species), did we begin to record the initial stomatal conductance as the control. At this time, although the fan had not been turned on but due to air circulation in the chamber, leaves were still exposed to a weak wind speed of 0.1~0.3 m s⁻¹. Three leaves were chosen for each of the 4 seedlings. The sampled leaves were young and fully expanded at the upper part of the seedlings. Then, the fan generated a wind speed of 1 m s⁻¹

for 10 min. Readings of the same leaves were then taken while the wind was still blowing. Normally all measurements of the 36 leaves could be completed before 11:00. We only examined 1 wind speed each measurement day; then, the following 2nd, 3rd, and 4th measurement days were for wind speeds of 2, 3, and 4 m s⁻¹, respectively. The difference in stomatal conductance of each species under a wind effect and before treatment (initial stomatal conductance, I_{g_s}) was presented as the variation in the percentage of g_s (Δg_s), which was calculated as follows:

$$\Delta g_s = [(g_s \text{ under wind effect} - I_{g_s}) / I_{g_s}] \times 100\%$$

A regression analysis of Δg_s versus wind speed was performed for each species. The slope of this linear regression line indicates the sensitivity of stomatal activities of each species to wind at speeds of 1~4 m s⁻¹.

Wind effects on leaf temperature

Three seedlings each of the 18 tested species were randomly chosen for this experiment conducted in February 2005. The temperature of a mature leaf at the upper part of the seedling was measured in the walk-in growth chamber. Microclimate conditions of the growth chamber were set to 25.5°C with an 80% RH. Seedlings received 700~800 μmol m⁻² s⁻¹ of light after being moved into the growth chamber. A metal thermosensor (MMS 3000-T6V4, Commtest, Christchurch, New Zealand) was attached to the lower epidermis of the tested leaf to monitor its leaf temperature. After the leaf temperature had stabilized, the seedling was exposed to a fixed wind speed of 6 m s⁻¹ generated by the 50-cm fan. Leaf temperatures were measured every 1 min for 10 min. Then the fan was turned off, but the leaf temperature was still recorded every 1 min until the leaf temperature had returned to the original state before wind exposure. We

compared the wind effects on leaf temperatures among species of the 3 habitat types.

Calculating the leaf area and LMA

We randomly picked 10 fully extended leaves from the upper part of seedlings from each of the 18 tested species and measured the leaf areas with an area meter (LI-3000A, LI-COR). Then, the leaves were dehydrated in an oven of 80°C, the dry weight was measured, and the LMA was calculated.

Data analysis

Differences in stomatal conductance before and after wind treatments were tested at the 5% significance level by *t*-test procedures. To analyze differences among the 3 habitat types with respect to variations in stomatal conductance, leaf temperatures, slopes of decreasing stomatal conductance versus increasing wind speeds, leaf areas, and LMA, analysis of variance (ANOVA) procedures in the SPSS software (SPSS, Chicago, IL, USA) were used.

RESULTS

Wind effects on stomatal conductance

The initial stomatal conductance (I_{gs}) of each species before wind treatments is listed in Table 1. Most of the windward and ubiquitous species had I_{gs} values of $< 150 \text{ mmol m}^{-2} \text{ s}^{-1}$, except that of *R. indica*, which was $207 \text{ mmol m}^{-2} \text{ s}^{-1}$. Most of the leeward species had I_{gs} values of $< 180 \text{ mmol m}^{-2} \text{ s}^{-1}$, with only *Mca. tanarius* showing $215 \text{ mmol m}^{-2} \text{ s}^{-1}$.

When exposed to a wind speed of 1 m s^{-1} , the stomatal conductance of 15 of the 18 tested species were lower than the stomatal conductance before wind treatment (the control), with 9 species (*G. axillaris*, *N. nagi*, *A. sieboldii*, *Bei. tsangii*, *I. arborescens*, *S. octophylla*, *E. sylvestris*, *F. septica*, and *Mch.*

japonica) showing significance; the other 3 species *R. indica*, *Mel. multiglandulosa* and *Mch. zuihoensis*, however, had increased their stomatal conductance, although significance was only detected in *Mch. zuihoensis* (Fig. 1). As the wind speed increased to 2 m s^{-1} , all species but *Mca. tanarius* (which showed no significance) had significantly decreased stomatal conductance compared to the control. When the wind speed was raised to 3 and 4 m s^{-1} , all species exhibited significantly lower stomatal conductance than the control (Fig. 1). The variation percentages of stomatal conductance under a 4-m s^{-1} wind speed are shown in Table 1. There were 5 species, including 4 windward species *L. akoensis*, *Mch. obovatifolia*, *Myr. adenophora*, and *N. nagi*, and 1 leeward species *Mch. zuihoensis*, that had $< 30\%$ decrease in stomatal conductance; 6 species, including 2 windward, 1 leeward, and 3 ubiquitous species were within the range of 30~40%; 7 species, including 2 ubiquitous species and 5 leeward species were $> 40\%$. Among the 18 species, *L. akoensis* and *Myr. adenophora* (both windward species) had the least (only 18 and 20% respectively), while *E. sylvestris* and *F. septica* (both leeward species) had the highest (59 and 55% respectively) decrease in stomatal conductance.

The mean I_{gs} of windward, ubiquitous, and leeward species were 139 ± 14 , 135 ± 6 , and $166 \pm 12 \text{ mmol m}^{-2} \text{ s}^{-1}$, respectively, and showed no significant difference (Table 2). At a 1-m s^{-1} wind speed, the variation in stomatal conductance was significantly larger in ubiquitous species than in either windward species or leeward species. With a 2-m s^{-1} wind speed, no significant differences in the percentages were observed among the 3 habitat types. With both 3- and 4-m s^{-1} wind speeds, the windward species had significantly smaller reductions than species of the other 2 habitat types (Table 2).

Table 1. Initial stomatal conductance before wind treatments (I_{g_s}), variations in stomatal conductance (Δg_s), slopes of decreasing g_s vs. increasing wind speeds, declines in leaf temperature (ΔT_{leaf}) after wind treatments, as well as leaf functional traits, including leaf mass per unit area (LMA) and leaf area (LA) in the 18 tested species

Species	I_{g_s} ($\text{mmol m}^{-2} \text{s}^{-1}$)	Δg_s ¹⁾ (%)	Slope	ΔT_{leaf} ²⁾ ($^{\circ}\text{C}$)	LMA (mg cm^{-2})	LA (cm^2)
Windward species						
<i>Gordonia axillaris</i>	124±3	-33	-5.40	4.2	14.1	29.3
<i>Lindera akoensis</i>	125±2	-18	-5.25	2.5	12.6	6.7
<i>Machilus obovatifolia</i>	126±3	-30	-8.47	2.9	9.3	7.5
<i>Myrica adenophora</i>	137±4	-20	-4.88	4.5	8.8	11.5
<i>Nageia nagi</i>	113±1	-26	-1.60	3.1	15.4	8.5
<i>Raphiolepis indica</i>	207±7	-35	-12.18	3.4	14.1	9.3
Ubiquitous species						
<i>Ardisia sieboldii</i>	130±2	-43	-4.38	4.1	10.2	20.7
<i>Beilschmiedia tsangii</i>	139±6	-40	-3.75	2.7	8.9	14.1
<i>Daphniphyllum glaucescens</i>	148±4	-33	-9.13	3.2	10.3	16.3
<i>Illicium arborescens</i>	115±2	-35	-4.33	2.9	12.0	13.1
<i>Schefflera octophylla</i>	124±11	-50	-4.25	3.5	9.1	18.3
Leeward species						
<i>Bischofia javanica</i>	160±9	-45	-9.87	5.4	6.1	49.0
<i>Elaeocarpus sylvestris</i>	175±9	-59	-10.69	4.7	8.9	24.3
<i>Ficus septica</i>	178±4	-55	-17.11	4.4	4.9	63.3
<i>Macaranga tanarius</i>	215±8	-37	-11.69	3.9	3.7	118.3
<i>Machilus japonica</i>	127±3	-48	-8.77	4.8	9.3	49.2
<i>Machilus zuihoensis</i>	131±3	-28	-11.31	4.8	5.4	37.3
<i>Melanolepis multiglandulosa</i>	179±9	-42	-12.81	5.5	4.1	62.0

¹⁾ with a wind speed of 4 m s^{-1} .

²⁾ with a wind speed of 6 m s^{-1} .

Slopes of the linear regressions between the variation in percentages of stomatal conductance and wind speeds

As wind speeds increased from 1 to 4 m s^{-1} , stomatal conductance of the 18 tested species accordingly decreased. The slopes, obtained by a linear regression analysis of the variation in percentages of stomatal conductance with increasing wind speeds, were all significant ($p < 0.05$), except that of a windward species, *N. nagi* ($p = 0.322$). For the other 5 windward species, 4 of them had slopes between -4.88 and -8.47, while *R. indica* had a slope of -12.18 (Table 1). Slopes of the ubiq-

uitous species were mostly between -3.75 and -4.38; only *D. glaucescens* showed a relatively steeper slope of -9.13. The slopes of the 7 leeward species were mostly > -10.0 (between -10.69 and -17.11), while only *Bis. javanica* and *Mch. japonica* had slopes of < -10.0 . Figure 2 shows 6 examples of this regression analysis, including *N. nagi* and *Myr. adenophora* (both windward species), *I. arborescens* and *D. glaucescens* (both ubiquitous species), as well as *Mch. japonica* and *F. septica* (both leeward species). The windward species *N. nagi* had the smoothest decline in stomatal conductance (the slope was only -1.6 and not significant)

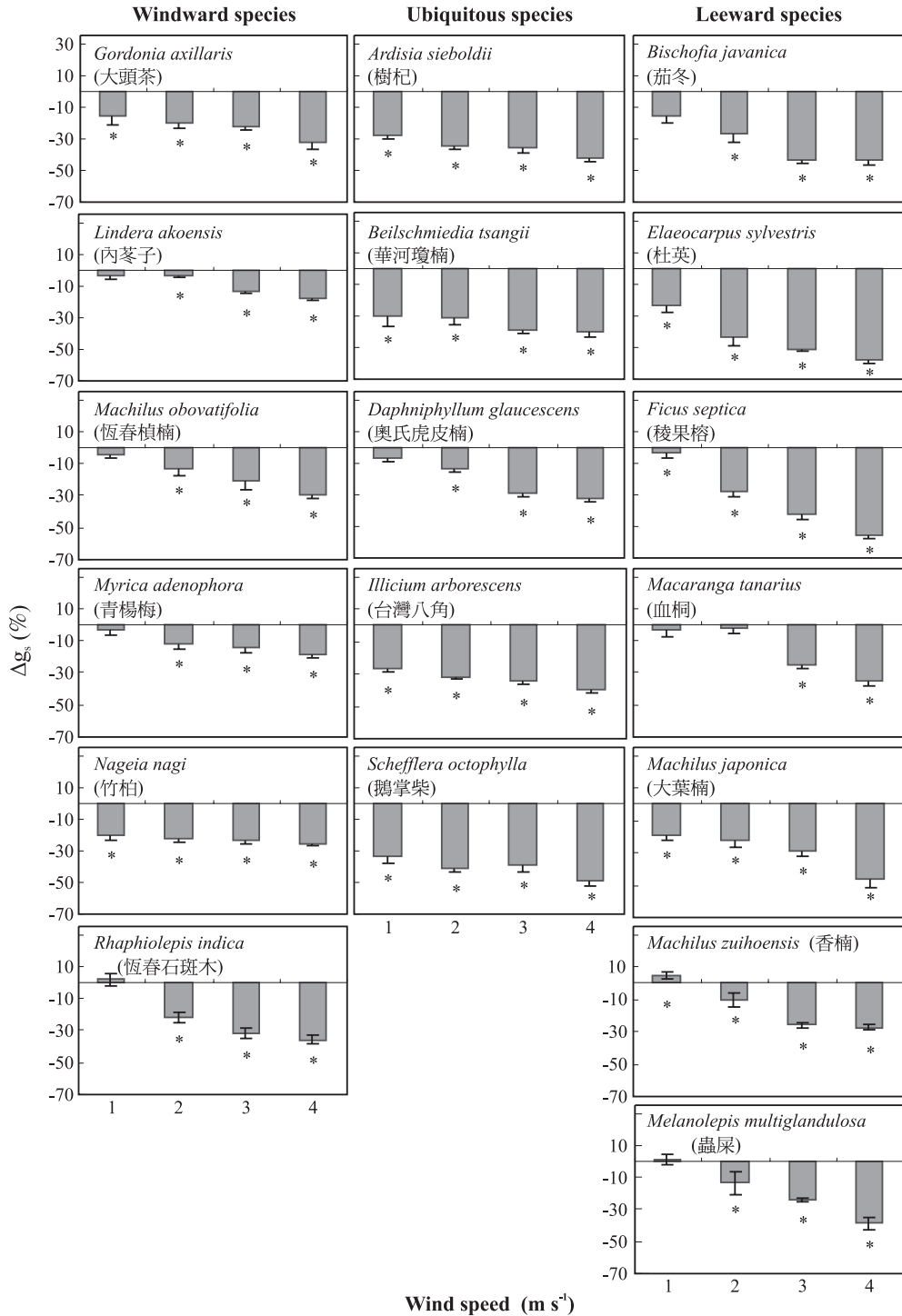


Fig. 1. Variations in stomatal conductance (Δg_s) under various wind speeds with each species classified as a windward, ubiquitous, or leeward species. * Denotes a significant difference ($p < 0.05$) between each wind treatment and the control.

with increasing wind speeds. Slopes of *Myr. adenophora* and *I. arborescens* were relatively smooth (-4.88 and -4.33, respectively) compared to -17.11 in *F. septica*. For the mean

slopes of the 3 habitat types, the windward (-6.3 ± 1.5) and the ubiquitous species (-5.2 ± 1.0) were both significantly smoother than the leeward species (-11.8 ± 1.0) (Table 2).

Table 2. Mean initial stomatal conductance (I_{g_s}) before wind treatments, mean variations in stomatal conductance (Δg_s) under various wind speeds, mean slopes of decreasing stomatal conductance vs. increasing wind speeds, and mean declines in leaf temperature (ΔT_{leaf}) after exposure to a wind speed of 6 m s⁻¹, as well as mean leaf functional traits, including leaf mass per unit area and leaf area, in species of the 3 habitat types

Item	Windward spp.	Ubiquitous spp.	Leeward spp.
I_{g_s} (mmol m ⁻² s ⁻¹)	139 ± 14 ^{a 1)}	135 ± 6 ^a	166 ± 12 ^a
Δg_s (%)			
1 m s ⁻¹ wind speed	-7.5 ± 3.5 ^b	-25.3 ± 4.7 ^a	-8.6 ± 4.2 ^b
2 m s ⁻¹ wind speed	-15.5 ± 3.0 ^a	-30.4 ± 4.7 ^a	-21.0 ± 5.2 ^a
3 m s ⁻¹ wind speed	-21.1 ± 2.7 ^b	-35.6 ± 2.6 ^a	-34.3 ± 4.1 ^a
4 m s ⁻¹ wind speed	-26.6 ± 3.0 ^b	-34.3 ± 4.1 ^a	-43.3 ± 4.1 ^a
Slope of decreasing g_s	-6.3 ± 1.5 ^b	-5.2 ± 1.0 ^b	-11.8 ± 1.0 ^a
ΔT_{leaf} (°C)	3.4 ± 0.3 ^b	3.3 ± 0.2 ^b	4.8 ± 0.2 ^a
Leaf mass per unit area (mg cm ⁻²)	12.4 ± 2.7 ^a	10.1 ± 1.2 ^a	6.1 ± 2.2 ^b
Leaf area (cm ²)	12.1 ± 8.6 ^b	16.5 ± 3.1 ^b	57.6 ± 30.0 ^a

¹⁾ Different letters in the same row indicate a significant difference ($p < 0.05$) among mean values of species of the 3 habitat types.

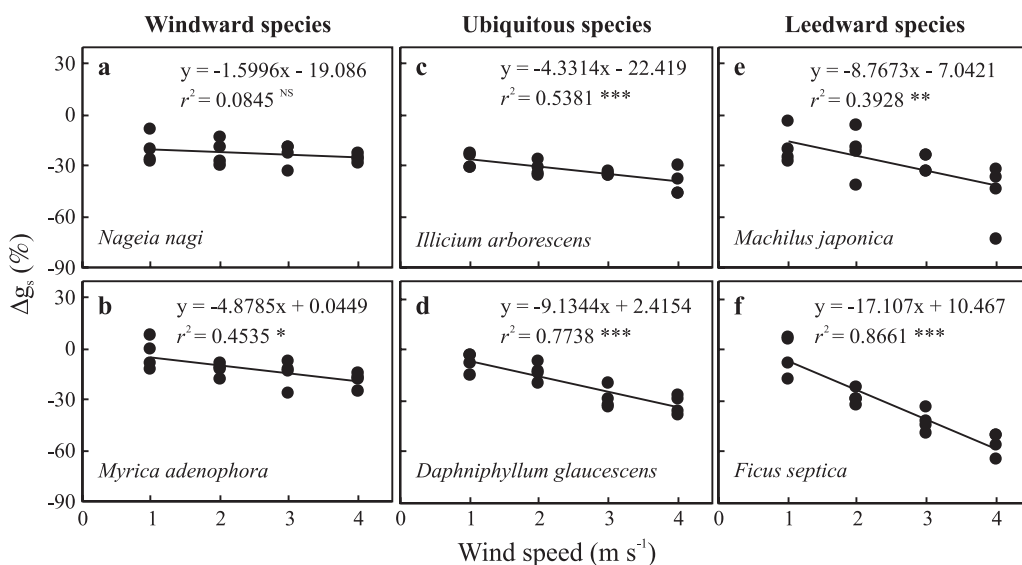


Fig. 2. Linear regressions of variations in stomatal conductance (Δg_s) vs. wind speeds in 6 representative species of the 3 habitat types. NS, *, **, * Denote no significant relationship and significance relationship at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively.**

Wind effects on leaf temperature

Our second experiment investigated wind effects on leaf temperatures of the 18 species. After being exposed to a 6-m s^{-1} wind speed, leaf temperatures of all species immediately dropped, but were restored to their initial values once the wind stopped (see examples in Fig. 3). Responses of leaf temperatures to wind differed among species of the 3 habitat types. As shown in Table 1, leaf temperatures of the windward species *L. akoensis* and *Mch. obovatifolia*, and ubiquitous species *Bei. tsangii* and *I. arborescens*, only dropped by $< 3^{\circ}\text{C}$. The leeward species of *Bis. javanica* and *Mel. multiglandulosa* had the highest declines of around 5.5°C (Table 1). On average, leaf temperatures of windward and ubiquitous species dropped 3.4 ± 0.3 and $3.3 \pm 0.2^{\circ}\text{C}$, respectively, while leaf temperatures of leeward species dropped $4.8 \pm 0.2^{\circ}\text{C}$, which was significantly higher than species of the former 2 habitat types (Table 2). Our hypothesis that the decreases in leaf temperature of the windward species would

be less than those of species of the other 2 habitat types was partially supported. Since, under a stronger wind, the reduction in leaf temperature of windward species was indeed significantly less than that of leeward species, this reduction was not statistically significant between windward and ubiquitous species.

Leaf morphology

The LMA of the 6 windward species ranged $8.8\text{--}15.4\text{ mg cm}^{-2}$, with *N. nagi*, *G. axillaries*, and *R. indica* having higher values; the LMA of the 7 leeward species ranged $3.7\text{--}9.3\text{ mg cm}^{-2}$, with *Mch. japonica* and *E. sylvestris* having higher values; and the LMA of the 5 ubiquitous species ranged $8.9\text{--}12.0\text{ mg cm}^{-2}$, with *I. arborescens* having a higher value (Table 1). The mean LMA of leeward species (6.1 ± 2.2) was significantly smaller than those of windward (12.4 ± 2.7) and ubiquitous species (10.1 ± 1.2) (Table 2). In terms of leaf area, 6 of 7 leeward species had leaf areas of $> 30\text{ cm}^2$, with *Mca. tanarius* being as large as 118 cm^2 ; leaf areas of windward

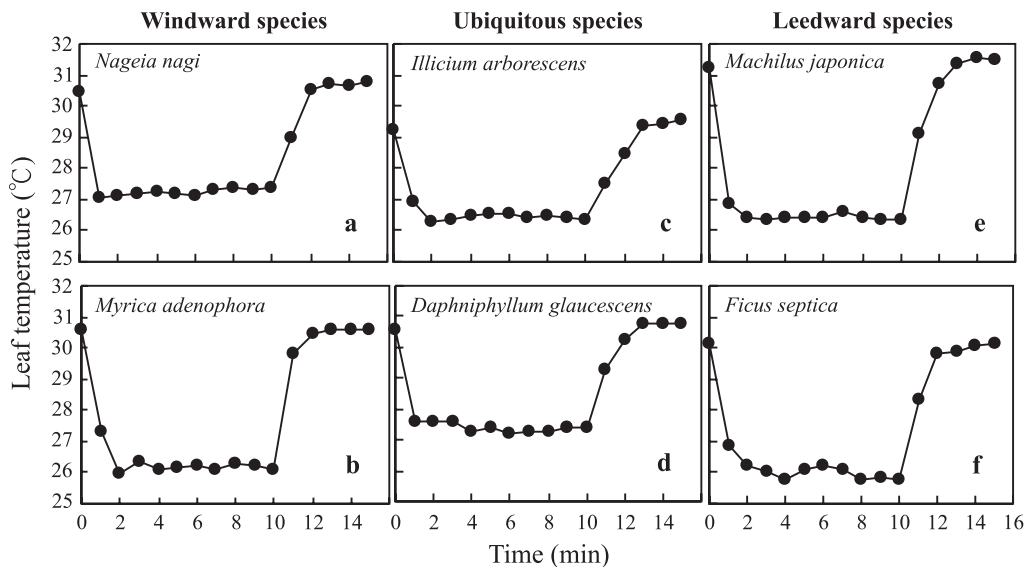


Fig. 3. Variation patterns in leaf temperatures of 6 representative species when exposed to a wind speed of 6 m s^{-1} for 10 min.

species and ubiquitous species were all < 30 cm², and among them, *L. akoensis*, *Mch. obovatifolia*, *N. nagi*, and *R. indica* (all windward species) had leaf areas of < 10 cm² (Table 1). Comparing the mean leaf area of species of the 3 habitat types, leeward species had a significantly larger mean leaf area (57.6 ± 30.0) than windward species (12.1 ± 8.6) and ubiquitous species (16.5 ± 3.1) (Table 2).

Relationships among stomatal conductance, leaf temperature, and leaf morphology

Combining data of all 18 species, the LMA showed no significant relationship (*p* = 0.108) with variations in stomatal conductance (Fig. 4a). But the LMA had significant negative relationships (*p* < 0.001) with slopes of decreasing stomatal conductance vs. increasing wind speeds (Fig. 4b) and with decreases in leaf temperature (Fig. 4c). On the other hand, leaf areas of the 18 species had significant positive relationships (*p* < 0.05) with variations in stomatal conductance, slopes, and the decreases in leaf temperature (Fig. 4d-f).

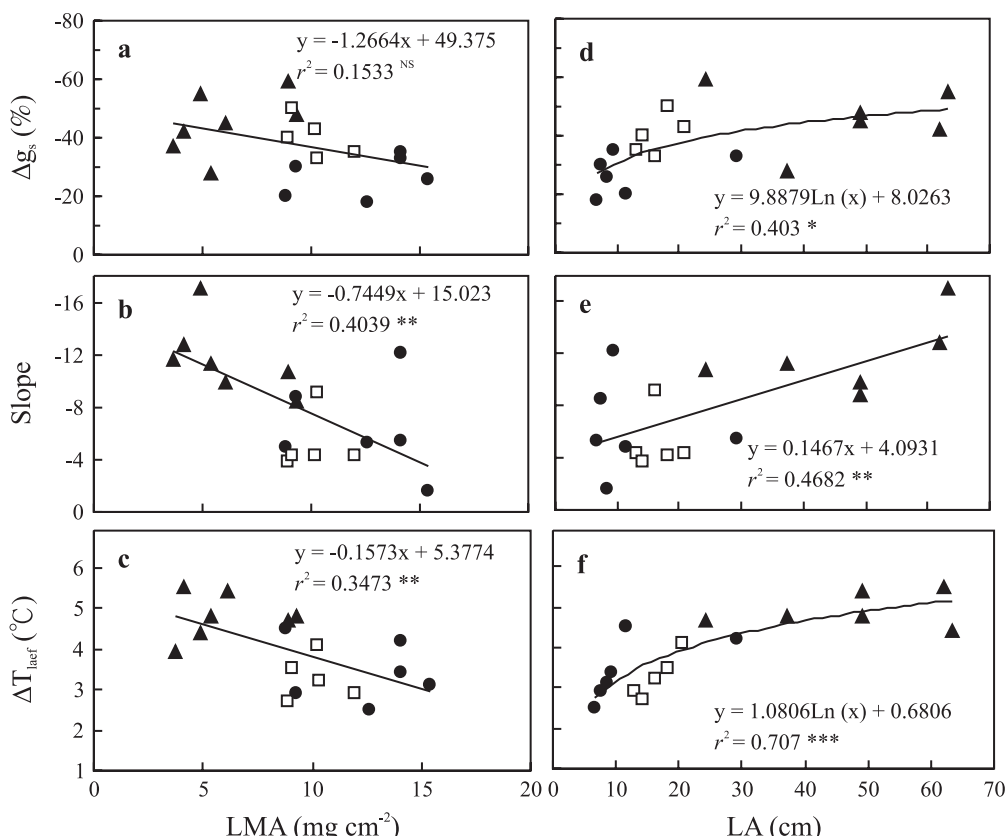


Fig. 4. Relationships between leaf mass per unit area (LMA), as well as between leaf area (LA), and variation in stomatal conductance (Δg_s), slopes of decreasing stomatal conductance vs. wind speeds, and decreases in leaf temperature (ΔT_{leaf}). ● Represents data of windward species; ▲ represents data of leeward species; and □ represents data of ubiquitous species. NS, *, **, *** Denote no significant relationship and significance relationships at *p* < 0.05, *p* < 0.01, and *p* < 0.001, respectively.

DISCUSSION

Stomata represent the principle pathway for diffusion of water and other gases between the leaf mesophyll and the external environment. Stomatal conductance is an estimate of the limitation of mass transfer, which is affected by various environmental factors including the wind (Van Gardingen and Grace 1991). Stomatal conductance of plants usually decreases with increasing wind speeds (Dixon and Grace 1984, Kozłowski et al. 1991, Van Gardingen and Grace 1991, Meinzer et al. 1996). Our results are consistent with this finding that most of the 18 tested species showed a significant decline in stomatal conductance at a wind speed of 2 m s^{-1} , and the decline became dramatic as the wind speed increased (Figs. 1, 2). The mechanisms of stomatal responses to wind are complicated since humidity, the boundary layer thickness, shaking, and CO_2 concentrations may all be involved (Nobel 1981, Grace 1988, Van Gardingen and Grace 1991, Gutierrez et al. 1994). Farquhar (1978) suggested that the responses of stomata to atmospheric humidity are the result of guard cells sensing the vapor pressure deficit (VPD) and closing to prevent water loss. The VPD increases in windy conditions and causes stomatal conductance to accordingly decrease (Bunce 1985, Gutierrez et al. 1994, Yasutake et al. 2001). A higher wind speed decreases the boundary layer thickness at the leaf surface, consequently increasing the boundary layer conductance. As the boundary layer conductance increases, CO_2 concentrations both at the leaf surface and in the leaf interior are elevated, and cause stomatal conductance to decline (Aphalo and Jarvis 1993, Gutierrez et al. 1994). In addition, mechanical stimuli such as shaking of twigs or rubbing of leaves against other plant parts during windy conditions might also trig-

ger the stomata to close (Grace and Thompson 1973, Mansfield and Davies 1985, Pappas and Mitchell 1985). Thus, under windy conditions, the 3 factors of increases in the VPD, elevated CO_2 concentrations, and mechanical stimuli, could all result in a decrease in stomatal conductance. Although various levels of decrease in stomatal conductance as affected by wind were observed in the 18 tested species, our experiment could not determine the major mechanisms causing the decrease.

As wind passes by leaves, the thickness of the boundary layer is reduced, and the convective transfer of heat increases, resulting in a smaller difference between the leaf and air temperatures (Grace 1988, Telewski 1995). That is why wind has cooling effects on leaves when the leaf temperature is higher than the air temperature in the daytime. Results of our study showed that leaf temperatures of all species immediately dropped, although different species had different degrees of reduction, with a 6-m s^{-1} wind speed. The leeward species showed more-substantial reductions in leaf temperatures than species from the other 2 habitat types (Tables 1, 2), possibly due to their larger leaf areas. With a larger area, the boundary layer of a leaf would be more disturbed by the wind, and hence more heat would be lost due to air convective effects (Nobel 1981).

The results clearly indicated that stomatal activities of the windward species were generally not sensitive to wind disturbances (Table 1). Variations in stomatal conductance with a 4-m s^{-1} wind speed and the slopes of decreasing stomatal conductance versus increasing wind speeds of windward species were relatively less severe compared to those of leeward species (Table 2). On the contrary, stomatal activities of leeward species, although showing no significant differences at wind speeds of 1 and 2 m s^{-1} , were significant-

ly reduced with wind speeds of 3 and 4 m s⁻¹ and had larger declining slopes compared to those of windward species (Table 2). This indicated that stomata of leeward species were sensitive to winds with speeds of > 3 m s⁻¹. Stomata of ubiquitous species had peculiar responses to wind disturbances. Except in *D. glaucescens*, stomatal conductance of the other 4 ubiquitous species all declined by 30% with a 1-m s⁻¹ wind speed (Fig. 1). But as the wind speed increased, the further reduction in the mean stomatal conductance of these 4 species was merely 10%, and the average slope was only -4.2. This is a unique pattern (a sudden drop of 30% under mild wind and no severe reductions afterwards even under higher wind speeds) of stomata responses to wind disturbances, a phenomenon worthy of further study.

With regard to responses in each species, the windward coniferous species *N. nagi* was the least sensitive to wind. Under wind speeds of 1~4 m s⁻¹, stomatal conductance of this species declined within a small range of 21~26% (Fig. 1). The regression analysis between the variation in percentages in stomatal conductance and wind speeds showed no significant relationship in this species ($p = 0.247$) (Fig. 2a), while the other 17 species all had significant negative relationships (the higher the wind speed, the lower the stomatal conductance). Yet *R. indica*, also a windward species, exhibited different responses to wind. Although with a 1-m s⁻¹ wind speed its stomatal conductance was still similar to that of the control, as the wind speed increased to 2 m s⁻¹, its stomatal conductance was greatly reduced by 23%, resulting in a very steep slope of -12.18 which greatly differed from the other 5 windward species (Table 1). This was probably due to the high I_g of this species, such that its guard cells would lose more water at higher wind speeds and it would greatly re-

duce the openness of its stomata in response. Among the 18 species studied, the most sensitive species to wind disturbance was *F. septica*, a leeward species. Its declining slope was as low as -17.11, indicating that stomata of this species had significantly strong reactions to increasing wind speeds.

Would the stomatal activities of plants growing in an environment with constant wind stress be less sensitive to wind? In addition to the intrinsic characteristics of each species, this would also depend on the environmental conditions of the habitat. For example, the stomata of *Cytisus scoparius* ssp. *maritimus*, a plant that grows on exposed windy cliffs with insufficient water availability, are very sensitive to wind. Within an hour of exposure to a wind speed of 0.4 m s⁻¹, its stomata would close up to save water (Davis et al. 1978). On the contrary, the stomata of *Rhododendron ferrugineum*, a plant growing in leeward environments, are not affected when exposed to a 1-m s⁻¹ wind speed, but would immediately close with a 15-m s⁻¹ wind speed. *Pinus cembra*, a plant that grows on windswept ridges, had only a slightly decrease in stomatal conductance when exposed to a wind speed of 15 m s⁻¹ for 24 h (Caldwell 1970). As shown in the above examples, when situated in a habitat of insufficient water supply, sensitivity of the stomata to wind was a favorable domesticating behavior to enhance the competitive advantages (Davies et al. 1978). However, in environments with sufficient water, the sensitivity of stomata to wind is not necessarily advantageous. This is because closing stomata inevitably reduces the intercellular CO₂ concentrations and the rate of CO₂ assimilation (Lambers et al. 1998), thus decreasing the productivity of the plant. In our study site, the Nanjenshan forest, windward species do not suffer soil water stress during the northeasterly monsoon

season (data not shown). Thus, when facing wind stress during that period, windward species do not need to close up their stomata so sensitively to save water, and so maintain their productivity.

In a plant community, wind speeds slow down due to serial blocking effects of vegetation (Jones 1986). Therefore, wind-caused physiological or mechanical damage would be less severe in plant communities of higher density (Retuerto et al. 1996). The mean stand density in windward sites of the Nanjenshan forest is as high as 16,610 stems ha^{-1} , which is 2.4-times higher than the density in leeward sites (4859 stems ha^{-1}) (Fan 1999). Numerous stems of trees provide favorable protective effects against the wind. Thus, from an ecological perspective, the windward forest already possesses a structure that minimizes adverse effects caused by the wind. From a species perspective, windward species have evolved leaves of smaller size, a larger leaf mass per unit area, and sclerophyllous structures to resist the physiological and mechanical damage caused by wind. From the perspective of physiological activities, stomatal conductance of windward species would not be substantially reduced because of wind, so they can maintain photosynthetic productivity at similar or even higher levels in the monsoon season than in the non-monsoon season (Hong 2003). In summary, windward species have adapted to the chronic stress of the northeasterly monsoon winds in the aspects of community structure, leaf structure, and physiological performance.

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