

Research paper

Photosynthetic Responses and Acclimation to Temperature in Seven Conifers Grown from Low to High Elevations in Subtropical Taiwan

Jen-Hsien Weng,^{1,3)} Tien-Szu Liao²⁾

[Summary]

Since most conifer species are commonly distributed in low-temperature regions, information of the photosynthetic response to temperature of conifers growing in high-temperature regions is little known. In order to obtain information on the photosynthetic response of conifers to global warming, the photosynthetic responses of 7 conifers grown from low to high elevations in subtropical Taiwan to both growth and measurement temperatures were studied. The results indicated that plants, except *Chamaecyparis obtusa* var. *formosana*, grown at high temperatures (30/23°C, day/night), exhibited lower inhibition of the light-saturated photosynthetic rate (P_N) at high temperature and an increase in the optimum temperature for photosynthesis (T_{opt}). The T_{opt} values of conifers with low- and high-elevational distributions grown at low temperatures (20/10°C) were 20~23 and 16~21°C, respectively; and T_{opt} values of these conifers grown at high temperatures were 23~27 and 21°C, respectively. Differences in T_{opt} values for 3 conifers (*Nageia nagi*, *Podocarpus macrophyllus*, and *Calocedrus macrolepis* var. *formosana*) with low-elevation (< 1000~1900 m) distributions, and 1 conifer (*Pinus taiwanensis*) with a broad-elevational (750~3000 m) distribution with low- and high-temperature acclimation were 2.2~7.7°C; those for 2 conifers with high-elevational distributions (*Cha. formosensis* and *Cha. obtusa* var. *formosana*, 1000~2900 m) were -0.7~2.3°C. In addition, 1 species with a high-elevational distribution (*Tsuga chinensis* var. *formosana*, 2000~3500 m) grown at low temperatures, and 1 species (*P. taiwanensis*) with a broad elevational distribution grown at high-temperatures both maintained relatively high P_N values ($\geq 90\%$ of the maximum) at wide temperature ranges (8~24 and 18~34°C, respectively). From the above results it was concluded that, just like broadleaf evergreen trees, the photosynthesis of conifer plants distributed at low and high elevations in Taiwan adapts to the temperature of their habitat through both genetic variations and thermal acclimation. Conifers with low- and broad-elevational distributions generally exhibited a higher potentiality for thermal acclimation of the T_{opt} when growth temperatures shifted from low to high.

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研究報告

原生於亞熱帶台灣從低至高海拔的七種針葉樹 之光合作用對溫度之反應及馴化

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摘要

由於針葉樹大多分布於低溫地區，對分布於高溫地區者較少研究。為提供地球暖化因應之基本資料，本研究以7種分布於台灣不同海拔之針葉樹為對象，探討其光合作用對其生長溫度及測定溫度之反應。結果顯示，當幼苗培養於高溫環境(30/23°C，日/夜)下，會減少測定時的高溫對其光合作用之抑制，使光合適溫(T_{opt})升高。分布於低及高海拔之針葉樹種，當生長於低溫(20/10°C)時，其 T_{opt} 分別為20~23及16~21°C，而生長於高溫時則分別為23~27及21°C。當同一物種分別培養於高溫及低溫環境下，其 T_{opt} 之差異，三種(竹柏、大葉羅漢松、台灣肖楠)分布於低海拔(< 1000~1900 m)及一種分布於廣海拔(台灣二葉松，750~3000 m)者為2.2~7.7°C，而兩種(紅檜、台灣扁柏)分布於高海拔(1000~2900 m)者為-0.7~2.3°C。此外，有一分布於高海拔樹種(鐵杉，2000~3500 m)當培養於低溫環境下，及另一廣海拔分布樹種(台灣二葉松)當培養於高溫環境下時，均可在較廣泛圍之溫度下(各為18~34及8~24°C)維持高光合速率(≥最大值之90%)。由以上結果可知，就如常綠闊葉樹，原生於亞熱帶台灣不同海拔之針葉樹種，其光合作用能藉基因分化及對溫度之馴化來適應其棲地的溫度。而且分布於低海拔及廣海拔者，當生長溫度上升時，其 T_{opt} 之熱馴化潛力通常較高。

關鍵詞：海拔、針葉樹、光合作用、溫度。

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INTRODUCTION

Temperature is a major limiting factor determining the elevational- and latitudinal-distributions of plants. Photosynthesis is readily influenced by temperature; when the ambient temperature is either above or below a certain range, photosynthesis increasingly becomes inhibited. The optimal temperature for photosynthesis (T_{opt}) is known to vary among species and within species with different origins that display either genetic vari-

ability or an acclimation to different growth temperatures (Slatyer 1977, Berry and Björkman 1980, Weng and Ueng 1997, Zhang et al. 2005, Hikosaka et al. 2006). Plants grown at high elevations or latitudes generally have a lower T_{opt} , compared to those grown in regions with high temperatures (Slatyer 1977, Weng and Ueng 1997, Zhang et al. 2005). On the other hand, some alpine plants show a much-broader T_{opt} range to cope with short-

term changes in temperature (Engel et al. 1986, Körner and Diemer 1987).

The response of photosynthesis to temperature was found to vary in the same individual subjected to different temperature regimes. In many species, the T_{opt} increases with an increasing growth temperature (Berry and Björkman 1980). This thermal acclimation was documented under both field conditions, based on seasonal trends in the temperature response (Slatyer and Morrow 1977, Lewis et al. 2001), and growth chamber conditions by changing the temperature (Slatyer 1977, Gunderson et al. 2000, Cunningham and Read 2002, Hikosaka et al. 2006).

Conifers are most commonly distributed in temperate and sub-arctic zones as well as in alpine and sub-alpine areas of subtropical regions. There are extensive mountainous areas higher than 3000 m in Taiwan (21°55'~25°18'N), a subtropical island, where many conifers are distributed in alpine and sub-alpine areas, and several conifers are also found at low elevations. For example, *Podocarpus macrophyllus* is distributed below 1000 m, and *Pinus taiwanensis* is distributed over a broad range of elevations, i.e., 750~3000 m. (Li and Keng 1994).

Differences between high- and low-temperature-region forests have long interested ecologists. In addition, with increases in global air temperatures induced by the greenhouse effect, plant responses to increasing temperatures have become a major area of concern in recent decades (Gunderson et al. 2000, Norby and Luo 2004). Unlike deciduous species, the leaves of which are exposed to less-extreme temperature fluctuations, conifers retain their needles for several years. Therefore, their photosynthetic apparatus must be able to withstand periods of severely low (high-latitude or high-elevation regions) or high (lowlands of tropical and subtropical areas)

temperatures and still retain the capacity for photosynthesis during intervening warm periods. Thus, it is important to elucidate the temperature dependency of photosynthetic rates for a basic understanding of environmental changes in the future. Because little information on the temperature response of photosynthesis of conifers distributed in high-temperature regions has been reported (Weng et al. 2009), in the present study, 7 species of conifers distributed from low to high elevations in Taiwan were used to determine their photosynthetic characteristics in response to various temperature regimes.

MATERIALS AND METHODS

Two or 3-yr-old trees of 7 conifer species distributed from low to high elevations in Taiwan (Table 1), including 2 populations of *P. taiwanensis* collected from 800 and 2600 m, were used as materials. The young trees were grown in pots (16 cm in diameter, 12 cm deep) filled with fine sandy loam, grown outdoors in a nursery at Taichung (24°10'N, ca. 70 m). In May 2002, 3~4 mo after being transplanted, the potted young trees were transferred to a growth-chamber and exposed to low (20/10°C, day/night) or high (30/23°C) temperatures for 3~4 wk. Both treatments were under the same day/night photo period of 12/12 h with 800 mol m⁻² s⁻¹ of photosynthetic photon flux density (PPFD), provided by a metal halogen lamp (HQI-TS 250W/D, Osram, München, Germany). One conifer with a high-elevational distribution, i.e. *Tsuga chinensis* var. *formosana*, was grown at the low temperature only.

The light-saturated photosynthetic rates (P_N) of young trees grown at different temperatures were measured on intact current-year needles, which were fully expanded before being transported to the growth chamber,

Table 1. Conifer species used in this study and elevations of their distribution (from Li and Keng 1994)

Species	Family	Distribution elevation (m)
<i>Nageia nagi</i>	Podocarpaceae	< 1000
<i>Podocarpus macrophyllus</i>	Podocarpaceae	< 1000
<i>Calocedrus macrolepis</i> var. <i>formosana</i>	Cupressaceae	300~1900
<i>Chamaecyparis formosensis</i>	Cupressaceae	1000~2900
<i>Chamaecyparis obtusa</i> var. <i>formosana</i>	Cupressaceae	1300~2800
<i>Pinus taiwanensis</i>	Pinaceae	750~3000
<i>Tsuga chinensis</i> var. <i>formosana</i>	Pinaceae	2000~3500

in an open gas exchange system (Liao and Weng 2002) by measuring the differential CO₂ concentration with an infrared gas analyzer (model-880, Rosemount Analytical, Solon, OH, USA) at temperatures of 10, 15, 20, 25, 30, and 35°C, 75% relative humidity, 1200 mol m⁻² s⁻¹ of PPFD provided by a metal halide lamp (D400, Toshiba, Tokyo, Japan), atmospheric CO₂ concentration, and a wind speed of 1.5 m s⁻¹. The air used for photosynthesis measurements was taken from outdoors, at a height 3 m above the roof level. The humidity of air entering the chamber was controlled by passing the flow through temperature-controlled water, and it was monitored by a flow-through hygrometer (1100AP, General Eastern, Watertown, MA, USA). The temperature in the chamber was controlled by circulating water through a radiator inside the chamber, and the temperatures of both the leaf (*T*) and air were measured with copper-constantan thermocouples. Shoots of 10 cm in length were used for each replication of each species and kept at each temperature for about 1 h until the CO₂ exchange of the needles had stabilized. One plant was designated a replicate, and 3 or 4 plants were measured for each temperature treatment. Because high and low temperatures might damage the photosynthetic function (Berry and Björkman 1980), during measurement, the temperature treatment of each plant was carried out in 2

stages, i.e., from 20 to 35°C and from 20 to 10°C. The plant, after going through the temperature treatment of 1 stage, was returned to the temperature-controlled growth chamber for 2 d before it underwent the 2nd-stage temperature treatment. For most plants grown at high temperatures, the 10°C treatment was omitted.

The relationship between the relative light-saturated photosynthetic rate (*P_N*%, using the maximum rate of the same shoot as 100%) and *T* was estimated by a polynomial regression, using Sigmaplot 9.0 software (Jandel Scientific, San Rafael, CA, USA). A 2nd-order polynomial equation ($P_N\% = a + bT + cT^2$) was found to give an adequate fit to all of the data, and the *T*_{opt} was calculated as $T_{opt} = -b/c/2$ (Leakey et al. 2003, Zhang et al. 2006). The slope between the *T*_{opt} and growth temperature of each species or population was calculated as $(T_{opt} \text{ grown at } 30/23^\circ\text{C} - T_{opt} \text{ grown at } 20/10^\circ\text{C}) / [(30 + 23) / 2 - (20 + 10) / 2]$.

Seasonal changes in air temperature at different elevations were obtained from meteorological data (<http://www.cwb.gov.tw/eng/index.htm>) recorded by meteorological stations at different elevations in central Taiwan (Taichung (24°09'N, 120°41'E, 78 m), Sun Moon Lake (23°52'N, 120°54'E, 1014 m), Alishan (23°31'N, 120°48'E, 2408 m) and Yushan (23°29'N, 120°57'E, 3858 m)).

RESULTS

According to the data collected in 1971~2000 by meteorological stations at different elevations in central Taiwan, the monthly mean air temperatures in the lowlands were ca. 28°C in the warm season and 16°C in the cool season; and temperature decreases by about 0.5°C per 100-m rise in elevation (Fig. 1).

Relationships between the $P_N\%$ and T for all tested conifer species or populations significantly fit a 2nd-order polynomial equation ($r = 0.615\sim 0.976$, $p < 0.05\sim 0.001$, Fig. 2). We herein used this equation to estimate the T_{opt} (Leakey et al. 2003, Zhang et al. 2006); above and below this temperature, photosynthesis becomes increasingly inhibited (Fig. 2). When grown at a low temperature, T_{opt} values of 3 conifers with low-elevation distributions and 3 conifers with high-elevation distributions were 20~23 and 16~21°C, respectively; when grown at high temperatures, T_{opt} values of

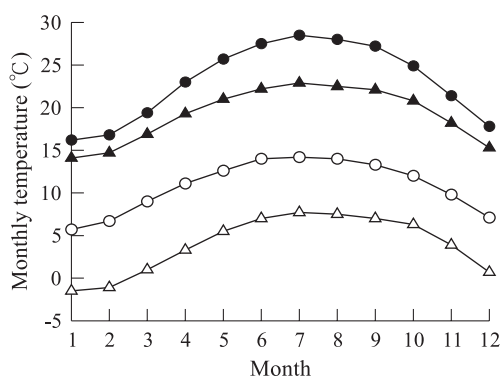


Fig. 1. Mean monthly air temperatures (1971~2000) from low to high elevations in central Taiwan. Data were collected by meteorological stations at different elevations [Taichung (24°09'N, 78 m, ●), Sun Moon Lake (23°52'N, 1014 m, ▲), Alishan (23°31'N, 2408 m, ○), and Yushan (23°29'N, 3858 m, △)].

these conifers were 23~27 and 21°C, respectively (*T. chinensis* var. *formosana* was not grown at the high temperature). For 1 conifer (*P. taiwanensis*) with a broad elevational distribution, T_{opt} values of populations sampled separately from low and high elevations were 19 and 18°C, respectively, when grown at low temperatures; and these temperatures were 26 and 23°C, respectively, when grown at high temperatures (Figs. 2, 3). These results indicate that in both low- and high-temperature-grown plants, T_{opt} values generally decreased as the distribution elevation increased; and acclimation to high temperatures increased the T_{opt} of each species. The difference in T_{opt} values within the same species grown at low and high temperatures was 2.2~6.0°C for 3 conifers with low-elevational distributions, -0.7~2.3°C for 2 conifers with high-elevational distributions; and 7.7°C for the population from a low elevation and 4.5°C for the population from a high elevation of a broadly distributed conifer (*P. taiwanensis*). Slopes between the T_{opt} and growth temperature of those conifers were 0.19~0.53, -0.06~0.20, 0.67, and 0.39°C °C⁻¹, respectively (Fig. 3B).

Curve fitting also indicated that $P_N\%$ values of plants grown at low temperature were maintained near ($\geq 90\%$) the maximum of the T range of 18~28 (*N. nagi*) to 8~24°C (*T. chinensis* var. *formosana*), and these ranges for plants grown at a high temperature were 21~33 (*N. nagi*) to 15~26°C (*Cha. obtusa* var. *formosana*) (Figs. 2, 3). In addition, *T. chinensis* var. *formosana*, the species with the highest elevational distribution in the present study grown at a low temperature, and *P. taiwanensis*, a species with a broad elevational distribution, grown at a high temperature maintained relatively high $P_N\%$ values for a wide temperature range.

When the T was above and below the T_{opt} , the decrease in P_N varied with species

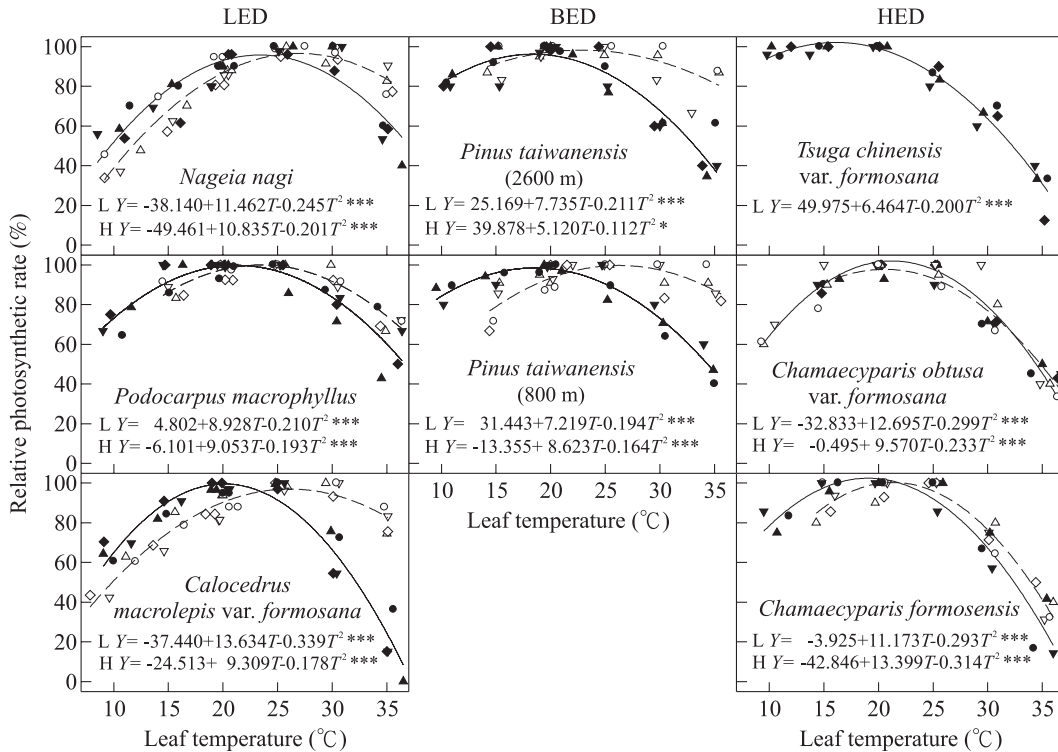


Fig. 2. Effect of measuring temperature (T) on the relative light-saturated photosynthetic rates (Y) of high- (H, 30/23°C, day/night, dotted line and open symbols) and low (L, 20/10°C, solid line and closed symbols)-temperature-grown conifer species. Different symbols represent different replicates. Regression lines were fitted using a 2nd-order polynomial equation ($r = 0.615\text{--}0.976$). * and *** are $p < 0.05$ and $p < 0.001$, respectively; LED, BED and HED are species with low-, broad-, and high- elevational distributions, respectively.

and growth temperature (Fig. 2). A comparison within the same species indicated that plants grown at a high temperature usually showed a higher $P_N\%$ than plants grown at a low temperature at a high measuring temperature. On the contrary, plants grown at a low temperature always showed higher $P_N\%$ values than plants grown at a high temperature at a low measuring temperature (Figs. 2, 3). However, for *Cha. formosensis* and *Cha. obtusa* var. *formosana*, which have high-elevation distributions, little difference in the $P_N\%$ - T relation was observed between plants grown at high and low temperatures. As to the difference in the temperature response

of $P_N\%$ among species, 3 species with high-elevation distributions, i.e., *T. chinensis* var. *formosana*, *Cha. Formosensis*, and *Cha. obtusa* var. *formosana*, and 1 species with a broad elevation distribution, *P. taiwanensis*, showed lower decreasing rates of P_N at a low measuring temperature (Fig. 2). Most species with either high- or broad-elevation distributions retained their P_N at more than 80% of the maximum at 10°C when grown at a low temperature. On the contrary, P_N values of 3 species with low-elevation distributions, i.e., *N. nagi*, *P. macrophyllus*, and *Cal. macrolepis* var. *formosana*, decreased to 70% of the maximum at the same temperature condition

(Fig. 2). In both high- and low-temperature-grown plants, P_N values of the 3 conifers with

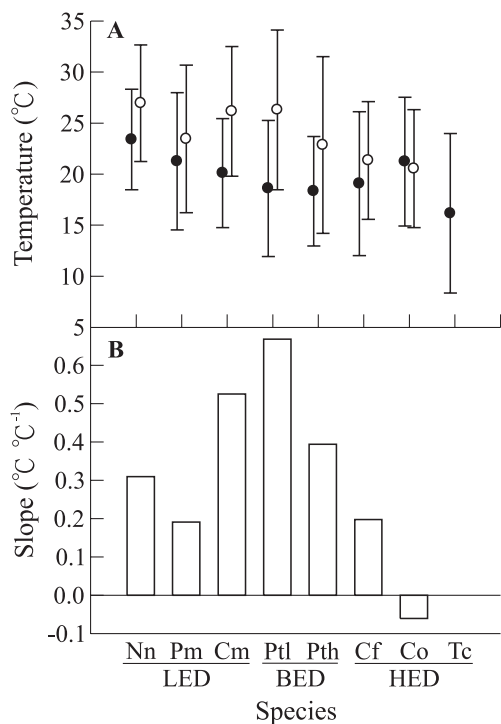


Fig. 3. A: Optimum temperature for photosynthesis (T_{opt} , closed and open circles) and the temperature range for the photosynthetic rate to be maintained at near the maximum ($\geq 90\%$) rate (vertical bars). Closed circles are plants grown at low temperatures (20/10°C, day/night), and open circles are plants grown at high temperatures (30/23°C). B: Slope between the T_{opt} and growth temperature. Nn, *Nageia nagi*; Pm, *Podocarpus macrophyllus*; Cm, *Calocedrus macrolepis* var. *formosana*; Ptl, *Pinus taiwanensis*, low-elevation population; Pth, *Pinus taiwanensis*, high-elevation population; Cf, *Chamaecyparis formosensis*; Co, *Chamaecyparis obtusa* var. *formosana*; Tc, *Tsuga chinensis* var. *formosana*; LED, BED and HED, species with low-, broad- and high-elevational distributions, respectively.

high-elevational distributions were sharply inhibited by high temperature (35°C). But P_N values of the 3 low- and 1 broad-elevational distribution conifers were slightly inhibited when they were grown at a high temperature (Fig. 2).

DISCUSSION

In central Taiwan, the long-term (1971~2000) mean temperatures of the warmest month (July) at Taichung (24°09'N, 78 m) and Alishan (23°31'N, 2408 m) are 28.5 and 14.2°C, respectively; while those of the coldest month (January) are 16.2 and 5.7°C, respectively (Fig. 1). The small monthly temperature difference (8.5°C) reflects the cool summers and warm winters at Alishan, compared to data from temperate and subarctic regions (Larcher 1995).

Temperature can have profound effects on the distribution and growth of woody plants. For example, climatic zones, which are largely determined by temperature variations in relation to elevation and latitude, support specific vegetation types that are determined by natural selection for various temperature regimes (Grace 1987). Rates of physiological processes are also generally affected by temperature. Plants often show photosynthetic acclimation to the temperature regimes in which they are grown (Slatyer 1977, Larcher 1995, Weng and Ueng 1997, Zhang et al. 2005). Results of the present study indicate that conifers with low-elevational distributions showed higher relative P_N values at higher temperatures than those with high-elevational distributions. This suggests an adaptation of photosynthesis in conifers with low-elevational distributions to the high temperatures of their native climate.

In temperate regions, T_{opt} values of conifers are 10~25°C (Alexander et al. 1995,

Larcher 1995, Lewis et al. 2001). Results of the present study indicate that T_{opt} of 3 conifers with high-elevational distributions that were grown at low temperature fell between 16 and 21°C (Figs. 2, 3). These values were within the range of the T_{opt} values of temperate conifer trees and some tropical and subtropical alpine broadleaf plants (Rawat and Purohit 1991, Cavieres et al. 2000).

However, information on the photosynthesis response to temperature of conifers distributed at low elevations of subtropical regions is still lacking. The current study demonstrated that T_{opt} values of high-temperature-grown conifers with a low-elevational distribution in Taiwan were 23~27°C (Figs. 2, 3). These values are lower than those of tropical or subtropical C_3 crops or plants, at 30~40°C (Berry and Björkman 1980, El-Sharkawy et al. 1984), but they are close to those of evergreen broadleaf trees of the tropics and subtropics (Larcher 1995, Cunningham and Read 2002, Leakey et al. 2003). These findings imply that photosynthesis of conifers with low-elevational distributions in Taiwan has adapted to high temperatures.

We herein found that *P. taiwanensis*, a species with a broad elevational distribution, maintained a relatively high P_N ($\geq 90\%$ of maximum) over a wide temperature range (18~34°C) when it was grown at a high temperature (Fig. 2). The same tendency was also found in our previous study (Liao and Weng 2002) for *Alnus formosana*, a deciduous broadleaf tree species with a broad elevational distribution (near 0~3000 m) in Taiwan. For another species with a relatively high P_N over a wide temperature range, Engel et al. (1986) reported that the T_{opt} of *Oxyria digyna* was similar for arctic, alpine, and moderate climate populations. Gunderson et al. (2000) also reported that despite a difference in the growing season temperatures

(4°C) at 2 source sites, no differences in T_{opt} among populations of *Acer saccharum* from the 2 sites were found. Thus, maintaining a near-maximum rate of photosynthesis over a broad range of temperatures would lessen the importance of ecotypic adaptations to specific climate patterns (Gunderson et al. 2000). Nevertheless, our previous study (Weng and Ueng 1997) indicated that the T_{opt} of *Miscanthus*, a perennial C_4 grass with a broad elevational distribution in Taiwan, varied with the temperature regime where it grows, i.e., low-elevation populations showed higher T_{opt} values than high-elevation populations. From the above results, it was concluded that in order to adapt to various temperature conditions of their habitats, species with broad elevational distributions possess at least 2 ways of adaptation. One is to maintain a near-maximum rate of photosynthesis over a wide range of temperatures, and the other is to differentiate into different inheritable characteristics to adapt to temperature environments at various elevations.

Unlike lowlands at high latitudes, tropical alpine environments are characterized by high-amplitude diurnal, rather than seasonal, temperature fluctuations. Plants must maintain their physiological activity on a daily basis year round. In order to adapt to alpine temperature conditions, some alpine plants show a much-broader T_{opt} range to cope with short-time changes in temperature (Engel et al. 1986, Körner and Diemer 1987). For low-temperature-grown plants, the same tendency was found only in *T. chinensis* var. *formosana*, the species with the highest elevational distribution in this study. It remained at near ($\geq 90\%$) the maximum as the T ranged 8~24°C, as calculated from the fitted 2nd order polynomial equation.

With changes in growth temperature, the photosynthetic characteristics of many

plants show considerable thermal acclimation. In general, plants grown at higher temperatures have higher T_{opt} values (Slatyer 1977, Slatyer and Morrow 1977, Berry and Björkman 1980, Gunderson et al. 2000, Lewis et al. 2001, Hikosaka et al. 2006). The response of the T_{opt} to growth temperature may vary within the same individual subjected to different temperature regimes. Slatyer (1977) found a linear relationship between the T_{opt} and growth temperature with a slope of $0.34^{\circ}\text{C }^{\circ}\text{C}^{-1}$ for *Eucalyptus pauciflora*. Similar slopes were observed for *Oxyria digyna* (Billings et al. 1971), *Ledum groenlandicum* (Smith and Hadley 1974), and *Euc. nitens* (Battaglia et al. 1996). But Battaglia et al. (1996) reported $0.59^{\circ}\text{C }^{\circ}\text{C}^{-1}$ for *Euc. globules*. Cunningham and Read (2002) also found an interspecific difference in the T_{opt} -growth temperature relationship. They pointed out that 4 tropical rainforest tree species showed greater shifts in the T_{opt} ($0.16\sim 0.48^{\circ}\text{C }^{\circ}\text{C}^{-1}$) than other 4 temperate rainforest tree species ($0\sim 0.35^{\circ}\text{C }^{\circ}\text{C}^{-1}$). Results of the present study indicate that the slopes between the T_{opt} and growth temperature of 3 conifers with low-elevational and 2 conifers with high-elevational distributions were $0.19\sim 0.53$ and $-0.06\sim 0.20^{\circ}\text{C }^{\circ}\text{C}^{-1}$, respectively; and that of 1 species with a broad elevational distribution was $0.39^{\circ}\text{C }^{\circ}\text{C}^{-1}$ for the population from a high elevation and $0.67^{\circ}\text{C }^{\circ}\text{C}^{-1}$ for the population from a low elevation (Fig. 3B). This tendency was similar to the difference in the shift in the T_{opt} between tropical and temperate rainforest tree species. According to Cunningham and Read (2002), temperate species maintain close to the maximum P_N over a larger span of growth temperatures than do tropical species, thus reducing the need for adjustments of temperature optima. However, results of the present study suggest that when the growth temperature shifts from low to high, the average T_{opt} of 3 conifers with

low-elevational distributions shifted from 21.6 to 25.5°C , while that for 2 conifers with high-elevational distributions shifted from 20.4 to 20.9°C . These results indicate that conifers with low-elevational distributions have a higher potential for thermal acclimation when growth temperatures vary. Also, the difference in T_{opt} between conifers with low- and high-elevational distributions was smaller for low-temperature-grown plants, and larger for high-temperature-grown plants.

From the results of the present study, we concluded that similar to findings of broadleaf evergreen trees, photosynthesis of conifers with high-elevational distributions in subtropical Taiwan is more adapted to low and diurnally harsh temperature conditions, and that of conifers with low-elevational distributions can adjust to high temperatures. When the growth temperatures shifted from low to high, most of the tested species raised their T_{opt} , especially for species with low- and broad-elevational distributions. In addition, species with broad elevational distributions can maintain relatively higher P_N values at a wide temperature range, when grown at high temperatures. These findings provide important information for pertinent research on the effects of global warming.

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