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Gas exchange and epidermal characteristics of *Miscanthus* populations in Taiwan varying with habitats and nitrogen application

J.-H. WENG* and F.-H. HSU**

*Department of Botany, National Chung-Hsing University, Taichung, Taiwan**
*Department of Forage Crops, Taiwan Livestock Research Institute, Council of Agriculture, Hsinhua, Taiwan***

Abstract

Seventeen clones of C_4 grass *Miscanthus* spp. collected from different climatic regions and elevations of Taiwan were transplanted in pots. 15-16 months after collection the plants received 0, 1, and 2 g of nitrogen fertiliser (N_0, N_1, and N_2, respectively) per pot. All the measurements were done 10-12 d after N application. The relationships between net photosynthetic rate (P_N) and photon flux density (PFD) showed a saturated curve, with PFD saturation at about 1 000 μmol m^{-2} s^{-1}. The ranges of PFD saturated P_N (P_{sat}) for all the tested clones with N_0, N_1, and N_2 were 8-16, 11-18, and 12-21 μmol m^{-2} s^{-1}, respectively. The clones from southern Taiwan, a tropical region, showed the highest P_{sat}, followed by the clones from northern Taiwan, a subtropical region, while those from mountainous area showed the lowest P_{sat}. The clones collected from southern Taiwan showed the highest frequency of stomata on the adaxial surface, and those collected from the high mountainous area showed the lowest frequency. Also the adaxial surface of leaves from the higher mountainous area had more wax deposited than the leaves from the lowland. Thus the low P_{sat} in mountain clones is limited by both stomatal and non-stomatal factors. Further, the lower leaf conductance and different epidermal characteristics of mountain clones might prevent excessive loss of heat through transpiration and provide production against ultraviolet-B radiation.

Additional key words: adaxial and abaxial leaf surfaces; altitude; C_4 plant; clone differences; ecotypes; leaf conductance; mesophyll conductance; photosynthesis; stomatal frequency.

Introduction

Miscanthus is a genus of rhizomatous, perennial C_4 grasses, which can be interbred with sugarcane to obtain new sugarcane cultivars (Chen *et al.* 1993). It is also used as a new biomass or fiber crop in Europe, currently being investigated for its biomass potential (McCarthy and Mooney 1995, Clifton-Brown and Jones 1997), because it requires a low input of nitrogen and achieves dry matter yield in excess of other C_4 crops in temperate climates (Beale *et al.* 1996, van der Werf *et al.* 1993).

Compared to C_3 plants, C_4 plants are usually more sensitive to low temperature (Long 1983), so there are few or no C_4 plants in cooler climates (Teeri and Stowe 1976). However, *Miscanthus* is distributed from Pacific Islands to Japan (up to 45°N). In Taiwan (21°55'N–25°18'N), it grows from the coastline up to 3 000 m above sea level (a.s.l.). Photosynthesis, one of the major determinants for biomass in higher plants, is easily influenced by environmental factors, but it can acclimate or adapt to the environment (Berry and Björkman 1980, Berry and Downton 1982, Engel *et al.* 1986, Schwarz and Redmann 1989, Weng 1988, 1993). Beale *et al.* (1996) reported that *Miscanthus*×*giganteus* was unlike other C_4 crops, since it showed high photosynthetic potential in both 120 kg(N) ha^{-1} and no nitrogen applications when grown under temperate field conditions. Previously Weng and Ueng (1997) showed that the temperature response in photosynthesis of *Miscanthus* grown in Taiwan varied with habitats. Optimum temperature of photosynthesis for the clones collected from the lowland was above 35 °C. However, the optimum temperature of P_N for the clone collected from the 2 550 m a.s.l. (mountainous site) was 28 °C, lower than that of most C_4 plants. Kao *et al.* (1998) also found that in Taiwan, *M. floridulus* collected from an altitude of 390 m showed better high-temperature adaptation of photosynthesis and growth than *M. transmorrisonensis* collected from an altitude of 2 700 m.

The above mentioned and other articles (Chou *et al.* 1987, Weng 1993) suggest that *Miscanthus* plants are

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*Fax: 886-4-2874740, e-mail: jhweng@dragon.nchu.edu.tw

differentiated into different ecotypes to adapt to the environment where they are grown, and some photosynthetic characteristics are different from the other C_4 plants. In order to obtain more information about the photosynthetic characteristics of different *Miscanthus* populations in Taiwan, the photosynthetic activities at different irradiances and nitrogen applications were compared.

Materials and methods

Five clones of *Miscanthus* spp. were collected from lowlands of northern Taiwan (24°50'N and 25°08'N, the subtropical region), seven clones from southern Taiwan (21°58'N to 23°05'N, the tropical region), and five clones from a mountainous area of central Taiwan (23°29'N–23°35'N, 120°50'E–120°53'E, 1 000–2 550 m a.s.l.). About 5 rhizomes of each clone were collected from the field between March and April, planted in pots (38 cm diameter) filled with sand loam, and placed outdoors in the campus of the National Chung-Hsing University, Taichung, Taiwan (24°10'N, 78 m). The plants were propagated and divided into 6-9 pots for each clone prepared for use until March, one year after collection. From June to August of this year, the N_0, N_1, and N_2 plants had 0, 1, and 2 g(N) [0, 88, and 176 kg(N) ha^{-1}, 50 % NH_4^++50 % NO_3^-, N concentrations in N_0 were 0.09-0.12 %] applied per pot, respectively. Net photosynthetic rate (P_N), transpiration rate (E), leaf chlorophyll (Chl) content, and leaf surface morphology were determined 10-12 d after N application. All the treatments were given in three replications, measurement was taken once a month for one replication.

P_N and E of the fully-expanded youngest leaves attached to the plants were determined in an open gas exchange system (Weng and Ueng 1997) by measuring CO_2 and H_2O concentrations with an infrared gas analyser (*Anarad, AR600*) at 30 °C, 80 % relative humidity, and wind speed of 1.5 m s^{-1}. A range of PFD from about 150 to 2 000 μmol m^{-2} s^{-1} was used from a metal halide lamp (*D400, Toshiba*, Japan) by cheese-cloth screens and measured with a quantum sensor (*LI-185A, LI-COR*, USA). Temperature in the chamber was controlled by water circulating through a radiator inside the chamber, and the temperatures of both leaf and air were measured with copper-constantan thermocouples. The humidity of air entering the chamber was controlled by passing temperature-controlled water and monitored with a hygrometer (*1100AP, General Eastern*, USA). Four to five leaves (30-40 cm^2) were used in each replication of each clone, and each PFD was kept for about 20 min until CO_2 and H_2O concentrations in the chamber were steady.

Leaf conductance (g_l) was calculated from vapour pressure deficits (VPD) of air to leaf and E of the leaves (Gaastra 1959). The VPD of air to leaf was calculated from temperature and humidity of the leaf and those of air in the chamber, and assuming the relative humidity in the inter-stomatal cavity is 100 % (Salisbury and Ross 1985). Mesophyll conductance (g_m) was calculated from CO_2 concentration of air, CO_2 compensation concentration, P_N, and g_l (Bravdo and Pallas 1982, Salisbury and Ross 1985).

Chl content was determined with a spectrophotometer after acetone extraction (Arnon 1949). Leaf surface morphology was determined by scanning electron microscope (SEM) (*Bausch and Lomb Nanolab 2100*).

Results

Comparison of photosynthetic characteristics among *Miscanthus* populations: The relationship between P_N of *Miscanthus* and PFD showed a saturated curve with a saturating irradiance of about 1 000 μmol m^{-2} s^{-1} (PAR). Photosynthetic capacity varied with different N applications and the regions where these samples were collected. PFD-P_N curves of the clones representing the maximum, medium, and minimum photosynthetic capacity are shown in Fig. 1, and the PFD-saturated photosynthetic rate (P_{sat}) of each clone for different N treatments is shown in Fig. 2. The P_{sat} values for all tested clones with N_0 were 8-16 μmol m^{-2} s^{-1}, with N_2 12-21 μmol m^{-2} s^{-1}, while those with N_1 were intermediate between N_0 and N_2.

The clones collected from southern Taiwan showed the highest P_{sat}, followed by the clones collected from northern Taiwan, and then by those from mountain area, showing the lowest P_{sat} in all N treatments (Table 1 and Fig. 2). Thus the P_{sat} significantly varied with the habitat.

Positive correlations were found for the relations between P_{sat}, g_l, g_m, and Chl content of all the tested *Miscanthus* clones in all N treatments (Fig. 3). However, there was no significantly difference in P_{sat} among the plants collected from different regions under the same g_l (Fig. 3*A*). On the contrast, at the same g_m and Chl content, there were different P_{sat} for plants collected from different regions. The clones from southern Taiwan showed higher P_{sat} than those from northern Taiwan and mountain area under the same g_m and leaf Chl contents (Fig. 3*B,C*).

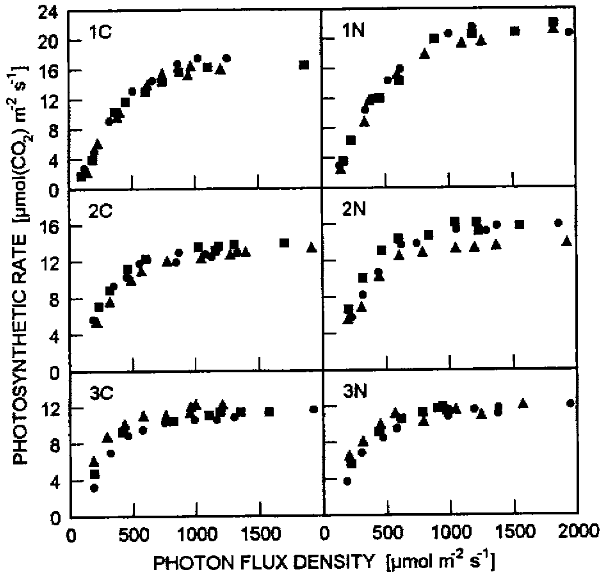

Fig. 1. Photosynthetic rates of *Miscanthus* clones grown with 0 (C) and 2 g (N) of nitrogen fertiliser per pot under various photon fluxes. Clones collected from various regions (1: southern Taiwan; 2: northern Taiwan; 3: 2550 m a.s.l.). Different symbols indicate different replications.

Comparison of epidermal characteristics for *Miscanthus* clones: The comparison of SEM photographs of leaf surface for *Miscanthus* clones showed that the adaxial surface of leaf from higher mountain site (2 550 m a.s.l.) had more wax than that of the lowland site (21°58'N) (Fig. 4). In addition, the clones collected from southern Taiwan showed the highest frequency of stomata on the adaxial surface, and those collected from the high mountain site showed the lowest frequency (Fig. 5). On the contrary, the stomatal frequency on the abaxial surface was remarkably higher than that on the adaxial surface, and no distinguishing clonal difference was observed. The N treatment could increase the stomatal frequency on the adaxial surface in most tested clones, however, no significant effect was observed on that of the abaxial surface (Fig. 5).

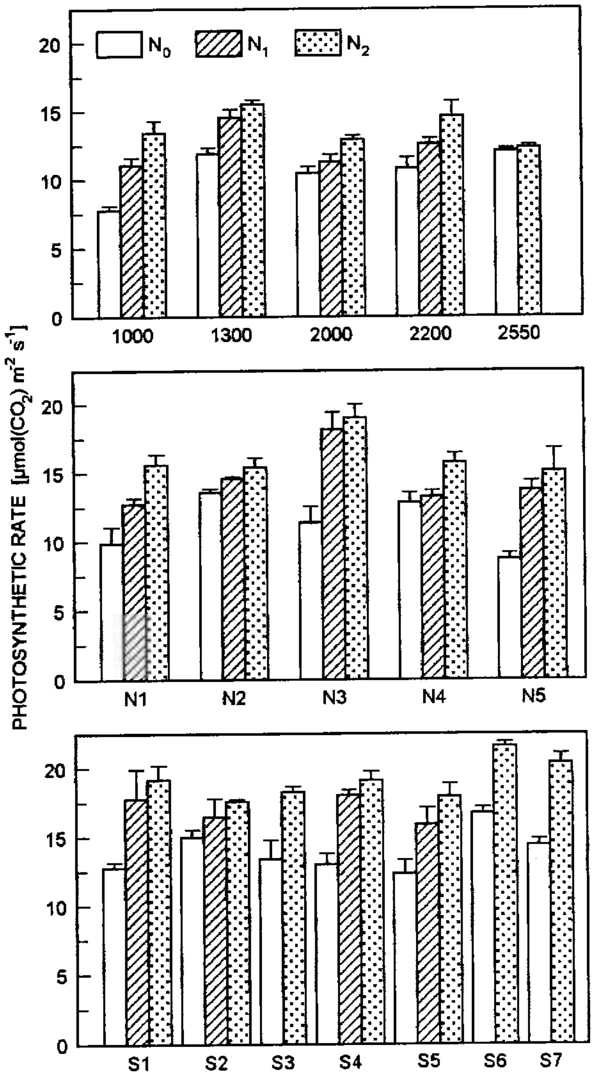

Fig. 2. The PAR-saturated photosynthetic rates of *Miscanthus* clones collected from different regions: 1 000–2 550: elevations [m], N1-N5: northern Taiwan, S1-S7: southern Taiwan. Different amounts of nitrogen fertiliser were applied. Means ± SE.

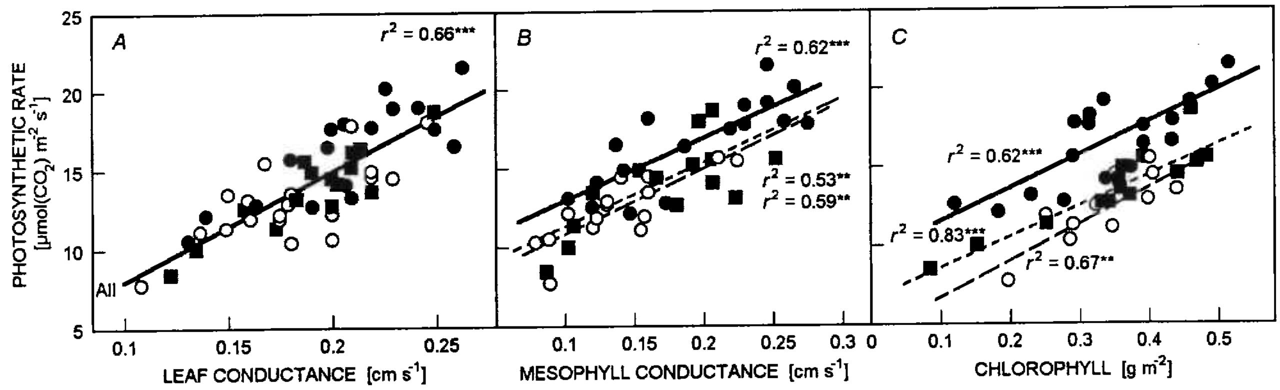

Fig. 3. Relationships between photosynthetic rate and leaf conductance, mesophyll conductance, and leaf chlorophyll content of *Miscanthus* clones collected from different climatic regimes and grown with different concentrations of nitrogen fertiliser. Clones collected from various locations (•: southern Taiwan; □: northern Taiwan; ○: mountainous area). $^{**}p < 0.01$, $^{***}p < 0.001$.

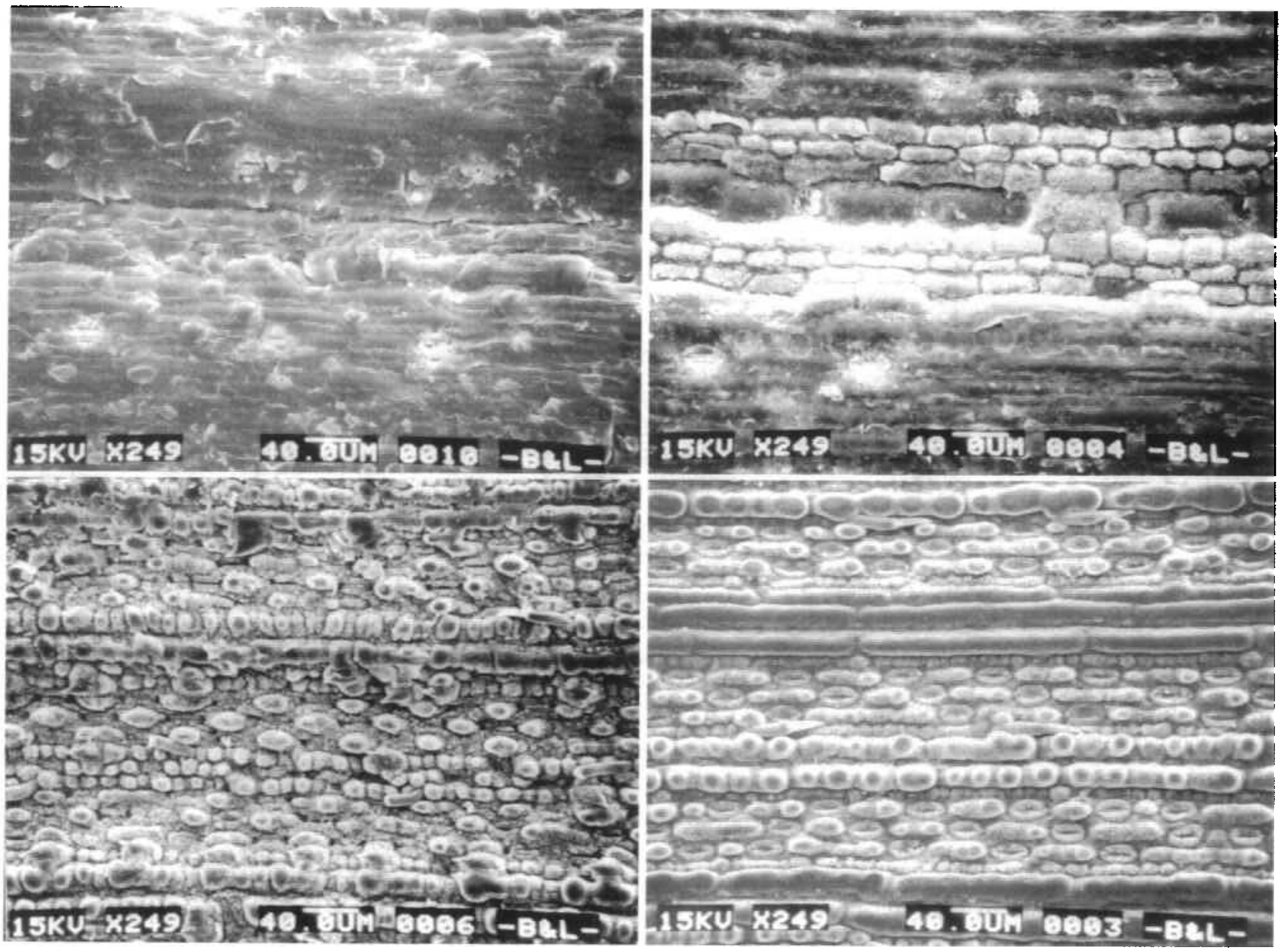

Fig. 4. Photographs from scanning electron microscope of leaf surfaces of *Miscanthus* clones collected from mountainous area (2 550 m above sea level, *left*) and from the lowland in southern Taiwan lowland (*right*). *Upper*: adaxial surface; *lower*: abaxial surface.

Discussion

Many C_4 plants are not saturated with PFD in photosynthesis, which is increased with irradiance up to full sunlight (Ray and Black 1979). *Miscanthus* grown in Taiwan tended to exhibit P_N saturated before reaching half of full sunlight (Fig. 1). This result was different from that observed in many C_4 plants, but was similar to that in *M. giganteus* (Beale *et al.* 1996) and some C_4 wild grass species (Singh *et al.* 1974, Weng *et al.* 1990). P_{sat} for all the tested *Miscanthus* clones with N_0 were 8-16 µmol m^{-2} s^{-1}, and for the N_2 ones were 12-21 µmol m^{-2} s^{-1} (Fig. 2). Hence the photosynthetic capacity of the tested *Miscanthus* of present study was lower than that of *M. sinensis* (van der Werf *et al.* 1993), *M. giganteus* (Beale *et al.* 1996), and other C_4 plants (Singh *et al.* 1974, Ray and Black 1979, Ramos and Hall 1982, Weng *et al.* 1990).

In addition, the photosynthetic capacity of *Miscanthus* varied in plants from different regions where the clones were collected. The clones collected from southern Taiwan, the tropical region, showed the highest P_{sat}, followed by the clones from northern Taiwan, the subtropical region, while those from the mountainous area showed the lowest rate. Cabrera *et al.* (1998) pointed out that the changes in photosynthetic characteristics along the altitude gradient might be due to lower CO_2 partial pressures or to soil nitrogen deficiency at higher altitudes. However, the P_{sat} of tested clones varied even if they were maintained in the same soil, with the same N application and the same CO_2 concentration. As compared at the same g_l, g_m, and Chl content, the clones from the mountainous area showed the lowest P_{sat} (Fig. 3). Thus the difference in photosynthetic capacity might be not due to CO_2 partial pressures or nitrogen in the soil.

Photosynthesis is affected by both stomatal and non-stomatal factors. No significant difference was observed in P_{sat} of *Miscanthus* clones under the same g_l. However, the clones from mountainous area showed lower P_{sat} than those from southern Taiwan at all g_m and Chl contents (Fig. 3). The values of g_l were lower in the clones from mountainous area and higher in the clones from southern

Taiwan. Thus photosynthesis of the clones from mountain clones was more limited by stomatal factor than that of the clones from southern Taiwan.

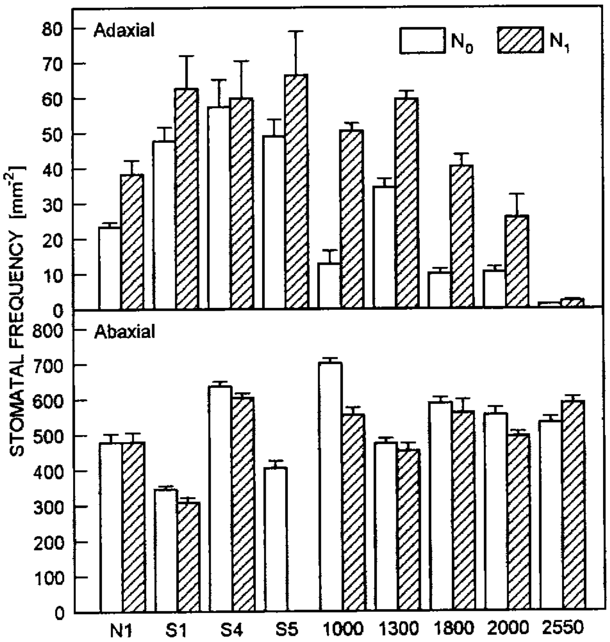

Fig. 5. Comparison of stomatal frequencies of adaxial and abaxial leaf surfaces of *Miscanthus* clones collected from different regions: N1: northern Taiwan, S1, S4, and S5: southern Taiwan, 1 000–2 550: the height [m a.s.l.] for mountainous area, and applied with different amounts of N fertiliser. Means ± SE.

Miscanthus is a perennial C_4 grass. The photosynthetic capacity of C_4 plants is significantly inhibited by low temperature, compared to that of C_3 plants (Berry and Björkman 1980). According to Weng and Ueng (1997), the optimum temperature of photosynthesis for *Miscanthus* clones collected from lowland was above 35 °C, while that for the clone collected from the 2 550 m at mountainous site was 28 °C. In July, the means of daily maximum and average air temperatures of Alishan meteorological station (23°31'N, 2 408 m) were 18.8 and 14.2 °C, respectively (Fig. 6, values from Central Weather Bureau of Taiwan, 1961-1990), which was much less than the optimum temperature of photosynthesis for *Miscanthus*.

Because *E* could dissipate a large amount of heat [2 258 kJ kg^{-1}(H_2O)], Engel *et al.* (1986) reported that alpine plants prevent excessive loss of heat through transpiration by closing the stomata. Epicuticular waxes may restrict *E* to prevent water loss (Kozlowski and Pallardy 1997). Indica type of rice (distributed in low latitudes) showed higher stomata aperture and/or higher frequency (Yoshida and Ono 1978, Maruyama and Tajima 1990) than the Japonica type (distributed in higher latitudes). We found that the clones from southern Taiwan, a tropical region, showed the highest P_{sat} and g_l, followed by the clones from northern Taiwan, a subtropical region, while those from mountainous area showed the lowest values. The clones from southern Taiwan showed the highest frequency of stomata on the adaxial surface, and those from the high mountain site showed the lowest frequency (Fig. 5). The adaxial leaf surface of the clone from higher mountain site had more wax than that of the clone from lowland. Thus the mechanisms for the clone of mountain area may prevent loss of excessive heat through transpiration.

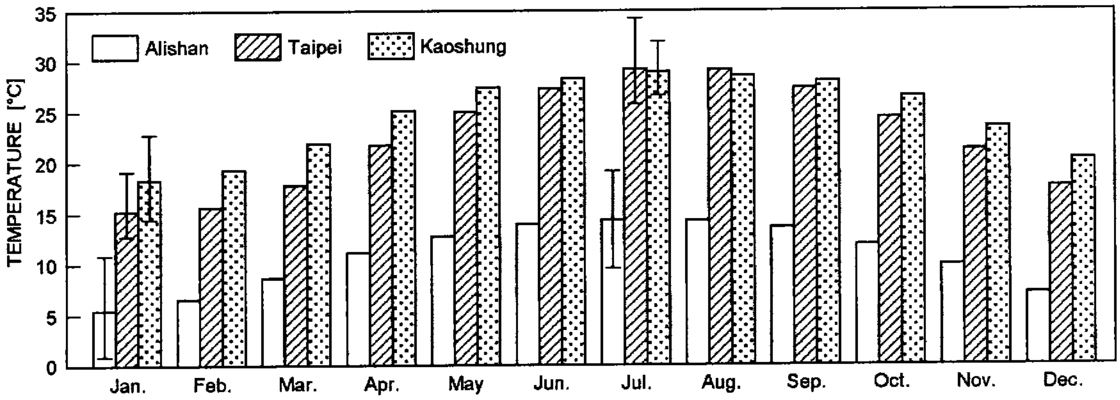

Fig. 6. Monthly mean air temperatures in Alishan (23°31'N, 2 408 m), Taipei (25°02'N, 9 m) and Kaoshung (22°34', 2.2 m) meteorological stations (values from Central Weather Bureau of Taiwan, 1961-1990). Bars represent the averaged daily maximum and minimum air temperatures.

In the lowland of Taiwan, *Miscanthus* plants grow throughout the year. The mean temperatures of the lowland were about 28 °C in July, while those in January were 15-20 °C (north-south) (Fig. 6). According to Weng and Ueng (1997), P_N of the *Miscanthus* clones from lowland at 20 °C was only about 45-65 % of that at 30 °C. Thus, *Miscanthus* plants in northern Taiwan may need a larger reduction of their g_l to prevent heat loss through transpiration as compared to those from southern Taiwan. However, the abaxial surface of *Miscanthus* leaf did not show a large clonal difference and remarkably higher frequency of stomata than that of the adaxial surface (Fig. 5). Thus, the difference of g_l in *Miscanthus* clones was not only affected by stomatal frequency, but it was also affected by stomatal aperature.

Table 1. The averaged PAR-saturated photosynthetic rates [μmol m^{-2} s^{-1}] for the *Miscanthus* clones collected from different regions and under different amounts of N applied [g per pot]. Means ± SE.

N	Mountain area	Northern Taiwan	Southern Taiwan
N_0	10.48±0.75	11.21±0.88	13.77±0.58
N_2	13.66±0.58	15.78±0.75	18.99±0.53

In addition, alpine plants are usually exposed to higher ultraviolet irradiation than lowland plants. UV-B significantly reduced stomatal density of rice (Dai *et al.* 1995) and faba bean (Visser *et al.* 1997) leaves. UV-B could also greatly reduce stomata density on the adaxial surface in comparison with the abaxial surface of rice leaves (Dai *et al.* 1995). Besides, cuticular waxes appear to protect some leaves from water loss, due to high radiation, *via* increased reflection and/or absorptive screening of the incoming radiation (Thomas and Barber 1974, Caldwell 1981). Some species and lines have more cuticular waxes when exposed to UV-B (Kraus *et al.* 1995, Gonzalez *et al.* 1996), and some high-altitude plants have highly reflective waxy layers (Thomas and Barber 1974). We show that the clones collected from the mountainous site had more wax deposited and lower stomatal frequency on the adaxial surface. Thus one of the mechanisms for the variation of epidermal characteristics in different clones of *Miscanthus* plants might be caused by the UV-B irradiation in mountain areas where the *Miscanthus* clones were collected.

All the plants were planted at the same location and grown for 15-16 months before determining the photosynthetic capacity and the characteristics of leaf surface. Nevertheless, the *Miscanthus* clones still expressed the adaptation characteristics to the environments where the clones were collected. Thus *Miscanthus* spp. was differentiated into different ecotypes to adapt to the habits in Taiwan.

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