Leaf photosynthesis of forage grasses in different seasons and temperatures

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(Received October 21, 1987; Accepted April 5, 1988)

Abstract. Five species of C₄ grasses, Digitaria decumbens cv. A24, Pennisetum purpureum cv. A214, Pennisetum caleaeimum, Panicum maximum cv. A27, and Paspalum notatum cv. A44, and a C₃ 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 (Pn) of most C₄ 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 Pn than the other C₄ species in January, while Panicum maximum had lower Pn than those of other grasses in February. The C₃ species Avena sativa, showed the same regression of Pn and leaf soluble protein content as most C₄ species at 20°C, but showed lower Pn than those of most C₄ species at 30°C. The Pn of C₄ species increased as leaf temperature increased from 15 to 37°C. A straight 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 regression line was higher in low temperature and lower in high temperature. Avena sativa showed a parabolic relation between Pn and leaf temperature in January and February, and had the highest Pn at 36°C. However, in May this species was the same Pn as leaf temperature increased from 21 to 32°C, but the Pn decreased at temperature above 35°C. The difference of Pn in response to leaf temperature among species and growth seasons were influenced mainly by non-stomatal factors.

Key words: C₄ 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, 1986; 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 decumbens and Paspalum notatum are all C₄ species. Photosynthetic rate of C₄ plants was reduced remarkably under low temperature as compared to that of C₃ 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 C₄ 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 C₃ 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 C₄ 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 µE m. s 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 CO₂ concentration of air, CO₂ compensation point, leaf photosynthetic rate and leaf conductance (Bravdo 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 (Pₙ) 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.
A: *Digitaria decumbens*; O: *Pennisetum purpureum*; ☐: *P. clandestinum*;
□: *Panicum maximum*; ■: *Paspalum notatum*; ○: *Avena sativa.*
* Except *Pennisetum purpureum* and *Panicum maximum*; b Except *Panicum maximum*; c Except *Avena sativa.*](image-url)
same level of leaf soluble protein, \( \text{Pn} \) varied in species and in seasons. In January, \( \text{Pn} \) was lower in \textit{Pennisetum purpureum} and \textit{Panicum maximum} and higher in \textit{P. calandestinum} than those of other species measured at 20 and 30\(^\circ\)C, respectively. \textit{A. sativa} showed higher \( \text{Pn} \) at 20\(^\circ\)C. In February, \textit{Panicum maximum} showed lower \( \text{Pn} \) at both 20 and 30\(^\circ\)C. In May, the \( \text{Pn} \) of all species studied were significantly correlated with leaf soluble protein content at 20\(^\circ\)C. However, at 30\(^\circ\)C, the \( \text{Pn} \) of \textit{A. sativa} was below the regression line of \( \text{Pn} \) against leaf soluble protein of the five \textit{C\(_4\)} species.

The \( \text{Pn} \) of \textit{C\(_4\)} species showed positive correlation with leaf conductance from January to July (Table 1; Fig. 2). \textit{A. sativa} had higher leaf conductance and lower \( \text{Pn} \) than those of \textit{C\(_4\)} species. Except \textit{A. sativa} in January, the \( \text{Pn} \) of all the tested species showed positive correlation with mesophyll conductance from January to July (Table 1, Fig. 2).

The \( \text{Pn} \) of grasses in response to leaf temperature varied with grass species and seasons. As shown in Table 2 and Fig. 3, \textit{A. sativa} showed a parabolic relationship between \( \text{Pn} \) and leaf temperature in January and February, it had maximum \( \text{Pn} \) at 26\(^\circ\)C. In May, \textit{A. sativa} maintained the same \( \text{Pn} \) between 21 and 32\(^\circ\)C, and decreased its \( \text{Pn} \) above 32\(^\circ\)C. On the contrary, the \( \text{Pn} \) of \textit{C\(_4\)} species increased as leaf temperature increased from 15 to 37\(^\circ\)C. A linear regression was found between \( \text{Pn} \) and leaf temperature in May and July. However, in January and February the regression line between \( \text{Pn} \) 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 \( \text{Pn} \) at 30\(^\circ\)C as 100\%, the relative \( \text{Pn} \) at 20\(^\circ\)C was 93 (in January) to 100\% (February).

**Table 1.** Correlation coefficients of photosynthetic rate (\( \text{Pn} \)) with leaf conductance (\( g_l \)) and mesophyll conductance (\( g_m \)) of all grasses tested in different growth periods

<table>
<thead>
<tr>
<th></th>
<th>( \text{Pn}-g_l )</th>
<th>( \text{Pn}-g_m )</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>0.84(^*)</td>
<td>0.92(^*)</td>
</tr>
<tr>
<td>February</td>
<td>0.70(^*)</td>
<td>0.95</td>
</tr>
<tr>
<td>May</td>
<td>0.81(^*)</td>
<td>0.84</td>
</tr>
<tr>
<td>July</td>
<td>0.74(^*)</td>
<td>0.75</td>
</tr>
</tbody>
</table>

Data were obtained at leaf temperature 30\(^\circ\)C.

* Except \textit{Avena sativa}, all the regression coefficients are significant at \( P=0.001 \).

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![Graph](image-url)

**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. ●: \textit{C\(_4\)} grasses; ○: \textit{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

<table>
<thead>
<tr>
<th>Month</th>
<th>Digitaria decumbens</th>
<th>Pennisetum purpureum</th>
<th>P. clandestinum</th>
<th>Panicum maximum</th>
<th>Paspalum notatum</th>
<th>Arena sativa</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$a$</td>
<td>-0.14</td>
<td>-0.04</td>
<td>-0.13</td>
<td>-0.06</td>
<td>-0.12</td>
<td></td>
</tr>
<tr>
<td>$b$</td>
<td>11.70</td>
<td>6.51</td>
<td>10.16</td>
<td>7.15</td>
<td>6.01</td>
<td></td>
</tr>
<tr>
<td>$c$</td>
<td>-128.64</td>
<td>-58.98</td>
<td>-89.05</td>
<td>-70.53</td>
<td>-26.58</td>
<td></td>
</tr>
<tr>
<td>$R$</td>
<td>0.98</td>
<td>0.95</td>
<td>0.98</td>
<td>0.97</td>
<td>0.81</td>
<td></td>
</tr>
<tr>
<td>$n$</td>
<td>24</td>
<td>26</td>
<td>24</td>
<td>25</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>P20</td>
<td>49</td>
<td>55</td>
<td>62</td>
<td>48</td>
<td>99</td>
<td></td>
</tr>
<tr>
<td>February</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$a$</td>
<td>0.13</td>
<td>0.09</td>
<td>0.09</td>
<td>0.16</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td>$b$</td>
<td>11.50</td>
<td>7.85</td>
<td>8.00</td>
<td>12.53</td>
<td>8.29</td>
<td>7.64</td>
</tr>
<tr>
<td>$c$</td>
<td>-127.97</td>
<td>-60.22</td>
<td>-64.66</td>
<td>-131.18</td>
<td>-92.59</td>
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<tr>
<td>$R$</td>
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<td>0.98</td>
<td>0.98</td>
<td>0.86</td>
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<tr>
<td>$n$</td>
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<td>21</td>
<td>21</td>
<td>22</td>
<td>39</td>
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</tr>
<tr>
<td>P20</td>
<td>50</td>
<td>61</td>
<td>59</td>
<td>51</td>
<td>45</td>
<td>93</td>
</tr>
<tr>
<td>May</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$a$</td>
<td>4.90</td>
<td>4.22</td>
<td>4.94</td>
<td>4.55</td>
<td>5.71</td>
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</tr>
<tr>
<td>$b$</td>
<td>51.40</td>
<td>28.78</td>
<td>26.39</td>
<td>49.06</td>
<td>71.60</td>
<td></td>
</tr>
<tr>
<td>$c$</td>
<td>0.99</td>
<td>0.98</td>
<td>0.99</td>
<td>0.98</td>
<td>0.99</td>
<td></td>
</tr>
<tr>
<td>$R$</td>
<td>21</td>
<td>20</td>
<td>13</td>
<td>21</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>$n$</td>
<td>47</td>
<td>56</td>
<td>54</td>
<td>48</td>
<td>43</td>
<td></td>
</tr>
<tr>
<td>P20</td>
<td>6.99</td>
<td>5.21</td>
<td>3.80</td>
<td>3.69</td>
<td>4.15</td>
<td></td>
</tr>
<tr>
<td>July</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$a$</td>
<td>112.08</td>
<td>60.34</td>
<td>16.22</td>
<td>10.95</td>
<td>27.94</td>
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<tr>
<td>$b$</td>
<td>0.98</td>
<td>0.97</td>
<td>0.98</td>
<td>0.97</td>
<td>0.98</td>
<td></td>
</tr>
<tr>
<td>$c$</td>
<td>24</td>
<td>32</td>
<td>24</td>
<td>30</td>
<td>32</td>
<td></td>
</tr>
<tr>
<td>$R$</td>
<td>28</td>
<td>44</td>
<td>60</td>
<td>63</td>
<td>55</td>
<td></td>
</tr>
</tbody>
</table>

$Y$: 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 seasones. 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).

![Graph](image)

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

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

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

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

4: \( Y = 0.32X^2 - 7.84X + 53.38 \) \( R = 0.95 \) (\( P < 0.001 \))
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 calandesinum* 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; Mustard et al., 1982), light reaction (Berry and Downton, 1982; Long, 1983; Potvin, 1983; 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 Silvius, 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.
Acknowledgements. This study was supported by a grant from the National Science Council of the Republic of China (NSC75-0291-B005). I thanked Prof. C. H. Chou and Dr. F. H. Hsu for their valuable discussion.

Literature cited


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

(Pn)。

幾乎所有供試 C₄ 型牧草之 Pn 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
草在四月，天堂草在四月及五月之 Pp 少其他 C₄ 型牧草為低。C₃ 型的燕麥，在 20°C 時，其 Pn 與葉片中之可溶性蛋
白質含量之關係與大部分 C₄ 型牧草相近，但在 30°C 時，其 Pn 則較 C₄ 型牧草為低。適溫從 15°C 升至 37°C 時，C₃ 型
牧草之 Pn 均隨溫度而上升，唯在四月及五月，Pp 係呈曲線上升，其斜率隨溫度上升而緩緩，而在五月及七月，Pn 則隨
溫度升高而呈直線上升。燕麥之 Pn 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，但五月，於 20 至
32°C 間，其 Pn 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。此差異是受
到非氣孔因子之影響。