Photosynthetic Response to the Low Temperature in Elephant Grass (Pennisetum purpureum) and Zea mays

Abdulkhaliq A. AL-Shoaibi
Department of Biology, Faculty of Science, Taibah University,
P.O. Box 30002, Almadinah Almunawwarah, KSA

Abstract: Photosynthetic CO₂ uptake and the quantum efficiency of PSII photochemistry (Fₚ/Fₛ) of C₄ grasses (Pennisetum purpureum and Zea mays) were studied at 14 and 25°C. P. purpureum showed superior photosynthetic rates at chilling temperature (14°C) than Z. mays. Growth at a chilling temperature compared to 25°C had no significant effect on the light saturated assimilation rate (Aₘₛ), the quantum yield (φ), the CO₂ saturated rate of CO₂ uptake (Aₘ₅₅) and the carboxylation efficiency of P. purpureum but caused more than 78% loss of those occurred in Z. mays. The values of Fₚ/Fₛ were significantly reduced only in Z. mays at 14°C compared to 25°C and as a result, the photosynthetic apparatus of P. purpureum was more resistant to chilling temperature than of Z. mays.

Key words: Zea mays, Pennisetum purpureum, chilling stress, gas exchange, Fₚ/Fₛ

INTRODUCTION

Low temperature is one of the most important factors which limit the growth, the distribution and the productivity of plants (Tambussi et al., 2004; Van Heerden et al., 2004; Hu et al., 2006). Most C₄ plants are restricted largely to warmer climates because their physiological processes are adversely affected by low temperatures (Long et al., 1983; Hund et al., 2007). However, few C₄ plants have been found to be adapted and naturally grow in the cool climates (Beale and Long, 1995). The ability of these plants to activate or to increase their physiological and photosynthetic processes at low temperatures enabled them to survive in these cooler environments (Long, 1999; Naidu et al., 2003; Sowinski et al., 2005).

The photosynthetic production of C₄ crops is 40% higher than C₃ plants under the optimum climate (Long et al., 1983). However, this advantage is not realised in C₄ plants under low temperature conditions. Low temperature damages thylakoid membranes, breaks down chlorophyll and induces reduction in the photosynthetic capacity of C₄ plants such as maize (Tambussi et al., 2004; Sowinski et al., 2005). The reduction in the photosynthetic capacity of Z. mays leaves at cool temperatures is associated with reductions in both the light-saturated rate of carbon dioxide assimilation (Aₘₛ) and the maximum quantum yield (φ) (Fryer et al., 1998; Foyer et al., 2002; Sowinski et al., 2005; Hund et al., 2007).

Photoinhibition of photosynthesis may occur when the absorption of light is in excess of that required by the plant photosynthetic demands (Savitch et al., 2000). Many studies have shown that plants subjected to photoinhibition at low temperatures, both in controlled environments and in the field (Haldimann, 1999; Tambussi et al., 2004; Van Heerden et al., 2004; Sowinski et al., 2005; Hu et al., 2006; Hund et al., 2007). The phenomenon of photoinhibition is characterized by a reduction of the quantum yield of CO₂ uptake (φ) and the ratio of variable to maximum chlorophyll a fluorescence (Fₚ/Fₛ) (Fryer et al., 1998; Hu et al., 2006). The reduction in Fₚ/Fₛ of dark-adapted leaves indicates photoinhibition of PSII. In addition, the percentage of reduction depends upon the environmental conditions prior to the photoinhibitory treatment and genotypic variability (Lee et al., 2002; Sowinski et al., 2005; Hund et al., 2007).

The previous results (AL-Shoaibi, 2007) showed that P. purpureum had significantly higher growth rate at 14°C compared to Z. mays. This higher growth rate of P. purpureum could be, in part, is due to the consequence of differences in photosynthetic capacity between the two C₄ grasses (AL-Shoaibi, 2007). Therefore, this study was carried out to determine the effect of low temperature on photosynthetic CO₂ uptake of both P. purpureum and Z. mays and to compare the responses of photosynthesis of the two grasses to low temperature.

MATERIALS AND METHODS

Plants and growth conditions: This research was conducted in Biology Department, Faculty of Science, Taibah University during 2006. Rhizomes of
*Pennisetum purpureum* originally derived from Africa and *Zea mays* cv. LG 80 were planted in pots containing a peat-based compost (F2, Levington Horticultural Ltd., Ipswich, UK.) and grown in high-light controlled environment chambers (Fitotron SG066. CHX, Sanyo Gallenkamp PLC, Leicester, UK.), at day/night temperatures of 25/20°C and 14/12°C. Fertilisation was provided once a week by irrigating with Hoagland’s nutrient solution (Arnon and Hoagland, 1940). The Vapour Pressure Deficit (VPD) was kept below 1 kPa. Photosynthetic Photon Flux Density (PPFD) at leaf height was 600 µmol m⁻² sec⁻¹ and the photo period was 14 h.

**Gas exchange and chlorophyll fluorescence measurements:** The CO₂ uptake was measured with an open gas-exchange system incorporating open path infrared, CO₂, and water vapour analysers (LI-6400, LI-COR Inc, Lincoln, USA). A Peltier cooling system maintained the leaf temperature at 20°C as described by Long *et al.* (1996) and VPD was controlled between 1 and 1.5 kPa. The most recently fully expanded leaf was used to measure photosynthetic CO₂ uptake at PPFD of 0-2000 µmol m⁻² sec⁻¹. Net photosynthesis per unit leaf area and intercellular CO₂ concentration (ε) were determined using the equations of Von Caemmerer and Farquhar (1981). The light saturated photosynthesis (Aₘ) was determined at saturating PPFD (1500 µmol m⁻² sec⁻¹) and at the ambient CO₂ concentration of 360 µmol mol⁻¹. Carbon dioxide response curves were made over the range of 50-550 µmol mol⁻¹ using PPFD of 1500 µmol m⁻² sec⁻¹, at a leaf temperature of 20°C. These curves were analysed according to the model of Collatz *et al.* (1992).

Chlorophyll fluorescence was measured using a portable fluorimeter (PEA, Hansatech, Kings Lynn, Norfolk). The initial (Fᵢ) and maximum (Fₘ) fluorescence emissions were measured after 20 min of dark adaptation and the ratio of variable to maximum fluorescence (Fᵥ/Fₘ) was calculated as (Fᵥ-Fᵢ)/Fₘ as described by Øquist and Wass (1988). The Fᵥ/Fₘ ratio was measured weekly for four replicates of each plant using the youngest fully expanded leaves.

**Statistical analyses:** The data obtained from various analyses and measurements were statistically analysed using analysis of variance (Systat, Inc., Evanston, Illinois, USA).

**RESULTS**

Leaves of *Z. mays* growing at 14°C showed a significant reduction in Fᵥ/Fₘ (p<0.001) compared to those of *Z. mays* and *P. purpureum* grown at 25°C (Fig. 1). Furthermore, the Fᵥ/Fₘ of *P. purpureum* leaves grown at 14°C was 64% greater than that of *Z. mays* leaves (p<0.001) growing at the same temperature (Fig. 1).

Growth at chilling temperature (14°C), compared to 25°C, had no significant effect on the light-saturated (Aₘ) or light-limited photosynthetic capacity (φ) of *P. purpureum*, but caused 78% loss (p<0.001) of both in *Z. mays* (Fig. 2-4). For leaves of *P. purpureum* grown at 14°C, the Aₘ and φ were significantly greater than those of *Z. mays* grown at the same temperature (Fig. 3-4).

The plateau of the A/ε curve (Aₘ) is co-limited by the amount of in vivo Rubisco or/and PPDK activity (Collatz *et al.*, 1992). Decreasing temperature from 25°C to 14°C did not significantly affect the Aₘ of *P. purpureum*, but caused 78% loss (p<0.001) of *Z. mays* leaves compared to those grown at 25°C (Fig. 5-6). In addition, the Aₘ of *P. purpureum* leaves grown 14°C was more than 7 times greater than that of *Z. mays* leaves growing at the same temperature (Fig. 5-6).

The carboxylation efficiency was calculated from the initial slope of A/ε curve (Fig. 5). Growth at 14°C, relative to 25°C, had no significant effect on the carboxylation efficiency of *P. purpureum*, but caused 83% loss (p<0.001) of *Z. mays* (Fig. 7). For leaves of *P. purpureum* grown at 14°C, the carboxylation efficiency was significantly greater (p<0.001) than those of *Z. mays* grown at the same temperature (Fig. 7).
Fig. 2: The response of photosynthetic CO₂ uptake (A), per unit leaf area, to photon flux (Q) for *P. purpureum* and *Z. mays* leaves. Measurements of CO₂ uptake were all made at 20°C and a c₅ of 360 μmol mol⁻¹. The data represent the mean of n = 3-6 leaves (±SE).

Fig. 3: The light-saturated photosynthetic rate (Aₛ), per unit leaf area, measured at 20°C and a photon flux of 1500 μmol mol⁻¹ sec⁻¹, for *P. purpureum* and *Z. mays*. The data represent the mean of n = 3-6 leaves (±SE). Different letters show significant difference between temperature treatments at p<0.05.

Fig. 4: The mean quantum yield (φ), measured at 20°C for *P. purpureum* and *Z. mays*. The data represent the mean of n = 3-6 leaves (±SE). Different letters show the significant difference between temperature treatments at p<0.05.
Fig. 5: The response of photosynthetic CO₂ uptake (A), per unit leaf area, to changes in intercellular CO₂ concentration (c) for *P. purpureum* and *Z. mays* leaves. Measurements of CO₂ uptake were made at 20°C and a photon flux of 1500 µmol mol⁻¹. Data illustrated are for one selected leaf of each plant.

Fig. 6: The mean plateau \(A_{\infty}\), per unit leaf area, measured at 20°C and a photon flux of 1500 µmol mol⁻² sec⁻¹, for *P. purpureum* and *Z. mays*. The data represent the mean of \(n = 3-6\) leaves (±SE). Different letters show significant differences between temperature treatments at \(p<0.05\).

Fig. 7: The mean carboxylation efficiency, measured at 20°C and photon flux of 1500 µmol mol⁻² sec⁻¹, for *P. purpureum* and *Z. mays*. The data represent the mean of \(n = 3-6\) leaves (±SE). Different letters show significant differences between temperature treatments at \(p<0.05\).
DISCUSSION

The results of this research provide a clear evidence that P. purpureum showed significantly greater resistance to photoinhibition at low temperatures than Z. mays. The low Fv/Fm in Z. mays grown at low temperature may not be related to the photoinhibition, but to the impaired development of the photosynthetic apparatus. Nie and Baker (1991) and Nie et al. (1995) showed that several chloroplast polypeptides were poorly expressed in Z. mays leaves developed at 14°C. These lesions, which included the D1 protein, could account for the low Fv/Fm even in the absence of direct photoinhibition.

The photosynthetic rates for all leaves grown at 25°C of both P. purpureum and Z. mays were similar and close to the rates recorded previously for healthy leaves of a range of NADP-malic enzyme type C₄ grasses (Ehleringer and Pearcy, 1983). This indicates that these plants were unstressed and not suffering any photoinhibition at the optimal growth temperatures and as indicated by high Fv/Fm. When grown at 25°C, P. purpureum had similar Aₘ, φ, Aₘ/τ, and carboxylation efficiencies to P. purpureum grown at 14°C, but Z. mays showed a very substantial decrease in all these measures. Moreover, rates of CO₂ uptake of P. purpureum grown at 14°C were in excess of Z. mays grown at 14°C at all light levels. The decrease in the photosynthetic performance in Z. mays grown at chilling temperatures was observed previously in controlled environments and in the field (Nie and Baker, 1991; Nie et al., 1992; Haldimann et al., 1996; Proulx, 1996; Fryer et al., 1998).

The sensitivity of C₄ photosynthesis to low temperature is frequently associated with the reduction in the rate of enzymatically controlled reactions (Long et al., 1983). This was investigated in vivo by A/α analysis. The Aₘ and carboxylation efficiency are controlled by activity of Ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) and activity of Phosphoenol pyruvate carboxylase enzymes (PEPC), respectively (Collatz et al., 1992). Also, the regulatory enzyme Pyruvate, Pi dikinase (PPDK) is another limitation for Aₘ decreased (Furubank et al., 1997). PPDK is known as a cold sensitive enzyme (Usami et al., 1995; Du et al., 1999). Research work with Flaveria bidentis and Amaranthus edulis indicates that, at 25°C, Rubisco accounts for 50-70% of the metabolic control over A at 360 μbar CO₂ while PPDK and PEPC account for only 20-30% (Dever et al., 1997; Furubank et al., 1997; Von Caemmerer et al., 1997). Results of the Aₘ and carboxylation efficiency of the 14°C grown P. purpureum leaves were similar to leaves grown at 25°C (Fig. 5-7). In contrast, the Aₘ and carboxylation efficiency of the 14°C grown Z. mays leaves suggested a reduction of 84% in the in vivo activity of these enzymes compared to leaves grown at 25°C. This suggests that in contrast to Z. mays, P. purpureum has similar activity of PEPC, PPDK and Rubisco regardless of whether it is grown at 25 or 14°C.

In conclusion, P. purpureum has superior photosynthetic rates at chilling temperatures than Z. mays. The values of Fv/Fm were significantly reduced only in Z. mays at 14°C compared to 25°C and as a result, the photosynthetic apparatus of P. purpureum was more resistant to chilling temperature than that of Z. mays. This high capacity of photosynthetic rates of P. purpureum at chilling temperatures may be responsible for the high growth rates of this grass at chilling temperatures.

ACKNOWLEDGMENT

The author is indebted to Professor Dr. Moustafa EL-Naggar for his critical reading and revision of the manuscript.

REFERENCES


