

Leaf photosynthesis of forage grasses in different seasons and temperatures

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Abstract. Five species of C_4 grasses, *Digitaria decumbens* cv. A24, *Pennisetum purpureum* cv. A214, *pennisetum. calandestinum*, *Panicum maximum* cv. A27, and *Paspalum notatum* cv. A44, and a C_3 species, red oat (*Avena sativa*), were used to study the leaf net photosynthesis in response to leaf temperature in different seasons.

The net photosynthetic rates of single leaf (P_n) of most C_4 species studied were positively correlated with leaf soluble protein content at both 20 and 30°C. However, based on the same level of leaf soluble protein, *Pennisetum purpureum* and *Panicum maximum* showed lower P_n than the other C_4 species in January, while *Panicum maximum* had lower P_n than those of other grasses in February. The C_3 species *Avena sativa*, showed the same regression of P_n and leaf soluble protein content as most C_4 species at 20°C, but showed lower P_n than those of most C_4 species at 30°C. The P_n of C_4 species increased as leaf temperature increased from 15 to 37°C. A straight linear regression was found between P_n and leaf temperature in May and July. However, in January and February the regression line between P_n and leaf temperature appeared to be curved, the slope of regression line was higher in low temperature and lower in high temperature. *Avena sativa* showed a parabolic relation between P_n and leaf temperature in January and February, and had the highest P_n at 26°C. However, in May this species was the same P_n as leaf temperature increased from 21 to 32°C, but the P_n decreased at temperature above 35°C. The difference of P_n in response to leaf temperature among species and growth seasons were influenced mainly by non-stomatal factors.

Key words: C_4 forage grass; Net photosynthetic rate; Season; Temperature.

Introduction

Photosynthesis is the major determinant of biomass production in higher plants. It is well known that the photosynthesis of plants is easily influenced by environmental factors (Bennett *et al.*, 1982; Berry and Bjorkman, 1980; Berry and Downton, 1982), but it could acclimate to environmental conditions (Bennett *et al.*, 1982; Berry and Bjorkman, 1980; Seemann *et al.*, 1986).

Taiwan is an island, located from N 21°55'

to 25°18', and covered by many mountains, in which more than 60 peaks are above 3000 m in elevation. Thus temperature of the island varies greatly due to latitude, topography, seasons and climate.

The dominant species of forage grasses in Taiwan, such as *Pennisetum purpureum*, *Digitaria decubens* and *Paspalum notatum* are all C_4 species. Photosynthetic rate of C_4 plants was reduced remarkably under low temperature as compared to that of C_3 plants (Long, 1983; Ray and Black,

1979). In order to improve the productivity of pasture in different locations and growth seasons, it is important to understand the photosynthesis of forage grasses in response to various temperatures under different seasons.

Materials and Methods

Five species of C_4 grasses, pangola grass (*Digitaria decumbens* cv. A24), napier grass (*Pennisetum purpureum* cv. A214), kikuyu grass (*Pennisetum clandestinum*), guinea grass (*Panicum maximum* cv. A27) and bahia grass (*Paspalum notatum* cv. A44); and one species of C_3 grass, red oat (*Avena sativa*) were used in this experiment. All the materials were planted in pots, out door at National Chung Hsing University, Taichung, Taiwan.

Two to three months after cutting of C_4 species and planting of *A. sativa*, the photosynthetic and transpiration rates of fully expanded youngest leaves attached to the plants were

measured in an open gas system by an infrared analyzer (Anarad, AR-600) as described (Weng and Chen, 1987), at 15–37°C, 80% RH, 1500 $\mu E m^{-2} s^{-1}$ photon fluence rate (PAR), and 1.5 m/s wind speed.

Leaf conductance was calculated from vapor pressure deficits and transpiration rate of the leaves (Graastra, 1959). Mesophyll conductance was calculated from CO_2 concentration of air, CO_2 compensation point, leaf photosynthetic rate and leaf conductance (Braydo and Pallas, 1982). The leaves used for determining soluble protein content were the same leaf as those of measuring photosynthesis, following the procedures described by Lowry *et al.* (1951).

Results

The net photosynthetic rate (P_n) of leaves in the tested grasses were increased with the increase in leaf soluble protein content at both 20 and 30°C (Fig. 1). When the rate was compared at the

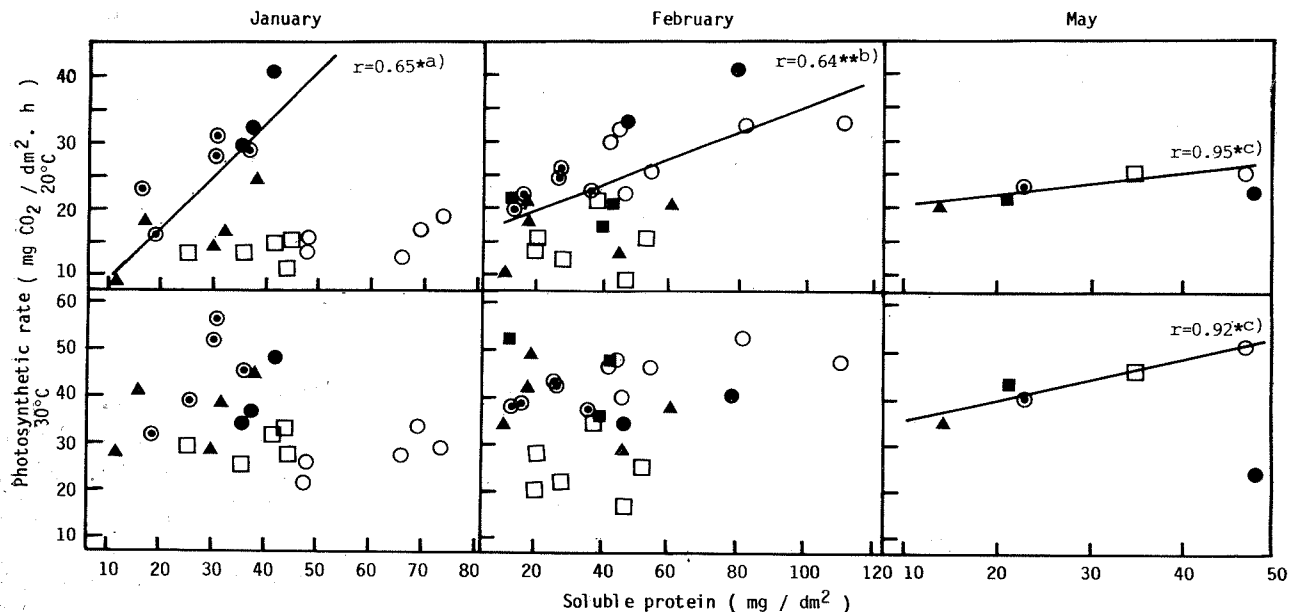


Fig. 1. The relationships between photosynthetic rate and leaf soluble protein content of grasses at 20 and 30 °C.

▲: *Digitaria decumbens*; ○: *Pennisetum purpureum*; ⊙: *P. clandestinum*; □: *Panicum maximum*; ■: *Paspalum notatum* ●: *Avena sativa*.

^a Except *Pennisetum purpureum* and *Panicum maximum*; ^b Except *Panicum maximum*; ^c Except *Avena sativa*.

same level of leaf soluble protein, Pn varied in species and in seasons. In January, Pn was lower in *pennisetum purpureum* and *Panicum maximum* and higher in *P. calandestinum* than those of other species measured at 20 and 30°C, respectively. *A. sativa* showed higher Pn at 20°C. In February, *Panicum maximum* showed lower Pn at both 20 and 30°C. In May, the Pn of all species studied were significantly correlated with leaf soluble protein content at 20°C. However, at 30°C, the Pn of *A. sativa* was below the regression line of Pn against leaf soluble protein of the five C₄ species.

The Pn of C₄ species showed positive correlation with leaf conductance from January to July (Table 1; Fig. 2). *A. sativa* had higher leaf conductance and lower Pn than those of C₄ species. Except *A. sativa* in January, the Pn of all the tested species showed positive correlation with mesophyll conductance from January to July (Table 1, Fig. 2).

The Pn of grasses in response to leaf temperature varied with grass species and seasons. As shown in Table 2 and Fig. 3, *A. sativa* showed a parabolic relationship between Pn and leaf temperature in January and February, it had maximum Pn at 26°C. In May, *A. sativa* maintained the same Pn between 21 and 32°C, and

decreased its Pn above 32°C. On the contrary, the Pn of C₄ species increased as leaf temperature increased from 15 to 37°C. A linear regression was found between Pn and leaf temperature in May and July. However, in January and February the regression line between Pn and leaf temperature appeared to be curved, the slope of the regression line was higher at low temperature and lower at high temperature. It indicated that the photosynthesis at higher temperature was influenced by winter season. The plants might show some climatical adaptation as climate changed.

If taking Pn at 30°C as 100%, the relative Pn at 20°C was 93 (in January) to 100% (February)

Table 1. Correlation coefficients of photosynthetic rate (Pn) with leaf conductance (gl) and mesophyll conductance (gm) of all grasses tested in different growth periods

	Pn-gl	Pn-gm
January	0.84 ^a	0.92 ^a
February	0.70 ^a	0.95
May	0.81 ^a	0.84
July	0.74 ^a	0.75

Data were obtained at leaf temperature 30°C.

^a Except *Avena sativa*, all the regression coefficients are significant at P=0.001.

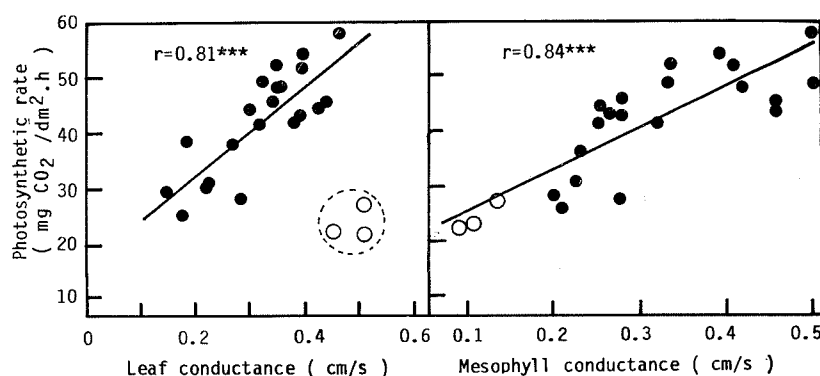


Fig. 2. The relationships of photosynthetic rate of single leaves to leaf and mesophyll conductance of grasses at different temperatures in May...All data were obtained at leaf temperature 30°C. ●: C₄ grasses; ○: *Avena sativa*; ***: Significant at 0.001 level.

Table 2. Information derived from regression equation $Y=aX^2+bX+C$ (Jan. and Feb.) or $Y=aX+b$ (May and July) for photosynthetic rates of grasses in different growth seasons

Month		<i>Digitaria decumbens</i>	<i>Pennisetum purpureum</i>	<i>P. clandestinum</i>	<i>Panicum maximum</i>	<i>Paspalum notatum</i>	<i>Avena sativa</i>
January	a	- 0.14	- 0.04	- 0.13	- 0.06	—	- 0.12
	b	11.70	6.51	10.16	7.15	—	6.01
	c	-128.64	- 58.98	- 89.05	- 70.53	—	26.58
	R	0.98	0.95	0.98	0.97	—	0.81
	n	24	26	24	25	—	14
	P20	49	55	62	48	—	99
February	a	- 0.13	- 0.09	- 0.09	- 0.16	- 0.07	- 0.14
	b	11.50	7.85	8.00	12.33	8.29	7.64
	c	-127.97	- 60.22	- 64.66	-131.18	- 92.59	- 3.93
	R	0.98	0.96	0.98	0.98	0.98	0.86
	n	20	21	21	22	19	25
	P20	50	61	59	51	45	93
May	a	4.90	4.22	4.04	4.85	5.71	—
	b	- 51.40	- 28.78	- 26.39	- 49.06	- 71.60	—
	r	0.99	0.98	0.99	0.98	0.99	—
	n	21	20	13	21	15	—
	P20	47	56	54	48	43	—
July	a	6.99	5.21	3.80	3.69	4.15	—
	b	-112.08	- 60.34	- 16.22	- 10.95	- 27.94	—
	r	0.98	0.97	0.98	0.97	0.98	—
	n	24	32	24	30	32	—
	P20	28	44	60	63	55	—

Y: Relative photosynthetic rate (30°C as 100%); X: Leaf temperature; R and r : Regression coefficient ($P<0.001$); n : Sample size; P20: Relative photosynthetic rate at 20°C (30°C as 100%).

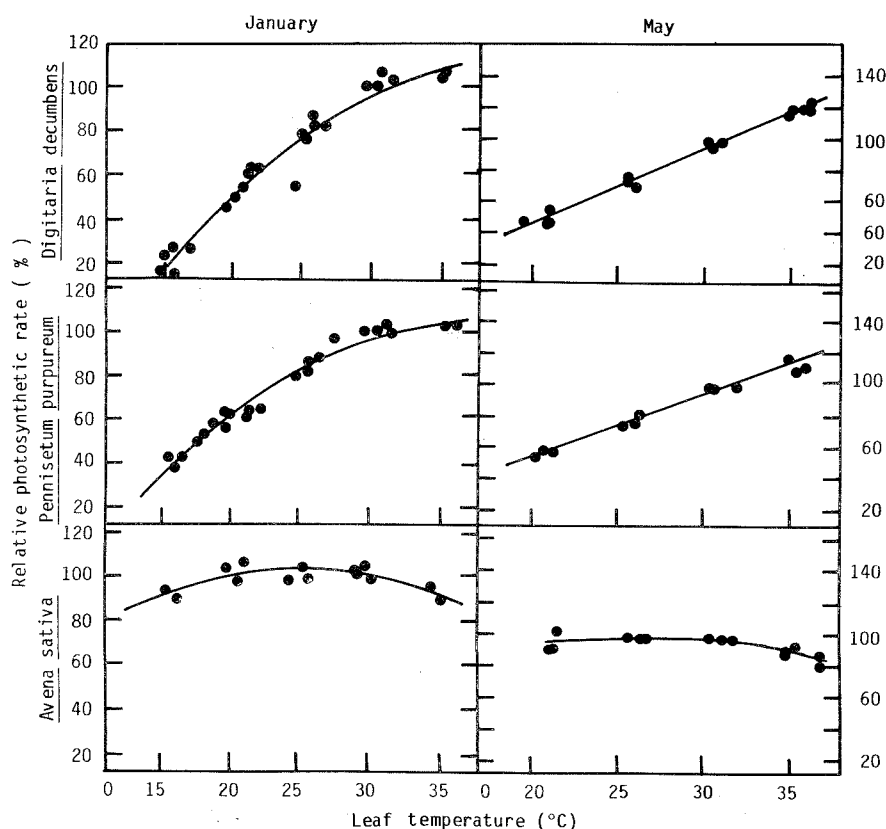


Fig. 3. Relationships between relative photosynthetic rates and leaf temperature of grasses (30°C as 100%) in different growth seasons. Regression coefficient see Table 2.

for *A. sativa*, 60% for *P. clandestinum* (January to July), 30% (July) to 50% (January to May) for *Digitaria decumbens*, 45 to 60% for the other species (Table 2). *P. clandestinum* showed a higher Pn at low temperature and was more stable than those of other C₄ species under different seasons.

In order to understand whether the stomatal and non-stomatal factors affecting Pn at different leaf temperatures and seasons, leaf and mesophyll conductances were determined. The C₄ species showed similar relationship between Pn and mesophyll conductance. *Digitaria decumbens* and *A. sativa* were chosen as examples as shown in Figs. 4 and 5, respectively.

The leaf conductance of tested grasses increased as leaf temperature increased, but it increased faster at low temperature than at high temperature. The mesophyll conductance to leaf temperatures was varied with species and seasons. In the C₄ species, the increased

rate of mesophyll conductance at high temperature was lower in January while it was higher in July. In *A. sativa* showed the highest mesophyll conductance at 22°C in January and May. The results indicated that the change of Pn for each species at different leaf temperatures and seasons were highly correlated to the performance of non-stomatal factors of photosynthesis.

Discussion

The results in this study indicates that photosynthesis is not favourable at high temperature in January and February, as compared to May and July. These results show that photosynthesis of grasses would acclimate to temperature changes as season advanced. This acclimation was mainly influenced by non-stomatal factors of photosynthesis (Figs. 4 and 5).

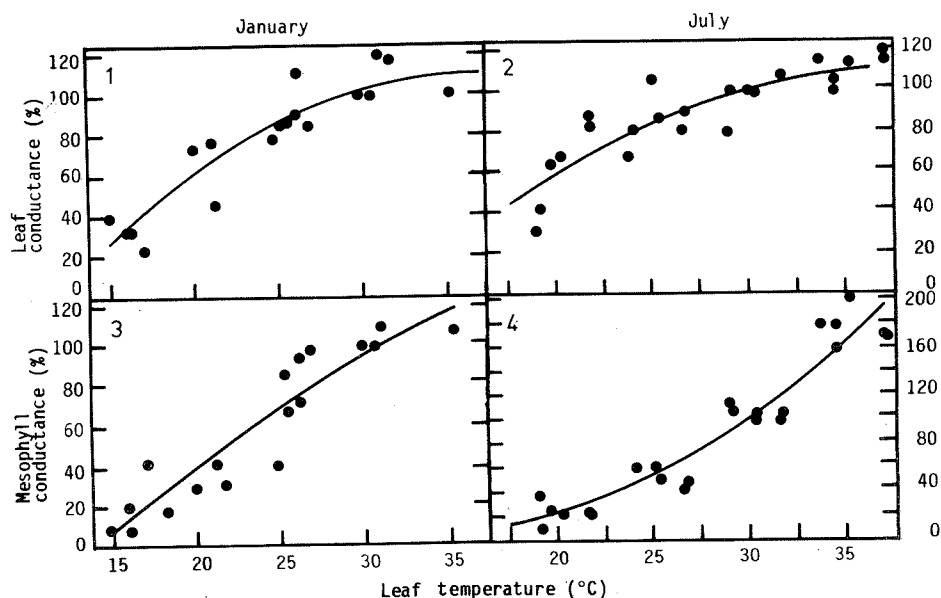


Fig. 4. The relative leaf and mesophyll conductance of *Digitaria decumbens* related to leaf temperatures (30 °C as 100%).

$$1: Y = -0.19X^2 + 13.46X - 133.76 \quad R = 0.92 \quad (P < 0.001)$$

$$2: Y = -0.15X^2 + 11.91X - 117.11 \quad R = 0.88 \quad (P < 0.001)$$

$$3: Y = -0.06X^2 + 8.75X - 109.37 \quad R = 0.93 \quad (P < 0.001)$$

$$4: Y = 0.32X^2 - 7.84X + 53.38 \quad R = 0.95 \quad (P < 0.001)$$

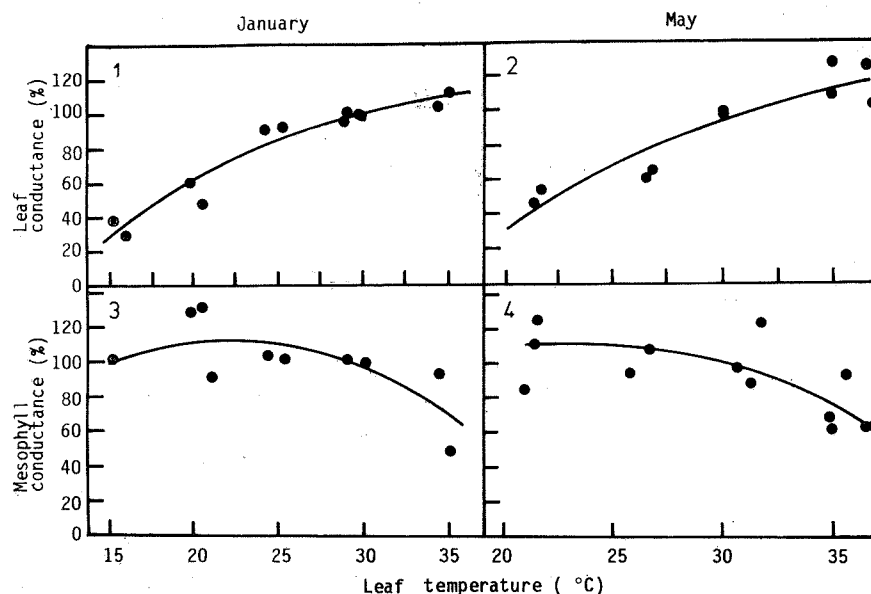


Fig. 5. The relative leaf and mesophyll conductance of *Avena sativa* related to leaf temperatures (30 °C as 100%).

1: $Y = -22.73/X + 1.75$

2: $Y = 1.39 \ln X - 3.79$

3: $Y = -0.27X^2 + 11.88X - 20.43$

4: Line is fitted by hand.

$R = 0.96$ ($P < 0.001$)

$R = 0.95$ ($P < 0.001$)

$R = 0.71$ ($P < 0.05$)

It was reported that Pn showed positive correlation with leaf soluble protein content in both C_3 and C_4 plants (Usuda *et al.*, 1984; Weng and Chen, 1987; Yang *et al.*, 1984). In this study, Pn was also significantly positive correlation with leaf soluble protein content in C_4 species in May. Based on the same leaf soluble protein level, *Pennisetum purpureum* in January, *Panicum maximum* in January and February showed lower Pn than those of other C_4 species (Fig. 1). It indicates that photosynthesis of *Pennisetum purpureum* and *Panicum maximum* was more influenced by low temperature in winter. Compared to other C_4 species, the Pn of *Pennisetum calandestinum* are less influenced by low temperature. It might be one of the reasons for this species to adapt to mountainous areas elevating 1,000 to 2,000 m above sea level in Taiwan.

It was reported that low temperature could

reduce the stomatal opening (Berry and Bjorkman, 1980; Mustardy *et al.*, 1982), light reaction (Berry and Downton, 1982; Long, 1983; Potvin, 1985; Yakir *et al.*, 1985) and dark reaction (Long, 1983; Robert *et al.*, 1983) of photosynthesis. Besides, low temperature and short day could decrease translocation of photosynthate (Chatterton and Silviu, 1980; Sato, 1976) and result in decreasing photosynthesis (Hanson and Yeh, 1979). This study shows that leaf conductance of all the grasses increased as leaf temperature increased. Further, leaf conductance shows the same tendency for each grass as temperature and season changed. However, mesophyll conductance in response to leaf temperature varied with species and seasons (Figs. 4 and 5). It suggests that the difference of Pn in species and seasons in response to leaf temperature be mainly influenced by non-stomatal factors of photosynthesis.

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Literature cited

- Bennett, K. J., H. G. McPherson, and I. J. Warrington. 1982. Effect of pretreatment temperature on response of photosynthesis rate in maize to current temperature. *Aust. J. Plant Physiol.* 9: 773-781.
- Berry, J. and O. Björkman. 1980. Photosynthesis response and adaptation to temperature in higher plants. *Ann. Rev. Plant Physiol.* 31: 491-543.
- Berry, J. A. and W. J. S. Downton. 1982. Environmental regulation of photosynthesis. In Govindjee (ed.), *Photosynthesis, Volume II*. Academic Press, New York, pp. 263-343.
- Bravdo, B. and J. E. Pallas, Jr. 1982. Photosynthesis, photorespiration and RuBP carboxylase/oxygenase activity in selected peanut genotypes. *Photosynthetica* 16: 36-42.
- Chatterton, N. J. and J. E. Silviu. 1980. Acclimation of photosynthate partitioning and photosynthetic rates to changes in length of the daily photosynthetic period. *Ann. Bot.* 46: 739-745.
- Gasstra, P. 1962. Photosynthesis of leaves and field crop. *Neth. J. Agric. Sci.* 10: 311-324.
- Hanson, W. D. and R. Y. Yeh. 1979. Genotypic differences for reduction in carbon exchange rates as associated with assimilate accumulation in soybean leaves. *Crop Sci.* 19: 54-58.
- Long, S. P. 1983. Photosynthesis in C_4 plants at low temperatures. In R. Marcelle, H. Clijsters and M. Vanpoucke (eds.), *Effects of Stress on Photosynthesis*. Martinus Nijhoff/Dr W. Junk Publishers, London, pp. 237-243.
- Lowry, O. H., N. J. Rosenbrough, A. L. Farr, and R. J. Randall. 1951. Protein measurement with folin reagent. *J. Biol. Chem.* 193: 265-275.
- Mustardy, L. A., T. T. Vu, and A. Faludi-Daniel. 1982. Stomatal response and photosynthetic capacity of maize leaves at low temperature. A study on varietal differences in chilling sensitivity. *Physiol. Plant.* 55: 31-34.
- Potvin, C. 1985. Effect of leaf detachment on chlorophyll fluorescence during chilling experiments. *Plant Physiol.* 78: 883-886.
- Robert, G., M. C. Vezeau, and J. P. Simon. 1983. Adaptation and acclimation of higher plants at the enzyme level: Thermostability of phosphoenolpyruvate carboxylase of population of a weedy C_4 grass species, *Echinochloa crusgalli* (L.) Beauv. *Photosynthetica* 17: 557-565.
- Sato, K. 1976. The growth responses of soybean plant to photoperiod and temperature. II. Responses in chemical constituents. *Proc. Crop Sci. Soc. Japan* 45: 450-455. (in Japanese with English summary)
- Seemann, J. R., W. J. S. Downton, and J. A. Berry. 1986. Temperature and leaf osmotic potential as factors in the acclimation of photosynthesis to high temperature in desert plants. *Plant Physiol.* 80: 926-930.
- Usuda, H., M. S. B. Ku, and G. E. Edwards. 1984. Rates of photosynthesis relative to activity of photosynthetic enzymes, chlorophyll and soluble protein content among ten C_4 species. *Aust. J. Plant Physiol.* 11: 509-517.
- Weng J. H. and C. Y. Chen. 1987. Differences between Indica and Japonica rice varieties in CO_2 exchange rates in response to leaf nitrogen and temperature. *Photosynthesis Res.* 14: 171-178.
- Yakir, D., J. Rudich, and B. Bravdo. 1985. Photoacoustic and fluorescence measurements of the chilling response and their relationship to carbon dioxide uptake in tomato plants. *Planta* 164: 345-353.
- Yang, C. Y., J. H. Weng, and C. Y. Chen. 1984. Studies on photosynthesis and dry matter production of soybean. II. The photosynthetic characteristics of winter crop soybean. *J. Agric. Assoc. China* 126: 34-43. (in Chinese with English summary)

不同季節及溫度下牧草葉片的光合作用

翁 仁 憲

國立中興大學植物系

選用五種 C_4 型牧草，盤固草 (*Digitaria decumbens* cv. A24)，狼尾草 (*Pennisetum purpureum* cv. A214)，克育草 (*Pennisetum calandestinum*)，天竺草 (*Panicum maximum* cv. A27)，百喜草 (*Paspalum notatum* cv. A44) 與一種 C_3 型牧草，燕麥 (*Avena sativa* cv. red oat) 為材料，測定其在不同季節及溫度下之單葉光合成速率 (P_n)。

幾乎所有供試 C_4 型牧草之 P_n 與其葉片中 之可溶性蛋白質含量呈正相關。於相同之葉片可溶性蛋白質含量下，狼尾草在一月，天竺草在一月及二月之 P_n 較其他 C_4 型牧草為低。 C_3 型的燕麥，在 20°C 時，其 P_n 與葉片中之可溶性蛋白質含量之關係與大部分 C_4 型牧草相近，但在 30°C 時，其 P_n 則較 C_4 型牧草為低。葉溫從 15°C 升至 37°C 時， C_4 型牧草之 P_n 均隨溫度而上升，唯在一月及二月， P_n 係呈曲線上升，其斜率隨溫度上升而趨緩，而在五月及七月， P_n 則隨溫度升高而呈直線上升。燕麥之 P_n 與葉溫之關係，在一月及二月係呈拋物線關係，於 26°C 時最高，但在五月，於 20 至 32°C 間，其 P_n 之變化少，超過 32°C 時始見下降。綜合以上結果，溫度對牧草葉光合作用之影響隨草種及季節而異。此差異主要是受到非氣孔因子之影響。