Differential photosynthetic acclimation pattern to limiting growth-irradiance in two types of C₄ plants

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Abstract

Photosynthetic acclimation to reduced growth irradiances (650 and 200 μmol m⁻² s⁻¹) in Eleusine coracana (L.) Garten, a nicotinamide adenine dinucleotide-malic enzyme (NAD-ME) C₄ species and Gomphrena globosa L., a nicotinamide adenine dinucleotide phosphate-malic enzyme (NADP-ME) C₄ species were investigated. E. coracana plants acclimated in 4 and 8 d to 650 and 200 μmol m⁻² s⁻¹, respectively, whereas G. globosa plants took 8 and 10 d, respectively, to acclimate to the same irradiances. The acclimation to reduced irradiance was achieved in both species by greater partitioning of chlorophyll towards the light-harvesting antennae at the expense of functional components. However, magnitude of increase in the light-harvesting antenna was higher in E. coracana as compared to G. globosa. Superior photosynthetic acclimation to reduced irradiance in G. globosa was due to the smaller change in functions of the cytochrome b₆/f complex, photosystem (PS) I and PS2 leading to the higher carbon fixation rates compared to E. coracana.

Additional key words: chlorophyll amount and fluorescence; cytochrome b₆/f; electron transport rates; net photosynthetic rate; photosystems 1 and 2; quantum efficiency of photosystem 2.

Introduction

Plants acclimated to high irradiance develop alterations at the molecular level when exposed to reduced growth irradiance (Anderson and Andersson 1988). They acclimate by changing their thylakoid membrane composition, the light-harvesting complex (LHC2), chloroplast ultrastructure, and conductances for gas exchange (Björkman 1973, Boardman 1977, Lichtenthaler 1981, Lichtenthaler et al. 1981, Melis and Harvey 1981, Rao and Rama Das 1982, Hodges and Barber 1983, Leong and Anderson 1984, Lichtenthaler and Meier 1984, Bhaskar and Rama Das 1987, Chow and Hope 1987, Burkey and Wells 1991, Evans 1993, Koesmarno et al. 1998). However, there have been some exceptions (Lee and Whitmarsh 1989, Chow et al. 1991, McKiernan and Baker 1991, Burkey and Wells 1996). The time course of acclimation has been studied in several C₄ plants, e.g., Solanum, Pismum, Lycopersicon, Phaseolus, Hordeum (Caemmerer and Farquhar 1984, Davies et al. 1986, Ferrar and Osmond 1986, Chow and Anderson 1987, De la Torre and Burkey 1990) and one NAD-ME C₄ dicot species, Amaranthus hypochondriacus (Sailaja and Rama Das 1995a). The present study is a comparison of the behaviour of other C₄ species, Eleusine coracana (an NAD-ME C₄) and Gomphrena globosa (an NADP-ME C₄) to reduced growth irradiance. In an earlier study we observed that down-regulation of C₄ metabolism was accomplished in identical time periods in plants of different C₄ metabolising types, rate-limiting steps being the decarboxylating enzyme(s) of the pathways (Sailaja and Rama Das 1995b). Therefore, the present major objective was to identify species specific characters, if any, between the two plant species by studying the modulation of thylakoid membrane composition and function.

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Abbreviations: Asc - ascorbate; BQ - benzoquinone; Chi - chlorophyll; Cyt - cytochrome; DCPIP - dichlorophenol indophenol; DCMU - 3,3'-dichloro-1,1'-dimesityl urea; F₆₆₀ - fluorescence when reaction centres are open; F₉₀₀ - variable fluorescence; F₉₀₀ - maximum fluorescence; F₆₅₀ - fluorescence at 690 nm measured at 77 K; F₇₃₅ - fluorescence at 735 nm measured at 77 K; HEPES - N-2-hydroxyethylpiperazine N-2-ethanesulfonic acid; MV - methyl viologen; HI - high irradiance; LI - low irradiance; NAD-ME - NAD-malic enzyme; NADP-ME - NADP-malic enzyme; PM - net photosynthetic rate; PS - photosystem.

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Materials and methods

Plant growth: Eleusine coracana (L.) Gaertn. and Gomphrena globosa L. plants that were raised from seed in the open field under natural conditions receiving full sunlight (2000 μmol m⁻² s⁻¹) for 45 d, were designated as high irradiance (HI) plants. Two other batches of plants were grown at one-third (650 μmol m⁻² s⁻¹) and one tenth of this irradiance (200 μmol m⁻² s⁻¹) and designated LI₁ and LI₂ plants, respectively. Reduced irradiances were obtained by screening full sunlight through appropriate wooden meshes. The photoperiod was approximately 12 h. For studying the time course of acclimation, HI plants were transferred to reduced irradiances (650 μmol m⁻² s⁻¹ and 200 μmol m⁻² s⁻¹) while LI₁ and LI₂ plants were transferred to full irradiance. Plants grown under HI transferred to LI were called HI→LI₁ and HI→LI₂, respectively, and those grown under LI transferred to HI were called LI₁→HI and LI₂→HI, respectively. The time course was measured with respect to controls on every day following transfer. The day temperature varied from 30 to 40 °C. Night temperature varied from 12 to 25 °C. Experiments were performed from October 1992 to May 1993. Hyderabad is situated at 17°10'N latitude and 78°23'E longitude at an altitude of 542.6 m above mean sea level. The values are means ± SD of ten independent measurements per trial and three such trials. Statistics was done using t-test.

Chlorophyll (Chl) content was estimated spectrophotometrically according to the procedure of Arnon (1949).

Chl fluorescence emission spectra of thylakoid mem-

branes were recorded at 490 nm excitation using a fluorescence spectrophotometer (Hitachi model 3010) with a liquid N₂ attachment. Chl fluorescence transients at 77 K were measured according to the procedure of Powles and Björkman (1982) using the same fluorescence spectrophotometer. Chl fluorescence transients in the field were measured using a portable Chl fluorimeter (model SF-30, Richard Branker, Canada).

Thylakoid membranes were isolated according to the procedure of Vainstein et al. (1989).

Photosynthetic electron transport rates: Whole chain electron transport rates (H₂O→MV) and PS1 (DCPIP→MV) were measured polarographically at 25 °C as O₂ uptake using Clark-type electrode in Gilson Oxygraph according to the procedure of De la Torre and Burkey (1990). PS2 activity was measured as DCPIP reduction at 590 nm using molar extinction coefficient for DCPIP which is 18.9 mM⁻¹ cm⁻¹.

Cytochrome (Cyt) f was determined according to the procedure of Bendall et al. (1971) in a dual-beam dual-wavelength spectrophotometer (Hitachi model 557). The Cyt f concentration was calculated using molar extinction coefficient of 19.7 mM⁻¹ cm⁻¹.

Net photosynthetic rate (Pₑ) was measured using open gas exchange system (ADC portable IRGA comprising LCA-2 analysers) in differential mode.

Results

The effect of reduced irradiances on the ratios Chl a/b, F₆₅₀/F₇₃₅ at 77 K, and Chl/Cyt f was studied to see if the light-harvesting antenna changed under these conditions. The values of the Chl a/b ratios decreased in LI₁ and LI₂ plants of E. coracana and G. globosa compared to HI plants (Fig. 1). HI→LI₁ and HI→LI₂ plants of both species showed a reduction in Chl a/b ratios while increases in the ratios were observed in LI₁→HI and LI₂→HI plants (Fig. 1). The time taken for HI→LI₁ and LI₁→HI plants to show changes in Chl a/b ratio in E. coracana was 4 d whereas it was 8 d in G. globosa. The time course of acclimation was 8 d in HI→LI₁ and LI₂→HI plants of E. coracana while it was 10 d for similar G. globosa plants (Fig. 1). Fluorescence spectra at 77 K in both species showed fluorescence emission peaks at 690 and 735 nm. The LI₁ and LI₂ plants of both E. coracana and G. globosa showed an increase in the F₆₅₀/F₇₃₅ ratio at 77 K compared to the HI plants (Table 1). The F₆₅₀/F₇₃₅ ratio increased in HI→LI₁ and HI→LI₂ plants of both E. coracana and G. globosa while it decreased in LI₁→HI and LI₂→HI plants of both species. However, the magnitude of change was larger in E. coracana compared to that of G. globosa. The time period of acclimation was identical for all parameters studied to that observed for the Chl a/b ratio. Therefore, the variation is presented for the last day of acclimation in the table. As expected, the Chl/Cyt f ratio increased in HI→LI₁ and HI→LI₂ plants of both E. coracana and G. globosa while the ratio decreased in LI₁→HI and LI₂→HI plants of both species. The magnitude of change in the ratio in G. globosa was not so great as in E. coracana.

The values of the variable Chl fluorescence ratio F₆₅₀/F₇₃₅ were measured in order to assess the effect of reduced irradiance on function of PS2. The values at field temperature were typically above 0.33±0.06 which is in accordance with the measurements of Sthapit et al. (1995) and Sailaja and Rama Das (1996b) on rice cultivars and diheliotropic plants, respectively, by using
a similar SF 30 fluorimeter. After correcting $F_0$, the mean $F_/F_m$ was 0.78 ±0.04 at field temperature in HI plants (Table 1). The determination of $F_0$ is problematic in non-modulated fluorescence induction at room temperatures especially if the exciting radiation is switched on slowly. An apparent $F_0$ measured after the shutter opening may contain a contribution of $F_v$ (Tyystjärvi and Karunan 1990). Making a correction to $F_0$ according to the procedure of Morissette and Popovic (1987) solved this problem. The $F_/F_m$ ratio was low in LI$_1$ and LI$_2$ plants of E. coracana and G. globosa. The ratio decreased in HI→LI$_1$ and HI→LI$_2$ and increased in LI$_1$→HI and LI$_2$→HI plants for both E. coracana and G. globosa. The decline in $F_/F_m$ was contributed from both increase in $F_0$ and decrease in $F_m$ rather than decrease in both $F_0$ and $F_m$ (values not presented). The effect of reduced irradiance on $F_/F_m$ at field temperature was higher than the effect seen at 77 K. The effect was more pronounced in E. coracana plants acclimated to reduced growth-irradiance compared to the similar plants of G. globosa.

Fig. 1. Effects of limiting-irradiance on the chlorophyll a/b ratio in E. coracana (A, B) and G. globosa (C, D). Acclimation to reduced irradiance of 650 μmol m$^{-2}$ s$^{-1}$ (A, C) or 200 μmol m$^{-2}$ s$^{-1}$ (B, D) in HI (◦), LI$_1$ (▲), LI$_2$ (▼), HI→LI$_1$ (●), LI$_1$→HI (△), LI$_2$→HI (■), and HI→LI$_1$ (○) plants.

The reduction in function of PS2 under reduced irradiances lead us to measure the electron transport rates under these conditions. The electron transport rates decreased in the LI$_1$ and LI$_2$ plants of both species in comparison with HI plants. A lesser change was observed in the whole electron transport chain comprising PS1 and PS2 in G. globosa, in response to reduction in growth irradiances, compared to that in E. coracana (Table 1). In HI→LI$_1$ and HI→LI$_2$ plants of E. coracana, the whole chain electron transport decreased by 57 and 72 %, respectively, while the decrease in similar G. globosa plants was 54 and 65 %, respectively. In LI$_1$→HI and LI$_2$→HI E. coracana plants, the electron transport increased by 130 and 256 %, respectively, whereas 118 and 184 % increase was observed in low irradiance grown G. globosa plants transferred to normal irradiance. PS1 electron transport rates decreased in HI→LI$_1$ and HI→LI$_2$ plants of E. coracana (63 and 77 %, respec-
tively) and G. globosa plants (52 and 73 %, respectively). In L1→HI and L2→HI plants of E. coracana and G. globosa, the PS1 electron transport rates increased. PS2 electron transport rates decreased to a greater extent compared to that of PS1 in HI→L1 and HI→L2 plants of both species. Likewise, the change in the PS2 rates was also higher in L1→HI and L2→HI plants compared to PS1 rates in both species.

The concentrations of Cyt f decreased in both species grown at reduced irradiances (Table 1). In HI→L1 and HI→L2 plants of E. coracana, the concentrations of Cyt f decreased by 41 and 78 %, respectively, while the decrease observed in similar G. globosa plants was 31 and 59 %, respectively. In L1→HI and L2→HI E. coracana plants the Cyt f concentrations increased by 69 and 361 %, respectively, whereas 46 and 148 % increases were observed in low irradiance grown G. globosa plants transferred to normal irradiance.

Table 1. Effect of reduced irradiance on the ratio of Chl fluorescence \(F_{685}/F_{735}\) at 77 K, the ratio Chl/cytochrome \(f\), quantum efficiency of photosystem 2 (PS2) at room temperature and 77 K, photosynthetic electron transport rates \([\text{mol} \text{kg}^{-1}(\text{Chl}) \text{h}^{-1}]\), cytochrome \(f\) concentrations \([\text{mol} \text{kg}^{-1}(\text{Chl})]^{-1}\), and net photosynthetic rate \([\text{mol} \text{kg}^{-1}(\text{Chl}) \text{s}^{-1}]\) in E. coracana and G. globosa. Values are means ± SD of ten independent measurements per trial and three such trials on the last day of acclimation to reduced irradiances. *\(p<0.001\), \(b=p<0.005\).

<table>
<thead>
<tr>
<th></th>
<th>HI</th>
<th>L1</th>
<th>L2</th>
<th>L1→HI</th>
<th>L2→HI</th>
<th>HI→L1</th>
<th>HI→L2</th>
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<tr>
<td>(F_{685}/F_{735})</td>
<td>E. coracana</td>
<td>0.40±0.02</td>
<td>0.85±0.04</td>
<td>1.08±0.02</td>
<td>52</td>
<td>67</td>
<td>113</td>
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<tr>
<td>G. globosa</td>
<td>0.51±0.09</td>
<td>0.87±0.04</td>
<td>1.18±0.02</td>
<td>41</td>
<td>54</td>
<td>70</td>
<td>121</td>
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<td>Chl/Cyt f</td>
<td>E. coracana</td>
<td>311±33</td>
<td>523±18</td>
<td>1234±180</td>
<td>40</td>
<td>77</td>
<td>68</td>
</tr>
<tr>
<td>G. globosa</td>
<td>526±34</td>
<td>485±58</td>
<td>821±106</td>
<td>32</td>
<td>60</td>
<td>48</td>
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<td>PS2 at room temperature</td>
<td>E. coracana</td>
<td>0.74±0.06</td>
<td>0.36±0.06</td>
<td>0.26±0.03</td>
<td>111</td>
<td>192</td>
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<tr>
<td>G. globosa</td>
<td>0.81±0.09</td>
<td>0.52±0.04</td>
<td>0.38±0.02</td>
<td>55</td>
<td>113</td>
<td>36</td>
<td>53</td>
</tr>
<tr>
<td>PS2 at 77 K</td>
<td>E. coracana</td>
<td>0.84±0.06</td>
<td>0.74±0.04</td>
<td>0.63±0.06</td>
<td>13</td>
<td>33</td>
<td>11</td>
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<tr>
<td>G. globosa</td>
<td>0.86±0.06</td>
<td>0.77±0.04</td>
<td>0.69±0.04</td>
<td>12</td>
<td>24</td>
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<tr>
<td>Whole chain ET</td>
<td>E. coracana</td>
<td>960±136</td>
<td>417±56</td>
<td>250±44</td>
<td>130</td>
<td>256</td>
<td>57</td>
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<tr>
<td>G. globosa</td>
<td>942±148</td>
<td>432±48</td>
<td>331±48</td>
<td>118</td>
<td>184</td>
<td>54</td>
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<td>PS1</td>
<td>E. coracana</td>
<td>2827±434</td>
<td>1038±148</td>
<td>637±120</td>
<td>256</td>
<td>343</td>
<td>63</td>
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<td>G. globosa</td>
<td>2142±178</td>
<td>1018±138</td>
<td>556±105</td>
<td>114</td>
<td>285</td>
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<tr>
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<td>184±19</td>
<td>53±12</td>
<td>24±6</td>
<td>247</td>
<td>660</td>
<td>71</td>
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<tr>
<td>G. globosa</td>
<td>142±20</td>
<td>58±8</td>
<td>28±6</td>
<td>144</td>
<td>407</td>
<td>59</td>
<td>80</td>
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<tr>
<td>Cyt f</td>
<td>E. coracana</td>
<td>3.60±0.30</td>
<td>2.12±0.23</td>
<td>0.78±0.08</td>
<td>69</td>
<td>361</td>
<td>41</td>
</tr>
<tr>
<td>G. globosa</td>
<td>3.38±0.40</td>
<td>2.33±0.30</td>
<td>1.36±0.16</td>
<td>46</td>
<td>148</td>
<td>31</td>
<td>59</td>
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<tr>
<td>(P_{N})</td>
<td>E. coracana</td>
<td>44±6</td>
<td>22±3</td>
<td>17±2</td>
<td>108</td>
<td>177</td>
<td>51</td>
</tr>
<tr>
<td>G. globosa</td>
<td>21±3</td>
<td>16±2</td>
<td>10±2</td>
<td>40</td>
<td>87</td>
<td>33</td>
<td>42</td>
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</tbody>
</table>

The effect of reduced irradiance on \(P_{N}\) was measured to study the photosynthetic capacity under L1 stress. \(P_{N}\) was lower in L1 plants than in HI plants (Table 1). The rates decreased to a greater extent in HI→L1 and HI→L2 plants of E. coracana compared to that of similar G. globosa plants. The increase in \(P_{N}\) was also higher in L1→HI and L2→HI E. coracana plants compared to similar G. globosa plants. However, \(P_{N}\) was higher in control HI plants of E. coracana compared to that of G. globosa.
Discussion

The Chl a/b ratio decreased whereas the Chl fluorescence ratio at 77 K, F_{680}/F_{735}, and Chl/Cyt f ratios increased in both species under reduced irradiances (Fig. 1, Table 1) suggesting an increase in LHC2 (Lichtenthaler et al. 1982a,b, Terashima and Inoue 1984, Anderson 1986, Krause and Weis 1991). The Chl fluorescence ratio F_{680}/F_{735} at 77 K reflects changes in pigment-protein complexes (Šesták and Šiffel 1997) while the same ratio at room temperature is an indicator of the in vivo Chl content and is inversely correlated to the Chl content in a curvilinear manner (Lichtenthaler et al. 1990). The ratio at room temperature is frequently applied to determine the Chl content of leaves in a non-destructive way (Hák et al. 1990). The increase in LHC2 under reduced irradiances was greater for E. coracana compared to G. globosa suggesting necessity for the greater investment in Chl towards light-harvesting in former species compared to the latter one. The time taken for E. coracana plants to acclimate to reduced irradiances (650 and 200 µmol m^{-2} s^{-1}) was 4 and 8 d, respectively, whereas in G. globosa the time period was 8 and 10 d, respectively (Fig. 1). The difference in time period of acclimation to reduced irradiances between the two species is in contrast to our earlier observation that the time taken by carbon metabolism to acclimate to reduced irradiances (650 and 200 µmol m^{-2} s^{-1}) was identical (Sailaja and Rama Das 1995b). F_{r}/F_{m} was reduced in both plant species under reduced irradiances but the decline in the ratio was greater in E. coracana compared to that of G. globosa at both room temperature and at 77 K (Table 1). However, the fluorescence measurements at 77 K and field temperatures were not identical. This may be due to the lack of the effect of metabolic reactions on fluorescence at 77 K (Ögren and Öquist 1984, Sailaja and Rama Das 1996b). The F_{r}/F_{m} ratio denotes the excitation energy captured by the open reaction centres in the absence of photochemical quenching (Genty et al. 1989, Adams et al. 1990). Therefore, the decrease observed in F_{r}/F_{m} in the plants grown under reduced irradiances is an indication of a decrease in the excitation energy capture by the open reaction centres. The number of light-harvesting antennae increased (Fig. 1, Table 1) to optimise the function of open reaction centres offsetting the decrease in the excitation energy capture (Table 1). The assemblage of light-harvesting complex was apparently larger in E. coracana compared to G. globosa grown at reduced irradiances (Fig. 1, Table 1) to offset the extra decrease in the efficiency of excitation energy capture by the open reaction centres (Table 1). Thus, the present study agrees with our previous study on Amaranthus (Sailaja and Rama Das 1995a) that there is impairment in functional open reaction centres under sub-optimal irradiance because of lowered excitation energy capture due to more closed reaction centres. In contrast to that, an increase in the efficiency of energy transfer is observed in a shaded habitat (Björkman and Demmig 1987). However, the excitation energy capture did not change in Silene dioica grown at reduced irradiance (McKeran and Baker 1991). The reduction in function of PS2 reaction centres under limiting-irradiance was restored to the full PS2 functional capacity when normal irradiance was provided along with a reduction in LHC2 (Table 1). Reduced antenna under high-irradiance in both species (Table 1) could lessen the susceptibility of damage to PS2 since plants with large light-harvesting antennae are exposed to greater photoinduction of photosynthesis under high-irradiance (Anderson and Andersson 1988, Park et al. 1997).

The percent decrease in whole chain, PSI, and PS2 electron transport rates due to changes in growth irradiance varied in both species (Table 1). E. coracana showed greater reduction in electron transport rates compared to G. globosa. The electron transport in E. coracana was reduced more to match the extra decrease in the performance of photosystems and redox carriers and was restored to normal when normal irradiance was available (Table 1). The dynamic modulation of electron transport in response to reduced growth-irradiance in E. coracana and G. globosa reiterates that species specificity exists to fine tune the process of photo-synthesis in plants acclimated to reduced irradiance. Under limiting irradiance the impairment of PS2 electron transport was higher compared to that of PSI (Table 1) confirming the fact that PS2 is more susceptible to stressing irradiance over PSI (Anderson and Andersson 1988, De la Torre and Burkey 1990, Sailaja and Rama Das 1996a). The observed smaller change in function of the Cyt b/f complex in G. globosa compared to that of E. coracana might be related to less decline in the electron transport and the functional PS2 reaction centres under reduced irradiances (Table 1). This in turn accounts for the observed more efficient P_{N} in G. globosa compared to that of E. coracana under limiting irradiances (Table 1). However, control HI plants of E. coracana had higher P_{N} consistent with the higher amounts of Cyt b/f compared to HI plants of G. globosa (Table 1). The more efficient photosynthetic performance of G. globosa was likely to be due to the increased allocation of metabolic energy towards assembly of the Cyt b/f under limiting irradiance, unlike E. coracana which shows a greater investment in the light-harvesting complexes. The prominent regulatory role of Cyt f in LI plants in determining P_{N} is in agreement with previous studies (Anderson 1992, Price et al. 1995, Evans 1997).

We identified two modes of acclimation to reduced irradiances: (1) the G. globosa type which combines modulation of composition and function of thylakoid membrane to relatively higher performance, and (2) the E. coracana type in which a greater investment in the light-harvesting apparatus is employed in order to achieve
a reasonable acclimation level. *Amaranthus*, an NAD-ME C₄ dicotyledonous plant grown under the same irradiances (650 and 200 µmol m⁻² s⁻¹) showed acclimation similar to *E. coracana* type which is an NAD-ME monocotyledon species (Sailaja 1994, Sailaja and Rama Das 1995a, 1996a) indicating that the observed difference between the two species in the present study is not because of structural differences between monocotyledon and dicotyledon plants. NADP-ME C₄ plants have superior mode of acclimation compared to NAD-ME type C₄ plants. The observation is meaningful in view of the fact that NADP-ME is considered to be an advanced form of C₄ that evolved from the relatively primitive NAD-ME type. Carbon assimilation and photosynthetic acclimation are co-ordinated under reduced growth irradiance (Walker and Sivak 1986). End product of carbon assimilation is crucial in biochemical feed back regulation of carbon assimilation by depriving the orthophosphate concentrations in chloroplasts of low irradiance grown plants (Walker and Sivak 1986). The orthophosphate is essential for regulating the electron transport and carbon metabolism (Walker and Osmond 1986, Walker and Sivak 1986, Foyer 1988). Efficient recycling of the orthophosphate is not possible under reduced ATP conditions (Walker and Sivak 1986). PSI electron transport rates decreased under the limiting irradiance in both *E. coracana* and *G. globosa* (Table 1) resulting in reduced ATP content and probable inefficient recycling of orthophosphate. The greater efficiency of orthophosphate recycling in NADP-ME C₄ plants compared to the NAD-ME C₄ plants due to a lesser reduction in the PSI electron transport rates (Table 1) could account for the observed more efficient photosynthetic performance at reduced growth irradiances. The efficiency of orthophosphate recycling in different types of C₄ plants under limiting-irradiance needs to be investigated further.

References


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