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ORIGINAL ARTICLE

Diurnal variations in gas exchange and chlorophyll fluorescence in rice leaves: the cause for midday depression in CO_2 photosynthetic rate

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Gas exchange and chlorophyll fluorescence analysis were carried out to investigate the diurnal variations in photosynthesis in leaves of rice (*Oryza sativa* L.). Leaf CO_2 photosynthetic rate (Pn) showed a bimodal diurnal pattern and midday depression in Pn was observed at 13:00 h. Depression in Pn at midday was mostly attributed to stomatal limitation since the reduction in Pn was followed by the significant reduction in stomatal conductance (Gs). Midday depression in Pn was found to be associated with reversible inactivation of Photo-system II (PS II) reaction centers and increase of photo-inhibition in response to high intensity as evidenced by the maximum efficiency of PS II (Fv/Fm) decreased with increase of light intensity from 6:00 h to 16:00 h of a day. The minimal fluorescence (Fo) gradually increased with increasing light intensity and reached its highest value at 13:00 h and on contrary the maximal fluorescence (Fm) decreased and reached its lowest value at 13:00 h. Quantification of several chlorophyll fluorescence parameters (JIP-test) like area above the fluorescence curve between Fo and Fm, phenomenological energy fluxes like electron transport per cross section (ETo/CS), active PS II reaction center per exited cross-section (RC/CSo) and performance index (Pi) were low in early morning, increasing with time and reaching a maximum at 9:00 h subsequently decreasing and reaching a minimum value at 13.00 h. On contrary the dissipation per cross-section (Dio/CS) gradually increased with increasing light intensity and reached its highest value at 13:00 h. It is likely that PS II down-regulation and heat dissipation co-operated together to prevent the chloroplast from photo damage.

Key words: Chlorophyll fluorescence; Photosynthesis; Photo-system II; Photo-inhibition

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Key words: Chlorophyll fluorescence; Photosynthesis; Photo-system II; Photo-inhibition

Photosynthesis as the primary process by which plants use light energy to drive the synthesis of organic compounds, is pivotal for plant growth. Under common field conditions, the assimilatory apparatus of photosynthesis are exposed to variable intensities of light, temperature and humidity that

may result in a typical midday depression of CO_2 assimilation or photo-inhibition of photosynthesis (Hirasawa and Hsiao, 1999). The midday depression in photosynthesis is a common phenomenon in many C_3 plants, including rice (Hirasawa et al., 1989), soybean (Huang et al., 2006), sunflower (Quick et al., 1992) and cotton (Pettigrew et al., 1990). Several early studies have shown that stomatal closure is at least partial responsible for the reduction in photosynthetic rate in rice (Hirasawa et al., 1989). Murchie et al., (1999) reported that the midday depression in photosynthesis in rice leaves coincided with photo-inhibition and increase of photorespiration. Further more some authors argued that the midday photo-inhibition is a protective mechanism of PS II, rather than the result of irreversible photo-damage of photosynthetic apparatus (Xu and Wu, 1996). Strong irradiance will inevitably induce photo-inhibition with the decrease of photochemical efficiency when the absorbed energy is much higher than that utilized by the photosynthetic organs (Long et al., 1994). The photo-inhibition will occur much frequently when strong irradiance is combined with high temperature, drought or other stresses in summer midday. Furthermore, the photo-inhibition could result in photo-oxidative damage, pigment bleaching and even irreversible damage to the photosynthetic apparatus (Ivanov et al., 2008). Super high-yield rice hybrid, could maintain greater CO_2 photosynthetic rate owing to the greater resistance to photo-inhibition (Wang et al., 2005). This shows the importance of resistance to photo-inhibition in improving the rice yield / biomass.

The diurnal variation of photosynthetic response in rice plant and its photosynthetic apparatus remains far from being understood so far. *In vivo* chlorophyll fluorescence has been used frequently in the past as a convenient and non-intrusive method to study the photosynthetic performances of different species to different environmental condition such as light intensity, temperature, drought, submergence, and chemical influences and reflects the kinetic process of PS II closure (Strasser, and Tsimilli-Michael, 2001; Pietrini et al., 2005; Panda et al., 2008; Sarkar, and Panda, 2009). Fluorescence parameters derived by the theory of fluxes have been suggested to describe changes of absorbed, dissipative, trapping and electron transport fluxes (Force et al., 2003). The analysis of these parameters named JIP test is performed under typical fluorescence induction from the basal emission Fo (O) to a maximum emission Fm (P) through two main intermediate steps i.e. J and I (Strasser et al., 1995).

The aim of this study was to elucidate the diurnal variation of photosynthesis and chlorophyll fluorescence in rice leaves to know the cause for midday depression in CO_2 photosynthetic rate. And also the overall effects were compared with two photosynthetic lowland rice varieties to judge the photosynthetic performances.

MATERIALS AND METHODS

Plant materials and growth conditions:

The experiment was conducted on two photosensitive *Indica* rice cultivars [*Oryza sativa* (L.)] namely FR 13A and IR 42. All cultivars were sown directly in earthen pots containing 2 kg of farm soil (sandy–clay–loam, pH 6.8) and farmyard manure in a 3:1 ratio. Each pot was supplied with 80 mg urea, 192 mg single super phosphate (P_2O_5) and 70 mg murate of potash (K_2O). Plants were thinned to five seedlings per pot 10 days after germination. All the pots were well watered. Each pot is considered one replicate.

Plants were grown in a greenhouse subjected to natural solar radiation, with daily maximum photosynthetic photon flux density, air temperature and relative humidity being about 2040 µ mol m^{-2} s^{-1} and 39.6 ^{o}C and 70-75% respectively. After 30 days of growth the plants were about 20 cm in height and had three leaves stage. All measurements were performed on the 2nd nearly full-expanded leaves. Gas exchange and chlorophyll fluorescence were analyzed in a typical sunny day at four different time intervals namely 06:00 h, 09:00 h, 13:00 h and 16:00 h. The average photon flux density and temperature at 06:00 h, 09:00 h, 13:00 h and 16:00 h was 550, 1140, 2040, 1350 µ mol m^{-2} s^{-1} and 26.6, 30.5, 39.6 and 36.2 ^{o}C respectively. The experiment was arranged in a randomized complete block design with three replicates for studies of the different physiological characteristics.

Measurement of leaf CO_2 photosynthetic rate:

Measurements of CO_2 photosynthetic rate (Pn) and stomatal conductance (Gs) were made on the fully expanded leaves of five different plants using an open system photosynthetic gas analyzer (PP Systems, USA) under normal ambient environmental conditions at 70-75% relative humidity and 370 µ mol mol^{-1} CO_2 concentration. The second and third leaf from the top was selected and kept inside the chamber under natural irradiance until stable reading was recorded (Panda et al., 2008).

Measurement of chlorophyll fluorescence:

After measuring the gas exchange, the same leaves were used for the measurement of chlorophyll fluorescence using a Plant Efficiency Analyzer, Handy PEA (Hansatech Instruments Ltd., Norfolk, UK) and data were recorded from 10 µs up to 1 s with a data acquisition of every 10 µs for the first 300 µs, then every 100 µs up to 3 ms and later every 1 ms. The signal resolution was 12 bits (0 to 4000). The maximal intensity of the light source, providing an irradiance saturating pulse of 3000 µ mol photons m^{-2} s^{-1} was used. For each treatment, the Chlorophyll fluorescence transients of 15 individual leaves were measured. Different chlorophyll fluorescence parameters were analyzed by the so-called JIP-test (Strasser et al., 1995; Force et al., 2003). Different chlorophyll fluorescence parameters like minimal fluorescence (Fo), maximal fluorescence (Fm), Maximum efficiency of PS II (Fv/Fm), the efficiency of excitation capture by open PSII centers (Fv'/Fm'), area above the fluorescence curve between Fo and Fm, electron transport per exited cross section (ETo/CS), number of active reaction center per exited cross section (RC/CSo), dissipation per excited cross section (DIo/CS) and performance index were calculated using the software supplied by the manufacture (for definition and derivations see Table 1).

Statistical analysis:

Differences between various gas exchange and chlorophyll fluorescence parameters were compared by ANOVA using IRRISTAT (International Rice Research Institute, Philippines) software's least significant difference (LSD*P<0.05), as this is a good test for determining whether means were significantly different.

RESULTS

Diurnal changes in leaf gas exchange parameters:

Leaf CO_2 photosynthetic rate (Pn) showed a bimodal diurnal pattern (Fig. 1A). Pn is low in early morning, increasing with time and reaching a maximum at 09:00 h. There after Pn decreased independent of the increase in photon flux density

and lowest value was observed at 13:00 h. Further significant increase of Pn was observed at 16:00 h but its value is significantly lower than first peak. Among the variety significantly more Pn was observed in FR 13A compared to IR 42 at 13:00 h and 16:00 h.

Table 1 : The JIP-test formulae using data extracted from the fast chlorophyll fluorescence O-J-I-P transient.

Fo = Minimal fluorescence- when all the reaction centers are open or in oxidized state
Fm = Maximal fluorescence- when all the reaction centers are closed or in reduced state
Fj = Fluorescence intensity at the J-step (at 2ms)
Fi = Fluorescence intensity at the I-step (at 30ms)
Mo = 4 .(F_{300} - Fo) / (Fm - Fo)
Sm = Area / (Fm - Fo)
Vj = (F_{2ms} - F_0) / (Fm - Fo)
Vi = (F_{30ms} – $F_{50\mu S}$)/(Fm-$F_{50\mu S}$)
Area = Area between fluorescence curve Fo and Fm
Fv/Fm =(1-Fo/Fm), Maximum photochemical efficiency of PS II
Fv'/Fm" = (1-Fo'/Fm'), The efficiency of excitation capture by open PS II centers
Fo' and Fm' = Minimal and maximal fluorescence at normal light
ETo/CSo = (Fv/Fm).(1-Vj).Fo
RC/CSo =(Fv/Fm).(Vj/Mo).Fo
DIo / CSo = (ABS / CS) - (TR_0 / CS)
Performance index (PI_{ABS})= (RC/ABS). [(Fv/Fm)/1-(Fv/Fm)]. [(1-Vj)/(1-(1-Vj)]

Leaf stomatal conductance (Gs) was at maximum at 09:00 h and decreased thereafter as the increase of photon flux density up to 13:00 h (Fig. 1B). Further significant increase of Gs was observed in FR 13A at 16:00 but not in IR 42. As like the Pn, Gs also found to be significantly more in FR 13A compared to that of IR 42 at 13:00 h and 16:00 h.

Diurnal changes in chlorophyll fluorescence parameters:

The minimal fluorescence (Fo) low in early morning gradually increased with increasing light intensity and reached its highest value at 13:00 h (Fig. 2A) on contrary the maximal fluorescence (Fm) decreased and reached its lowest value at 13:00 h (Fig. 2B). There was no significant difference among variety on the basis of Fo but more Fm values observed in FR 31A at 09:00 h to 16:00 h. The maximal efficiency of PS II (Fv/Fm) was 0.82 in the early morning; afterward it decreased with the increase of photon flux density (Fig. 2C). Although Fv/Fm fell at midday 13:00 and it recovered to some extend at 16:00h. The midday decrease of Fv/Fm was more in IR 42 than that of FR 13A.

As like the Fv/Fm similar changes were also observed for the efficiency of excitation capture by open PS II centers (Fv'/Fm') (Fig. 3A). The area above the fluorescence curve between Fo and Fm was highly sensitive to diurnal changes (Fig. 3B). Area was low in early morning, increasing with time and reaching a maximum at 09:00 h. There after it decreased independent of the increase in photon flux density and lowest value was observed at 13:00 h. Further it was increase at 16:00 h but its value is significantly lower than first peak. The initial stage of photosynthetic activity of a reaction center complex is regulated by three functional steps namely absorption of light energy, trapping of the

excitation energy and the conversion of excitation energy to electron transport. Combining these three steps a multi parametric expression of over all performance index (PI) of PS II was calculated. The PI, found to be more in the morning decreased and reached its lowest value at 13:00 h (Fig. 3C).

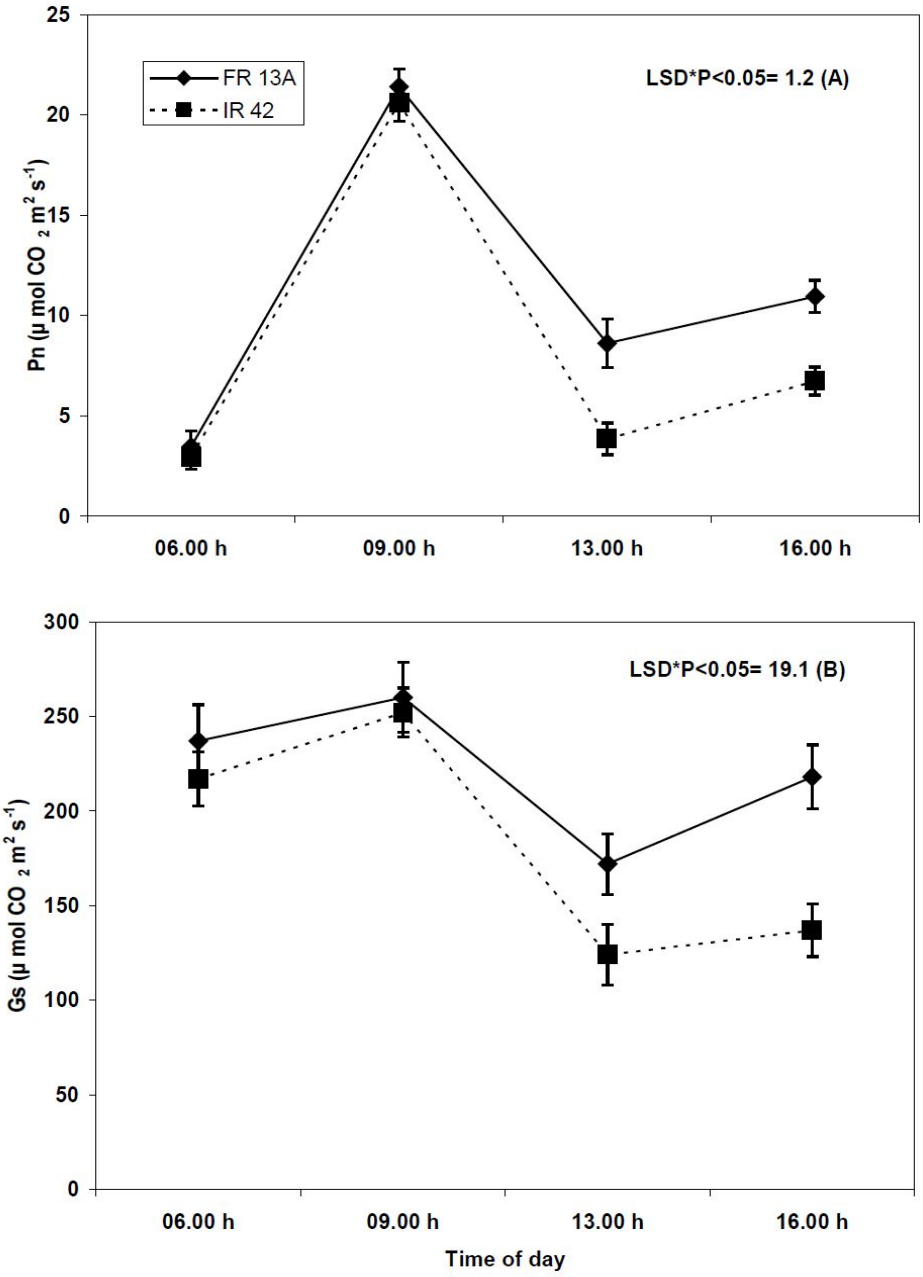

Figure 1. Diurnal variation of CO_2 photosynthetic rate (Pn) and Stomatal conductance (Gs) in rice leaves. Data are the mean of four replicates with standard deviation shown by vertical bars.

The phenomenological fluxes like electron transport per cross-section (ETo/CS) and active reaction center per cross-section (RC/CSo) were found to be more at 09:00 h and further decreased and reached its lowest value at 13.00 h. and further increased up to 16:00 h (Fig. 4AB). The dissipation per excited cross section (DI/CSo) on contrary was increased with the increase of photon flux density (Fig. 4C). Maximum dissipation was observed at 13:00 h and further it was decreased.

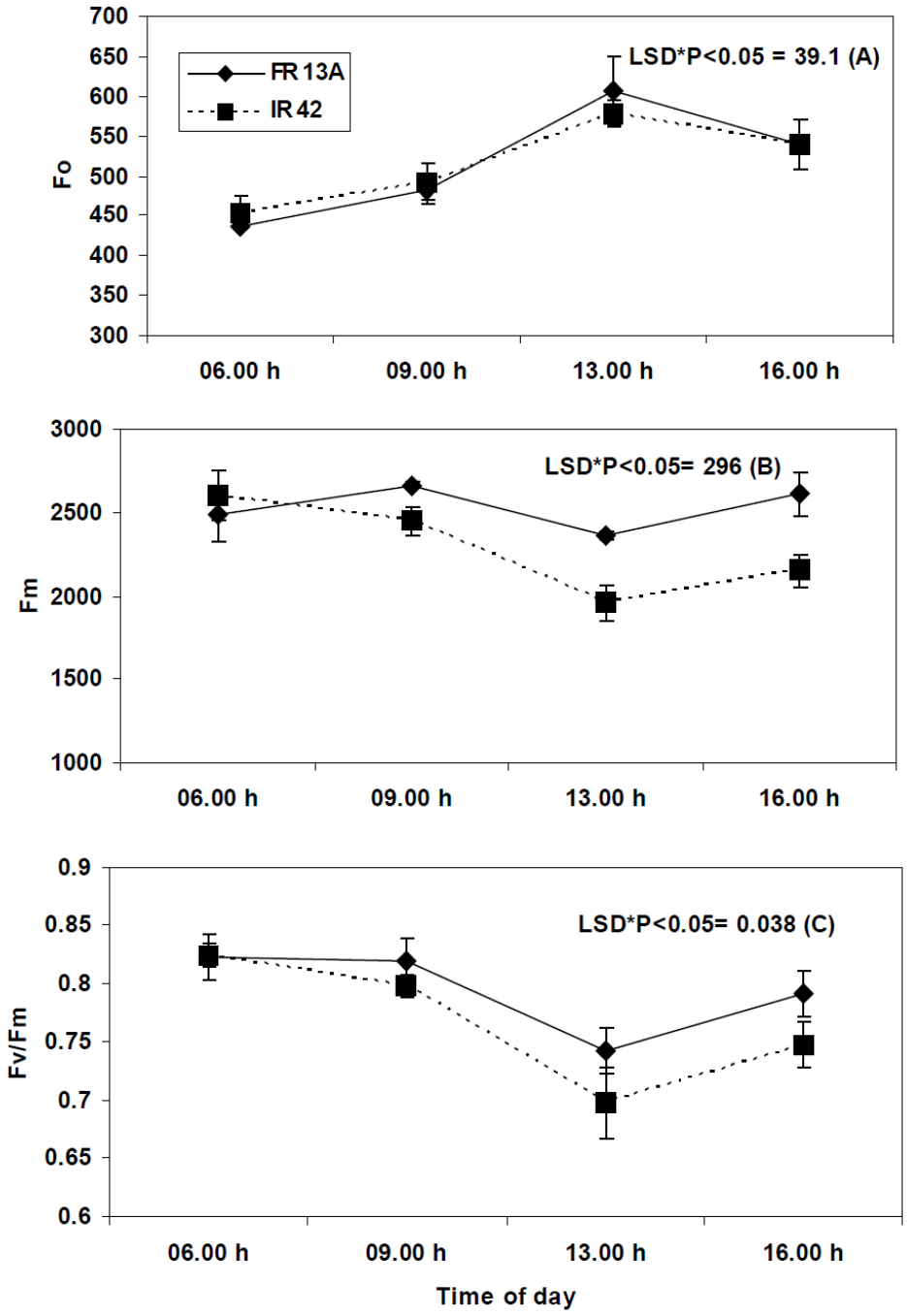

Figure 2. Diurnal variation in minimal fluorescence (Fo), maximal fluorescence (Fm) and maximum photochemical efficiency of PS II (Fv/Fm) in rice leaves. Data are the mean of three replicates with standard deviation shown by vertical bars.

DISSUSSION

Leaf CO_2 photosynthetic rate (Pn) showed a bimodal diurnal pattern and midday depression in Pn was observed at 13:00 h. Depression in Pn at midday was mostly attributed to stomatal limitation since the reduction in Pn was followed by the significant reduction in stomatal conductance (Gs) (Fig. 1). But several other studies have shown that stomatal closure is least partial responsible for the reduction in photosynthesis in rice and soybean (Hirasawa et al., 1989; Hirasawa and Hsiao, 1999). In contrast the midday depression of photosynthesis

predominately causes by closure of stomata and intracellular CO_2 concentration (Spunda et al., 2005).

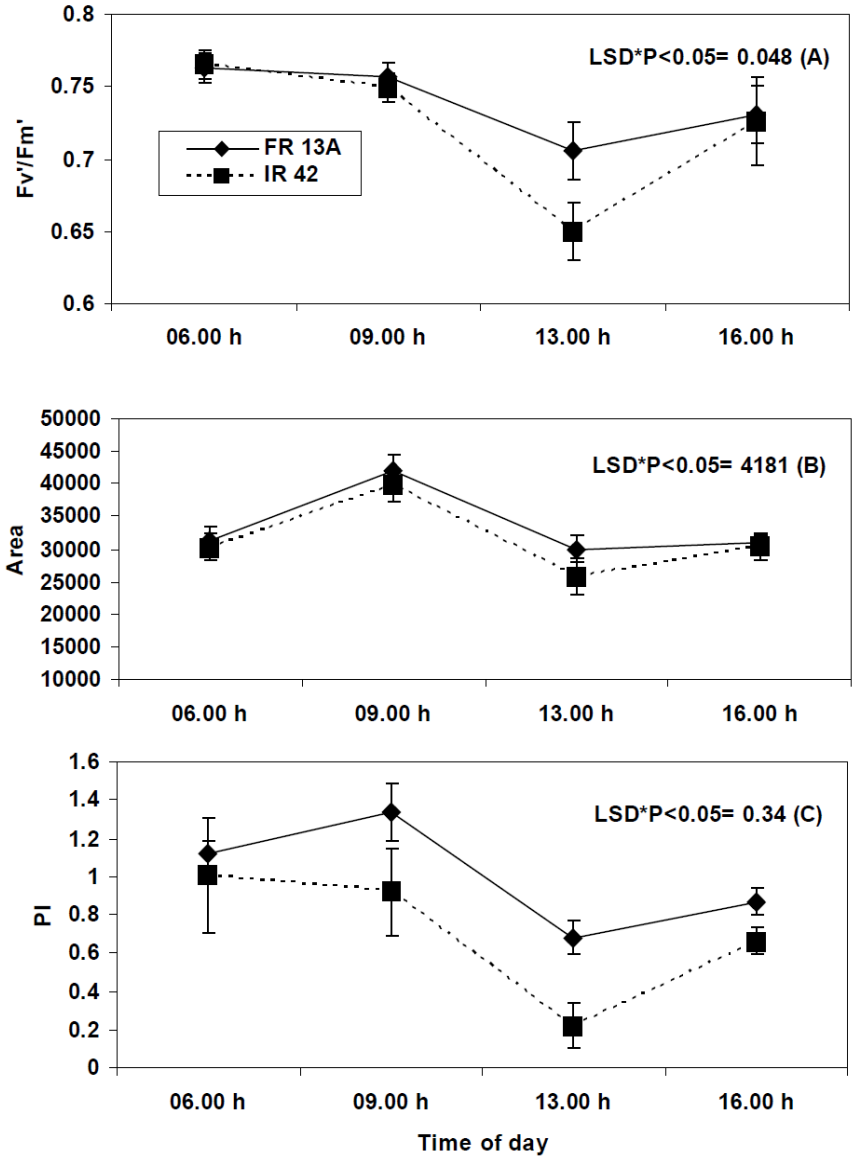

Figure 3. Diurnal variation in efficiency of excitation capture by open PS II (Fv'/Fm'), area above the fluorescence curve between Fo and Fm and performance index (PI) in rice leaves. Data are the mean of three replicates with standard deviation shown by vertical bars.

The present investigation characterizes the main effect of light intensity on the function of PS II in two photosensitive cultivars of rice as observed by the chlorophyll fluorescence induction kinetics. Photo-inhibition is characterized by the decline of photosynthetic quantum efficiency and photochemical efficiency, and Fv/Fm value is widely used as an index to evaluate the extent of photo-inhibition (Krause and Weis, 1991; Maxwell and Johanson, 2000; Sayed 2003). In this study decrease in Fv/Fm was found at 13:00 h (Fig. 2C) is indicative of photo-inhibition as well as damage to photosynthetic apparatus. It is also known to decrease due to high temperature or other abiotic

stresses (Prakash et al., 2003). But reversible change in Fv/Fm was found during the day, suggesting that photo-protection rather than photo-damage occurred. The decrease in Fv/Fm is likely due to the reversible inactivation or down regulation of PS II rather than the photo-damage to PS II or loss of D1 protein (Demming-Adam and Adams, 1996; Huang et al., 2006). The sharp increase in Fo and decrease in Fm was observed at 13:00 h of the day (Fig. 2BC) was likely to be caused by PS II inactivation (Demming-Adam and Adams, 1996). An increase in Fo fluorescence has been recognized as one of the most direct signs of photoinhibition (Aro et al., 1993). The decline in the value of Fm reflects a reduction in the ability of PS II to reduce the primary acceptor Q_A (Calatayud and Barreno, 2001).

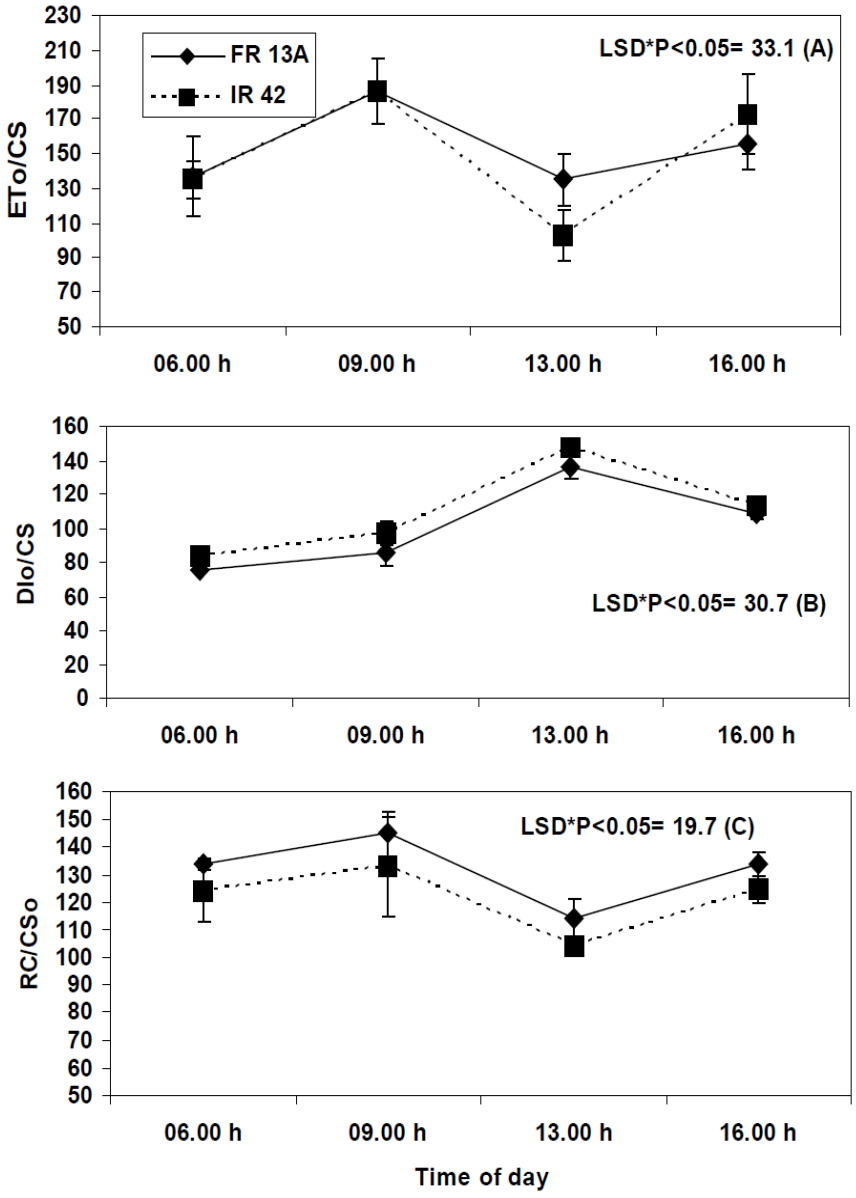

Figure 4. Diurnal variation in efficiency of electron transport (ET/CSo), Dissipation (Dio/CS) and active reaction center (RC/CSo) per excited cross section in rice leaves. Data are the mean of three replicates with standard deviation shown by vertical bars.

The area above the fluorescence curve between Fo and Fm represents the electron acceptor pool size of PS II that includes Q_A and Q_B and PQ (Joliot and Joliot, 2002), decreased with high light intensity at 13:00 h (Fig. 3B). This reduction in pool size is reflected in the observed deleterious effects of excess light intensity on PS II. Electron transport in a PS II cross section (ETo/CS) that represents the re-oxidation of reduced Q_A via electron transport over a cross-section of active and inactive RCs (Force et al., 2003) also decreased at 13:00 h (Fig. 4A). It showed that both the donor and acceptor side of PS II got damaged due to high light, which was more pronounced in the cultivar IR 42 (Fig. 4). The decrease in number of active reaction centre in a PS II cross-section (RC/CSo) supports the contention of damage to donor side (Fig. 4C).

Based on *in vitro* studies, two mechanisms of photo-inhibitory damage have been proposed Ohad et al., (2000). Acceptor side photo-inhibition begins from the over-reduction of the primary quinine acceptor, Q_A that occurs when the electron flow between Q_A^- and Q_B, the secondary quinine acceptor, is blocked. The other mechanism of photoinhibitiory damage is the donor side inhibition (Govindachary et al., 2003). It has been suggested that only one general mechanism of photo-inhibition predominates *in vivo* (Anderson et al., 1998), however under high light intensity both donor and acceptor sides got damaged. The initial stage of photosynthetic activity of a reaction center complex is regulated by three functional steps namely absorption of light energy, trapping of the excitation energy and the conversion of excitation energy to electron transport. Combining these three steps a multi parametric expression of over all performance index (PI) of PS II was calculated. The PI, found to be more in the morning decreased and reached its lowest value at 13:00 h (Fig. 3C) suggesting that the down regulation of PS II photochemistry at 13:00 h.

Although photon flux density was highest at 13:00 h, a drop of Pn was observed (Figure 1). Apparently light absorbed by the plants exceeded the photo-utilization capacity in chloroplast. Plants have developed several strategies to minimize the harmful effect of excess energy (Ort and Baker, 2002). In our experiment, there was a significant decrease in Fv'/Fm' i.e., an increase in the proportion of closed PS II centers and a decrease in the efficiency of excitation capture by open PS II center at 13:00 h (Fig. 3A) indicating the xanthophylls cycle dependant energy dissipation operated coessentially (Demming-Adam and Adams, 1996). In this study the active reaction per excited cross section RC/CSo decreased with the increase of photon flux density (Fig. 4B) and dissipation Dio/CS increased with the photo flux density (Fig. 4C). It was suggesting that heat energy dissipation is an important mechanism required for the rice plant to cope with the changes in light intensities.

In conclusion leaf CO_2 photosynthetic rate in rice showed a bimodal diurnal pattern. The midday depression is mainly due to stomatal limitation as closure of stomata. Down regulation of PS II photochemistry and photo-inhibition in the midday is occurred as a photo-protective mechanism rather than photo-damage, which induce a reversible inactivation of PS II centers and increased thermal energy dissipation in the antennae preventing photosynthetic apparatus from photo-damage.

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REFERENCES

Anderson, J.M., Park, Y.I., Chow, W.S. (1998) Unifying model for the photoinactivation of photosystem II in vivo under steady-state photosynthesis. *Photosynth. Res.*, **56**, 1-13.

Aro, E.M., Virgin, I., Anderson, B. (1993) Photoinhibition of photosystem II. Inactivation, protein damage and turnover. *Biochimica Biophysica Acta*, **1143**, 113-134.

Demming-Adam, B., Adams, I.I.I. (1996) Photosynthesis: harvesting sunlight safely. *Nature,* **384**, 557-560.

Force, L., Critchley, C., van Rensen, J.J.S. (2003) New fluorescence parameters for monitoring photosynthesis in plants. *Photosynth. Res.*, **90**, 1-19.

Govindachary, S., Bukhov, N.G., Joly, D., Carpentier, R. (2004) Photosystem II inhibition by moderate light under low temperature in intact leaves of chilling sensitive and tolerant plants. *Physiol. Planta.*, **121**, 322-333.

Hirasawa, T., Hsiao, T.C. (1999) Some characteristics of reduced leaf photosynthesis at midday in maize growing in the field. *Field Crop Res.,* **62**, 53-62.

Hirasawa, T., Iida, Y., Ishihara, K. (1989) Dominant factor in reduction of photosynthetic rate affected by air humidity and leaf water potential in rice plants. *Jap. J. of Crop Sci.*, **58**, 383-389.

Huang, I.F., Zheng, J.H., Zhang Y.Y., Hu, W.H., Mao W.H., Zhou, Y.H., Yu, J.Q. (2006) Diurnal variation in gas exchange, chlorophyll fluorescence quenching and light allocation in soybean leaves: The cause for midday depression in CO_2 assimilation. *Sciencetia Horticuture*, **110**, 214-218.

Ivanov, A.G., Hurry, V., Sane, P.V., Цquist, G., Huner, N.P.A. (2008) Reaction Centre Quenching of Excess Light Energy and Photoprotection of Photosystem II. *J. of Plant Biol.,* **51**, 85-96.

Joliot, P., Joliot, A. (2002) Cyclic electron transport in plant leaf. *PNAS*, **99**, 10209-10214.

Krause, G.H., Weis, E. (1991) Chlorophyll fluorescence and photosynthesis: the basics. *Ann. Rev. of Plant Physiol. Plant Mol. Biol.,* **42**, 313-349.

Long, S.P., Humphries, S., Falkowski, P.G. (1994) Photoinhibition of photosynthesis in nature. *Ann. Rev. of Plant Physiol. Plant Mol. Biol.,* **45**, 633-662.

Maxwell, K., Johanson, G.N. (2000) Chlorophyll fluorescence – a practical guide. *J. of Exp. Bot*. **51**, 659-668.

Murchie, Chen, Y., Hubbart, S., Peng, S., Horton, P. (1999) Interactions between Senescence and Leaf Orientation Determine in Situ Patterns of Photosynthesis and Photo-inhibition in Field-Grown Rice. *Plant Physiol.*, **119**, 553-563.

Ohad, I., Sonoike, K., Andersson, B. (2000) Photoinactivation of the two photosystems in oxygenic photosynthesis: mechanisms and regulations, In: M. Yunus, U. Pathre, P. Mohanty, (eds.): Probing Photosynthesis: Mechanisms, Regulation and Adaptation. Taylor and Francis Publishers – London, pp. 293-309.

Ort, D.R., Baker, N.R. (2002) A photoprotective role for O_2 as an alternative electron sink in Photosynthesis. *Curr. Opi. in Plant Biol*, **5**, 193-198.

Panda, D., Sharma, S.G., Sarkar R.K. (2008) Chlorophyll fluorescence parameters, CO_2 Photosynthetic rate and regeneration capacity

as a result of complete submergence and subsequent re-emergence in rice (*Oryza sativa* L.). *Aquatic Bot.*, **88**, 127-133.

Pettigrew, W.T., Hesketh, J.D., Peters, D.B., Woolley, J.T. (1990) A vapour pressure deficit on crop canopy photosynthesis. *Photosynth. Res.*, **24**, 27-34.

Pietrini, F., Chaudhuri, D., Thapliyal, A.P., Massacci, A. (2005) Analysis of chlorophyll fluorescence transients in mandarian leaves during a photo-oxidative cold shock and recovery. *Agricul. Eco. Env.*, 106, 189-198.

Prakash, J.S.S., Srivastava, A., Strasser R.J., Mohanty, P. (2003) Senescence-induced alterations in the photosystem II functions of *Cucumis sativus* cotyledons: probing of senescence driven alterations of photosystem II by chlorophyll a fluorescence induction O-J-I-P transients. *Ind. J. of Biochem. Biophy.*, **40**,160-168.

Qiang, W., Congming, L.U., Qide, Z., Naibin, H., Qiaoying, G.E., Fengqin, D., Kezhi, B., Tingyun, K. (2009) Characterization of photosynthesis, photoinhibition and the activities of C4 pathway enzymes in a superhigh-yield rice. *Sci. in Chinna (Series C)*, **45**, 468-476.

Quick, W.P., Chaves, M.M., Wender, R. (1992) The effects of water stress on photosynthetic carbon metabolism in four species grown under field conditions. *Plant Cell Env.*, **15**, 25-35.

Sarkar, R.K., Panda, D. (2009) Distinction and characterisation of submergence tolerant and Sensitive rice cultivars, probed by the fluorescence OJIP rise kinetics. *Fun. Plant Biol.,* **36**, 1-12.

Sayed, O.H. (2003) Chlorophyll fluorescence as a tool in cereal crop research. *Photosynthetica,* **41**, 321-330.

Spunda, V., Kalina, J., Urban, O., Luis, V.C., Sibisse, I., Puertolas, J., Sprtova, M., Marck, M.V. (2005) Diurnal dyanamics of photosynthetic parameters of Norway spruce trees cultivated under ambient and elevated CO_2: The reason of midday depression in CO_2 assimilation, *Plant Sci.*, **168**, 1371-1381.

Strasser, R.J., Srivastava, A., Govindjee, (1995) Polyphasic chlorophyll a fluorescence transient in plants and cyanobacteria. *Photochem. Photobiol.,* **61**, 32-42.

Strasser, R.J., Tsimilli-Michael, M. (2001) Stress in plants, from daily rhythm to global changes, detected and quantified by the JIP-test. *Chimie Nouvelle (SRC),* **75**, 3321-3326.

Wang, Q.A., Lu, C.M., Zhang, Q.D. (2005) Midday photoinhibition of two newly developed super-rice hybrids. *Photosynthetica*, **43**, 277-281.

Xu, D.Q., Wu, S., (1996) Three phases of dark recovery course from photo-inhibition resolved by the chlorophyll fluorescence analysis in soybean leaves under field condition. *Photosynthetica*, **32**, 417-423.