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Adaptation of photosynthesis under iron deficiency in maize

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Summary

This paper explores the effects of high light stress on Fe-deficient plants. Maize (*Zea mays*) plants were grown under conditions of Fe deficiency and complete nutrition. Attached, intact leaves of Fe-deficient and control plants were used for gas exchange experiments under suboptimal, optimal and photoinhibitory illumination. Isolated chloroplasts were used to study photosynthetic electron transport system, compromised by the induction of Fe deficiency. The reaction centers of PS II (measured as reduction of Q, the primary electron acceptor of P 680) and PS I (measured as oxidation of P 700) were estimated from the amplitude of light induced absorbance change at 320 and 700 nm, respectively. Plants were subjected to photoinhibitory treatment for different time periods and isolated chloroplasts from these plants were used for electron transport studies. Carbon dioxide fixation in control as well as in Fe-deficient plants decreased in response to high light intensities. Total chlorophyll, P 700 and Q content in Fe-deficient chloroplasts decreased, while Chl a/b ratio and Q/P 700 ratio increased. However, electron transport through PS II suffered more after photoinhibitory treatment as compared to electron transport through PS I or whole chain. Electron transfer through PS I+PS II, excluding the water oxidation complex showed a decrease in Fe-deficient plants. However, electron transport through this part of the chain did not suffer much as a result of photoinhibition, suggesting a defect in the oxidising side of PS II.

Introduction

Fe deficiency causes chlorosis in plants due to decreased chlorophyll biosynthesis (Chen and Barak, 1982). Light-dependent synthesis of δ-amino levulinic acid (δ-ALA) is impaired under conditions of Fe deficiency (Miller et al., 1982). Light-saturated

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Abbreviations: Chl a and b, Chlorophyll a and b; Cyt, Cytochrome; DCPIP, dichlorophenol indophenol; DPC, diphenylcarbazide; EDTA, ethylenediaminetetraacetic acid; HEPES, hydroxyethyl piperazine ethanesulfonic acid; MV, methyl viologen; P 700, reaction centre of PS I; PBQ, *p*-benzoquinone; PQ, plastoquinone; PQH_2, plastoquinol; PS I, photosystem I; PS II, photosystem II; Q, -primary electron acceptor of PS II; WOC, water oxidation complex

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rates of electron transport have been found to decrease during conditions of Fe deficiency as a consequence of reduction in reaction centers and electron carriers (Terry, 1980; Nishio et al., 1985). A loss in photosynthetic capacity would render the photosynthetic electron transport system susceptible to damage by light intensities normally encountered during growth, with PS II being especially susceptible due to the rapid degradation of D1. The photosynthetic system exhibits short term as well as long-term adaptation mechanisms in response to elevated temperatures and/or irradiance to avoid photoinhibitory damage (Anderson and Osmond, 1987; Anderson and Andersson, 1988). The more important characteristics of the acclimation response are a change in the PS II/PS I ratio (Anderson, 1986), change in antenna size and distribution (Anderson and Andersson, 1988) and a change in the relative amounts of photosystem II (PS II) in the appressed and nonappressed regions of the thylakoid (Hundal et al., 1990). Photosystem PSI appears to be a prime target of Fe deficiency and cyanobacteria are known to surround their PS I centers by the isiA protein that binds chlorophyll and could function either as a light-harvesting system (Bibby et al., 2001) or as a nonradiative dissipater of light energy (Sandstrom et al., 2001). In maize plants, the component of the photosynthetic electron transport system showing greatest decrease in activity is the Cyt *bf* complex (Sharma and Sanwal, 1992). Adaptive alteration in electron transport efficiency has been attributed to deficiency-induced remodeling of the light-harvesting apparatus (Moseley et al., 2002; Naumann et al., 2005). Reduced rates of carbon dioxide fixation in Fe-deficient plants could be attributed to decreased electron transport capacity leading to reduced availability of ATP and the reductant for carbon fixation. This could also be related to photoinhibitory damage in plants with reduced amount of chlorophyll.

The present paper is an attempt to explore the Fe deficiency response on photosynthetic electron transport, P 700 (reaction center of PS II), Q (primary electron acceptor of P 680 and therefore a measure of PS II) and CO_2 fixation rates under normal and photoinhibitory conditions.

Materials and methods

Plant growth

Maize (*Zea mays* L. var.Ganga 5) was grown on refined sand in glass house during April–August, when PAR levels at noon approached 1500–1700 μM quanta $m^{-2}s^{-1}$. The control plants were supplied with nutrient solution containing in mM: 4 $Ca(NO_3)_2$, 2 $MgSO_4$, 1.33 $(NH_4)_2HPO_4$, 0.1 NaCl, 0.1 Fe-EDTA; and in μM: 10 $MnSO_4$, 1 $CuSO_4$, 1 $ZnSO_4$, 33 H_3BO_3, 0.2 Na_2MoO_4, 0.1 $CoSO_4$ and 0.1 $NiSO_4$. The sand and the nutrients were purified against Fe (Hewitt, 1966). Fe deficiency was induced in a set of plants by growing with reduced (0.05 mM) supply of iron. Plants were harvested 21 d after sowing. Chloroplasts were isolated from second and third leaves from the top – which, in Fe-deficient plants, showed chlorosis. For photoinhibitory treatment, intact plants were moved to a growth chamber (Hereaus) and the shelf height and illumination adjusted to provide 2500 μmol quanta $m^{-2}s^{-1}$. The chamber temperature was maintained at 30 °C. All experiments were conducted in six sets of plants grown in different pots in the same time period.

Chloroplast isolation, chlorophyll, Q and P 700 estimation

Chloroplasts were isolated by grinding chopped, deveined leaves in a medium containing 0.33 M sorbitol, 10 mM $MgCl_2$, 10 mM $Na_4P_2O_7$, 20 mM HEPES pH 6.5 with an Ultra-Turrax suspended probe homogenizer. The slurry was filtered through eight-fold muslin and centrifuged at 1200*g* for 3 min. The pellet was suspended in a medium containing 0.33 M sorbitol, 2 mM EDTA, 2 mM $MgCl_2$, 2 mM $MnCl_2$, 5 mM $Na_2P_4O_7$, 10 mM $NaHCO_3$ and 50 mM HEPES (adjusted to pH 7.6 with KOH). Chlorophyll was extracted in 80% acetone and estimated spectrophotometrically, using extinction coefficients for chlorophyll a (Chl *a*) and chlorophyll a (Chl *b*) (Lichtenthaler, 1987). Since chlorophyll content is reduced in chlorotic plants, all results have been expressed on chlorophyll basis for establishing the stoichiometric relationship between PS I (P 700) and PSII (Q). CO_2 fixation rates were measured on area basis and finally expressed on chlorophyll basis. For this, chlorophyll content per unit leaf area was measured by extracting chlorophyll from 4 cm^2 pieces of comparable leaves in 80% acetone and estimating Chl a and b as discussed.

Before making P 700 measurements, secondary electron transport to P 700 from plastocyanin was inhibited by incubating the thylakoids with 100 mM KCN for 1.5 h (Ouitrakul and Izawa,1973). P 700 and Q measurements were carried out in SLM – AMINCO DW-2000 spectrophotometer interfaced to an IBM PS/2 -30 computer for collection and post-acquisition data treatment. Actinic radiation was provided by quartz halogen lamp and passed through Hilger-4 filter, which allows light transmission between 520 and 620 nm. Green light was chosen because it is absorbed uniformly by P 700 and P 680 (Melis and Anderson, 1983). The photomultiplier was shielded from actinic radiation by Wratten 88A filter for P 700 measurement and by Corning 3–96 filter for Q measurements. The intensity of the actinic beam was attenuated by neutral density filters to 6.5 K erg $cm^{-2} min^{-1}$. A water filled quartz cylinder placed in the path of the actinic beam served as a heat filter. The sample cuvette was