

Sensitivity to chilling temperatures and distribution differ in the mangrove species *Kandelia candel* and *Avicennia marina*

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Summary We compared the effects of short-term (hours) and long-term (days) exposure to chilling temperatures on the photosynthetic gas exchange, leaf characteristics and chlorophyll a fluorescence of seedlings of the mangrove species *Kandelia candel* Druce and *Avicennia marina* (Forsk.) Vierh. Both species occur along the west coast of Taiwan, but *K. candel* occurs further north than *A. marina*. We hypothesized that temperature was one of the major environmental factors limiting the northern distribution of *A. marina*. *Avicennia marina* was more sensitive to chilling temperatures than *K. candel*. Leaves of both species showed reductions in light-saturated photosynthetic rates (A_{\max}), stomatal conductance (g_s) and quantum yield of photosystem II after a 1-h exposure to 15 °C, with *A. marina* showing significantly greater reductions in A_{\max} and g_s than *K. candel*. No significant differences in A_{\max} , g_s and electron transport rate (ETR) were found between leaves of *K. candel* grown at 15 and 30 °C for 10 days. However, leaves of *A. marina* grown for 10 days at 15 °C had significantly lower A_{\max} , g_s and ETR than plants grown at 30 °C. After 20 days at 15 °C, leaf mass per area of both species was increased significantly, whereas area-based chlorophyll concentrations were reduced, with significantly greater changes in *A. marina* than in *K. candel*. We concluded that sensitivity to low winter temperatures is a primary limiting factor in the distribution of *A. marina* along the western coast of Taiwan.

Keywords: chlorophyll a fluorescence, photosynthetic gas exchange.

Introduction

Mangroves grow in the tidal waters of tropical and subtropical coastlines. There are four mangrove species, *Kandelia candel* Druce, *Avicennia marina* (Forsk.) Vierh., *Rhizophora mucronata* Lam. and *Lumnitzera racemosa* Willd., growing on the west coast of Taiwan (Liu 1982). Among them, *A. marina* is the dominant species in the southern part of Taiwan, whereas *K. candel* dominates the northern part of the island but can also be found in patches in central and southern Taiwan. The envi-

ronmental factors responsible for this distribution pattern have not been identified.

Aridity and temperature are two of the most important factors limiting the distribution of mangrove species (Tomlinson 1986). The coastal sediment in the southern and northern parts of Taiwan have similar salinity and pH values (Shae 1995), hence it is unlikely that these variables are major factors affecting mangrove distribution in Taiwan. However, mean monthly air temperature in January is about 15 °C for northern Taiwan and 17 °C for southern Taiwan, with differences of up to 5 °C in some years (Climatological data annual report, Central Weather Bureau, R.O.C.). Low temperature stress often affects leaf membranes and may damage the photosynthetic apparatus of higher plants, especially when combined with exposure to high light (Krause 1994, Kao et al. 1998). Markley et al. (1982) have documented within-species variation in the chilling response for *Avicennia* and *Rhizophora*. Furthermore, a decrease in leaf temperature results in reductions in the rate of photosynthetic CO₂ assimilation in chilling-sensitive plants (Larcher 1994). Thus, temperature could be a major factor affecting the distribution of mangrove species in Taiwan. To our knowledge, comparisons of sensitivity to chilling temperatures have not been conducted for *K. candel* and *A. marina*.

The amount and kinetics of chlorophyll a fluorescence emitted from leaves in response to actinic irradiation can be used to assess the primary photochemistry of photosynthesis (Krause and Weis 1991). In particular, measurements of chlorophyll a fluorescence can determine the potential quantum yield of photosystem II (PSII) (F_v/F_m), the efficiency of excitation capture by open PSII reaction centers (effective quantum yield of PSII) and the electron transport rate (ETR). These variables are tightly associated with the corresponding light responses and light-saturated rates of whole-leaf photosynthetic carbon dioxide (CO₂) uptake (Krall and Edwards 1992, Björkman and Demmig-Adams 1994). Hence, measurements of chlorophyll a fluorescence provide rapid, nondestructive estimates of photosynthetic performance. Chilling-induced changes in chlorophyll a fluorescence *in vivo* have been utilized to assess plant response to low, non-freezing temperatures (Schapendonk et al. 1989).

To test the hypothesis that air temperature is a major factor affecting the differential distribution of mangrove species in Taiwan, we compared the effects of long-term (days) and short-term (hours) exposure to chilling temperatures on *K. candel* and *A. marina*. Specifically, we determined if there were differences between *K. candel* and *A. marina* in the responses of photosynthetic gas exchange, leaf characteristics and chlorophyll a fluorescence to chilling temperatures, and attempted to identify possible mechanisms underlying any differential temperature responses found between these two mangrove species.

Materials and methods

Seedlings of *K. candel* (with 3–4 pairs of leaves) and *A. marina* (with 2 pairs of leaves) were transplanted in June 1998 from Chu-wei Natural Reserve (25°9' N, 121°26' E) in Taipei County and in October 1998 from Hwong-mau harbor in Hsin-Chu County (24°49' N, 121°00' E), respectively, to a greenhouse at Academia Sinica, Taipei. For the period 1988–1998, mean annual temperature and precipitation were 26.2 °C and 2500 mm, and 27.0 °C and 2100 mm for Taipei and Hsin-Chu county, respectively (Climatological Data Annual Report, Central Weather Bureau, R.O.C.). Seedlings were planted in 18-cm-diameter pots filled with sand and the pots were immersed in modified Hoagland's solution (Haines and Dunn 1976) containing 0.5% NaCl. The solution was renewed every 2 weeks. Plants were grown in the greenhouse in natural sunlight until measurements started in March 2000. Ten plants from each species were chosen randomly from the greenhouse populations for experimental measurements.

To evaluate the effect of short-term chilling temperature on photosynthesis, plants were brought to the laboratory and the most recent fully expanded leaf was enclosed in a climatically controlled cuvette (PAC System, Data Design Group, La Jolla, CA) with leaf temperature maintained at 25 °C, leaf-to-air vapor pressure difference at 1.5 kPa, CO₂ concentration at 360 cm³ m⁻³ and photosynthetic photon flux (PPF) at 1200 μmol m⁻² s⁻¹. After a steady-state value of light-saturated photosynthetic rate (A_{\max}) and stomatal conductance (g_s) were recorded (after about 40 min), leaf temperature was lowered to 15 °C, with all other conditions unchanged. The leaf was kept in the cuvette at a leaf temperature of 15 °C for 1 h, after which A_{\max} and g_s were remeasured. To measure chlorophyll a fluorescence, plants were placed in growth chambers maintaining

temperatures of 15 and 25 °C, respectively, for 1 h before effective quantum yield of PSII (Φ_{PSII}) to PPF was measured with a modulated fluorimeter (PAM 2000, Waltz, Effeltrich, Germany). The electron transport rate through PSII at a given PPF was then estimated as (ETR) = $\Phi_{\text{PSII}} \times 0.84 \times 0.5 \times \text{PPF}$.

To compare the responses of *A. marina* and *K. candel* to long-term chilling temperatures, five seedlings of similar size per species were transferred to two growth chambers (Conviron GC 108, Winnipeg, Canada) controlled at 15 or 30 °C. After 4 and 10 days of treatment, A_{\max} , g_s , F_v/F_m and the response of Φ_{PSII} to PPF were measured at a leaf temperature of 25 °C. Leaves were dark-adapted for 30 min before measurement of F_v/F_m . The initial chlorophyll fluorescence (F_0) was excited with a dim red light (about 1 μmol m⁻² s⁻¹) modulated at a frequency of 600 Hz. Maximal chlorophyll fluorescence (F_m) was induced by a 0.8-s pulse of 5000 μmol m⁻² s⁻¹ PPF. After 20 days in the growth chambers, leaves were collected and total chlorophyll concentration and leaf mass per leaf area (LMA) determined. Total leaf chlorophyll concentration was measured by extracting chlorophyll from the leaf with 96% ethyl alcohol, and subsequent spectrophotometric (Model V-560, Jasco, Tokyo, Japan) analysis of the extract at wavelengths of 649 and 665 nm (Wintermans and Mots 1965). A 2 × 2 cm² leaf sample from each experimental plant was collected and dried at 50 °C for 48 h and then weighed. The LMA was calculated as dry mass per unit leaf area.

All statistical tests were performed with the computer software SYSTAT (Statistical Solution, Cork, Ireland). Significant differences are reported as $P < 0.05$.

Results

Short-term chilling effects

At a leaf temperature of 25 °C, *A. marina* and *K. candel* had similar A_{\max} and g_s (Table 1). After exposure to a leaf temperature of 15 °C for 1 h, A_{\max} and g_s for both species were reduced (Table 1), and the reduction in A_{\max} was proportional to that in g_s . However, the reductions in A_{\max} and g_s were significantly greater in *A. marina* than in *K. candel*.

For both species, there was no significant change in F_v/F_m between leaves exposed to 15 and 25 °C for 1 h. However, the Φ_{PSII} at any given PPF was significantly lower in leaves held at 15 °C than in leaves held at 25 °C (Figures 1C and 1D). Consequently, in both species, ETR at PPF > 400 μmol m⁻² s⁻¹, light-saturated ETR, and the PPF required to saturate ETR were all

Table 1. Mean ± SE ($n = 5$) of light-saturated photosynthetic rate (A_{\max} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) and stomatal conductance (g_s ; $\text{mmol m}^{-2} \text{s}^{-1}$) of *K. candel* and *A. marina* measured at 25 and 15 °C. Values within the same column followed by different letters are significantly different at $P = 0.05$, *t*-test.

	<i>K. candel</i>		<i>A. marina</i>	
	A_{\max}	g_s	A_{\max}	g_s
25 °C	14.4 ± 0.6 a	192 ± 11 a	15.1 ± 0.7 a	191 ± 7 a
15 °C	12.1 ± 1.0 b	159 ± 16 a	8.2 ± 1.1 b	107 ± 12 b
Proportional change	-16%	-17%	-46%	-44%

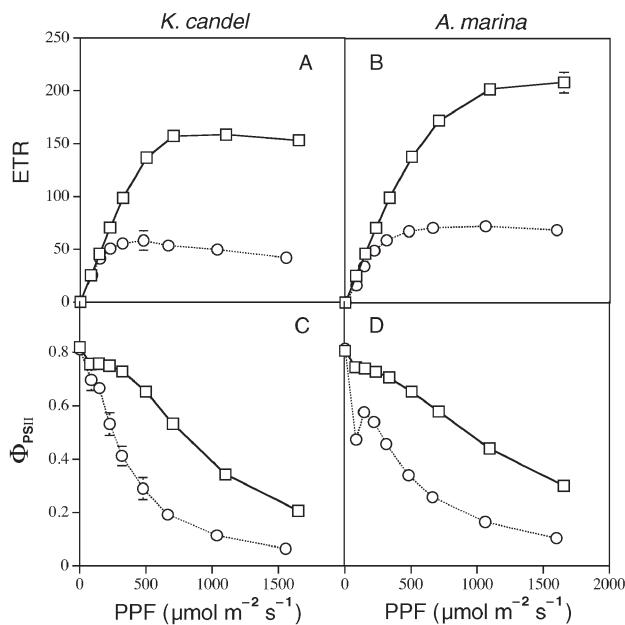


Figure 1. Response of electron transport rate (ETR) and effective quantum yield of photosystem II (Φ_{PSII}) to photosynthetic photon flux (PPF) in leaves of *K. candel* (A, C) and *A. marina* (B, D) measured at air temperatures of 15 °C (○) or 25 °C (□).

significantly reduced in leaves held at 15 °C compared with leaves held at 25 °C (Figures 1A and 1B).

Long-term chilling effects

Leaves of *K. candel* and *A. marina* grown in temperature-controlled chambers at 15 or 30 °C for 4 days had similar A_{max} and g_s (Figure 2). However, after 10 days, there were significant differences in photosynthetic gas exchange responses between the species. Both A_{max} and g_s in leaves of *A. marina* grown at 15 °C for 10 days were reduced significantly compared with values in the 30 °C treatment (Figures 2B and 2D), whereas the 15 and 30 °C treatments had no significant effect on A_{max} and g_s in leaves of *K. candel* (Figures 2A and 2C). Leaves of *K. candel* grown at 15 or 30 °C did not differ in the response of ETR to PPF (Figures 3A and 3C) after 4 or 10 days of treatment. In contrast, leaves of *A. marina* grown at 15 °C showed significant reductions in ETR at PPF > 400 μmol m⁻² s⁻¹ after 4 days of treatment compared with values in the 30 °C treatment (Figure 3B) and the reduction in ETR was even greater after 10 days of growth at 15 °C (Figure 3D).

Plants of both species had significantly lower F_v/F_m ratios after 4 days of growth at 15 °C compared with plants grown at 30 °C (Table 2). The reduction in F_v/F_m was 25 and 28% for *K. candel* and *A. marina*, respectively. After 10 days, F_v/F_m in leaves of *K. candel* was reduced by 20% in the 15 °C chambers compared with the 30 °C chambers, whereas F_v/F_m in leaves of *A. marina* was reduced by 30%.

Leaf mass per area increased significantly in plants grown for 20 days at 15 °C compared with plants grown at 30 °C (Table 3). The proportional increase in LMA was similar in both species, 57 and 54 % for *K. candel* and *A. marina*, respectively.

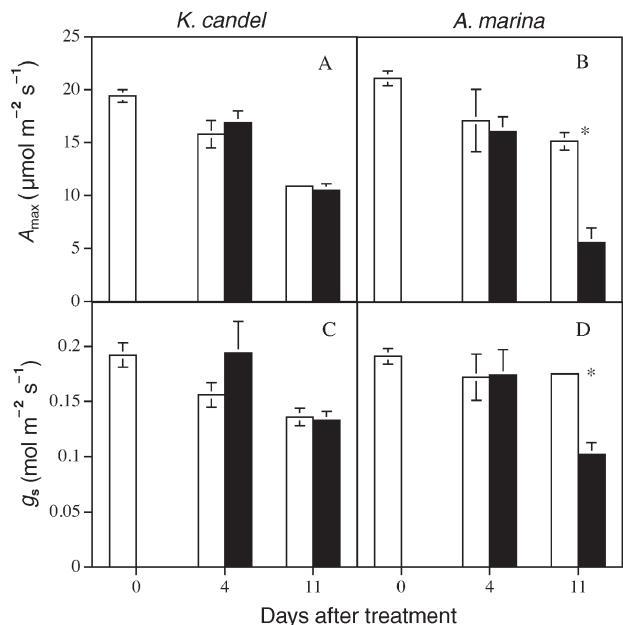


Figure 2. Light-saturated photosynthetic rate (A_{max}) and stomatal conductance (g_s) of leaves of *K. candel* (A, C) and *A. marina* (B, D) after 4 and 10 days of growth in chambers at 15 °C (closed bars) and 30 °C (open bars). Vertical bars represent 1 SE of treatment means ($n = 5$). An asterisk indicates significant differences ($P < 0.05$) between temperature treatments.

There was no significant change in total leaf chlorophyll concentration between *K. candel* grown for 20 days at 15 and 30 °C (Table 3). In contrast, *A. marina* had significantly lower

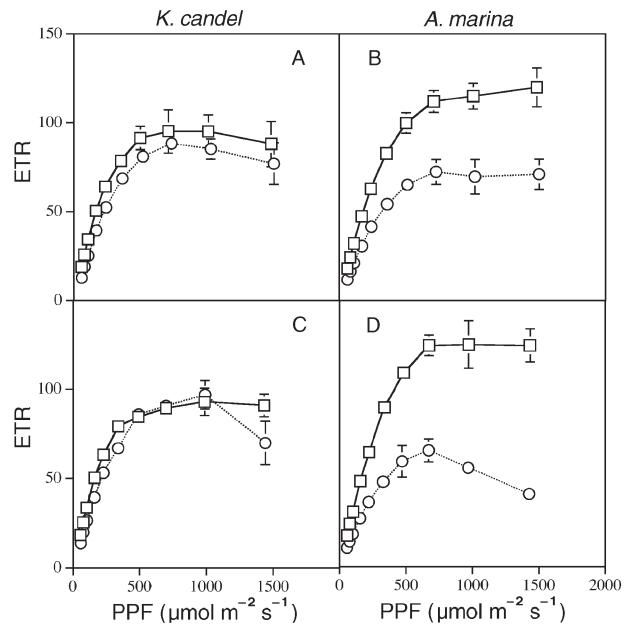


Figure 3. Response of electron transport rate (ETR) to photosynthetic photon flux (PPF) in leaves of *K. candel* (A, C) and *A. marina* (B, D) after 4 (A, B) and 10 (C, D) days of growth in chambers at 15 °C (○) and 30 °C (□).

Table 2. The F_v/F_m ratio (mean \pm SE, $n = 5$) of *K. candel* and *A. marina* after 4 and 10 days of growth in controlled environment chambers at 15 and 30 °C. Values within the same row followed by different letters are significantly different at $P = 0.05$, *t*-test.

Days of growth	<i>K. candel</i>		<i>A. marina</i>	
	30 °C	15 °C	30 °C	15 °C
4 Days	0.81 \pm 0.01 a	0.61 \pm 0.02 b	0.79 \pm 0.01 a	0.57 \pm 0.02 c
10 Days	0.83 \pm 0.01 a	0.66 \pm 0.03 b	0.80 \pm 0.01 a	0.56 \pm 0.03 c

total leaf chlorophyll concentrations when grown for 20 days at 15 °C than at 30 °C (Table 3).

Discussion

Temperature is one of the most important environmental factors affecting plant distribution (Berry and Björkman 1980). Many plants of tropical and subtropical origin are chilling-sensitive, showing impaired photosynthesis and breakdown of chlorophyll after exposure to temperatures of 15 °C or less. We found that exposure of the mangrove species, *A. marina* and *K. candel*, to 15 °C for 1 h resulted in reductions in A_{max} and g_s (Table 1) in both species. The similar proportional decreases in A_{max} and g_s suggest that the depression of light-saturated photosynthetic rate by short-term exposure to chilling temperature was caused by low-temperature-induced stomatal closure. Greater reductions in g_s for *A. marina* compared with *K. candel* indicate that stomata of *A. marina* are more sensitive to chilling temperatures than those of *K. candel*.

In addition to causing decreases in A_{max} and g_s , chilling temperatures also caused significant decreases in quantum yield of PSII and ETR in both species (Figure 1). However, in both species, the reductions in light-saturated ETR were greater than the reductions in A_{max} . The fluorescence-derived ETR values, which reflect the relative rate of energy conversion in PSII (Genty et al. 1989, Schreiber et al. 1994) do not necessarily correspond to the rate of CO₂ fixation. There are other forms of electron transport passing through PSII, such as photorespiration, nitrite reduction and the Mehler ascorbate peroxidase cycle. Our results indicate that there might be a significant flux of electrons through alternative routes under high light + low temperature conditions in both species. This might represent an initial response to short exposure to chilling temperature, acting to dissipate excess excitation energy in the short-term.

Results consistent with this mechanism were found in the long-term results as well. Though there were no significant differences in A_{max} between *A. marina* plants grown at 30 and 15 °C for 4 days (Figure 2), light-saturated ETR was significantly reduced in plants grown at 15 °C, perhaps indicating that a significant flux of electrons occurs through alternative routes to PSII.

After transfer to the temperature-controlled chambers for 4 days, A_{max} and g_s decreased from pre-transfer values even in the 30 °C chamber. This decrease may have been associated with the lower irradiances in the growth chamber (about 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$) compared with the greenhouse. Nevertheless, *K. candel* and *A. marina* responded differently in their photosynthetic gas exchange (Figure 2), chlorophyll fluorescence (Figure 3) and chlorophyll contents (Tables 2 and 3) to the growth temperature treatments, with *A. marina* demonstrating greater sensitivity to changes in growth temperatures between 30 and 15 °C.

Photoinhibition, defined as reduced photosynthesis at high PPF (Powles 1984), leads to decreases in the efficiency of light capture and lower carbon acquisition by leaves, and hence reduced plant growth (Laing et al. 1995, Werner et al. 2001). Photoinhibition of PSII is indicated by reductions in the ratio of F_v/F_m . We measured reductions in F_v/F_m in leaves of both species grown at 15 °C, and found significantly greater reductions for *A. marina* than for *K. candel* (Table 2). Though *K. candel* showed a 20% reduction in F_v/F_m ratio after 10 days at 15 °C (Table 2), ETR and A_{max} were not significantly affected (Figure 3). In contrast, *A. marina* grown at 15 °C for 10 days showed significant reductions in A_{max} , g_s , quantum yield of PSII and F_v/F_m ratio. The greater relative reduction in A_{max} than in g_s suggests that stomatal closure cannot fully account for the depression in A_{max} (Figure 3). Other factors, e.g., light inactivation of PSII or reduction in the amount or activity

Table 3. Chlorophyll concentration (Chl; g m^{-2} , mean \pm SE, $n = 5$) and leaf mass per area (LMA; g m^{-2}) of *K. candel* and *A. marina* after 20 days in controlled environment chambers at 30 and 15 °C. Values within the same column followed by different letters are significantly different at $P = 0.05$, *t*-test.

Temperature	<i>K. candel</i>		<i>A. marina</i>	
	Chl	LMA	Chl	LMA
30 °C	0.45 \pm 0.02 a	78.3 \pm 4.6 a	0.51 \pm 0.12 a	96.3 \pm 6.1 a
15 °C	0.40 \pm 0.01 a	122.8 \pm 5.4 b	0.20 \pm 0.02 b	147.8 \pm 11.6 b
Proportional change	-11%	+56.8%	-60.8%	+53.5%

of Rubisco, may also contribute to the depression in A_{max} . Generally, photoinhibition of PSII is recoverable only through synthesis of new D1 protein (Greer et al. 1986, Nishiyama et al. 2001). Reductions in F_v/F_m in leaves of both species grown at 15 °C indicate that the rate of synthesis of new D1 protein may be inhibited at chilling temperatures, as has been found in maize grown at chilling temperatures (Fryer et al. 1995). A reduction in Chl a fluorescence in response to low temperatures has also been observed in chilling-sensitive plants such as bean (Hetherington et al. 1989), tomato (Bruggemann et al. 1992) and maize (Hetherington et al. 1989, Janda et al. 1994, Haldimann et al. 1996).

The reductions in ETR and A_{max} (Figure 2) in *A. marina* after 10 days at 15 °C may have been due to photoinhibition of PSII (Table 2). However, there are studies showing little correspondence between reductions in photosynthesis under high light + low temperature conditions and the loss of PSII activity (Hodgson and Raison 1989, Tyystjärvi et al. 1989). Several studies have shown that PSI is the site of chilling damage in chilling-sensitive plants (Havaux and Davaud 1994, Terashima et al. 1994, Ivanov et al. 1998, Tjus et al. 1998, Sonoike 1998, Kudoh and Sonoike 2002). Photoinhibition of PSI may occur under relatively weak illumination at chilling temperatures (Terashima et al. 1994, Sonoike 1996). Because we did not measure PSI activity, we cannot identify which of these two mechanisms might be responsible for the reductions in ETR and A_{max} .

We found that chilling temperatures differentially affected our study species. At 15 °C, *A. marina* seedlings had reduced light-saturated rates of photosynthesis, potential quantum yields, light-saturated rates of electron transport and total leaf chlorophyll concentration. From these results, we predict that, in nature, the growth of *A. marina* seedlings will be significantly reduced when air temperature drops below 15 °C. In northern Taiwan, mean monthly air temperatures in January and February are about 14–16 °C and mean minimum air temperatures can drop to 12 °C. In contrast, in southern Taiwan, mean monthly air temperatures in January and February are about 17–19 °C and mean minimum air temperatures seldom drop below 15 °C (Climatological Data Annual Report, Central Weather Bureau, R.O.C.). Thus, chilling temperatures that occur during the winter months in northern Taiwan potentially limit the growth of *A. marina*. In addition, *A. marina* blooms between May and July, with seed maturation in October (personal observation). Generally, therefore, *A. marina* seedlings have only 2 months of favorable growth conditions in northern Taiwan before mean monthly air temperatures drop to 15 °C, implying that environmental selection for chilling tolerance in mangrove species is greater in northern Taiwan than in southern Taiwan. Species differences in response to chilling temperatures may thus explain the differences in the northern limits to the distribution of *K. candel* and *A. marina* in Taiwan. It is unclear which factors are limiting the growth of *K. candel* in southern Taiwan. Currently, we are investigating differences in nutrient requirements and salinity tolerances between these two species.

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