

## Effects of Flooding Treatments on Photosynthetic Activity of Different Greengram (*Vigna radiata* (L.) Wilczek) Cultivars

Takuya ARAKI<sup>1</sup>, Thay Thay OO<sup>2</sup> and Fumitake KUBOTA<sup>3</sup>

<sup>1</sup> Faculty of Agriculture, Ehime University, Matsuyama 790–8566, Japan

<sup>2</sup> Yezin Agricultural University, about 18 km north of Pynmana, Naypyidaw, Myanmar

<sup>3</sup> Faculty of Agriculture, Kyushu University, Fukuoka 812–8581, Japan

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The response in growth and gas exchange to a flooding condition was characterized with 8 cultivars of greengram (*Vigna radiata* (L.) Wilczek). Pot-grown plants were subjected to 6-d flooding and 6-d recovery treatment. The flooding treatment had serious effects on the gas exchange and electron transport of 7 cultivars except for cv. KP, while the damages were lenient in cv. KP. KP was characterized by maintaining relatively higher stomatal conductance, mesophyll conductance and photochemical efficiency of photosystem II, which was attributed to sustaining the CO<sub>2</sub> assimilation under flooding stress. KP was also superior in photosynthetic sustainment than other 7 cultivars under recovery treatment, which was attributable to the fact that this cultivar recovered stomatal conductance, mesophyll conductance, electron transport and the ratio of photorespiration to total carbon assimilation. These results in cv. KP lead to higher plant growth in relation to leaf area extension and dry matter.

Keywords : flooding tolerance, gas exchange, greengram, photochemical system II

### INTRODUCTION

In Myanmar, greengram is an important component of the rice-based cropping system and this crop sown area has dramatically increased due to the export market demand. A problem of greengram cultivation in such a condition is excessive moisture and flooding after rain. Under those circumstances, the understanding of the physiological features and identifying genotypic differences for tolerance to flooding are indispensable to solve such an agronomical problem. By introducing flood-resistant cultivars into the rain-fed areas in Myanmar, the production of greengram is expected to be significantly improved and stabilized.

Growth and productivity of crops are often severely affected by flooding. It has been known that by flooding treatments, greengram cultivars suffered several physiological impacts, such as the reduction of leaf photosynthesis, stomatal closure and growth inhibition of leaves, stems and roots (Ahmed et al., 2002). Yadav and Saxena (1998) also reported a drastic reduction in seed yield of greengram as a result of flooding, and the reason for this reduction was attributable to the inhibitory effect on the symbiotic nitrogen fixation of root nodules. *Vigna radiata* species is suggested to be unsuitable in the wet tropics where the annual rainfall is more than 1,000 mm (Jain and Mehra, 1980).

In accordance with a reduction in stomatal conductance ( $G_s$ ), the photosynthesis of sensitive species decreased rapidly following flooding (Pezeshki and Chambers, 1985). This phenomenon has been observed in a number of different species, including important crops

such as tomato, wheat, pepper and bean (Pezeshki, 1994). A reduction of  $G_s$  in flooding limits water loss by transpiration decrease, but simultaneously it decreases the carbon assimilation and retard the growth. In flooded plants, a signal from roots to leaves, probably a combination of reduced cytokinin synthesis along with an increased transport of ABA and ethylene induces stomatal closure (Nelsen and Orcutt, 1996).

The energy production-consumption balance between chlorophyll and stroma in chloroplasts is the element strongly affecting the functional situation in the entire photosynthetic apparatus. This situation is usually investigated by monitoring fluorescence from chlorophylls. Chlorophyll fluorescence measured with a leaf can be used as an indicator of the stress tolerance or the damage severity in photosynthetic apparatus (Mexwell and Johnson, 2000). Light energy absorbed in photosystem II is utilized on various energy consumers, not only carboxylation but also photorespiration, alternative reactions such as thermal dissipation which contribute to dissipation and reduction of excessive light energy. This energy partitioning has been evaluated by the simultaneous measurement of gas exchange and chlorophyll fluorescence under stress conditions, such as nitrogen deficiency (Kumagai et al., 2010), salinity (Brugnoli and Björkman, 1992) and drought (Flexas and Medrano, 2002). Kumagai et al. (2010) showed that the difference in rice productivity under nitrogen deficiency condition could depend on the carboxylation and H<sub>2</sub>O<sub>2</sub> scavenging capacities. Thus, CO<sub>2</sub> gas exchange rate ( $CER$ ),  $G_s$ , mesophyll conductance ( $G_m$ ) and chlorophyll fluorescence are important parameters for clarifying

Corresponding author : Takuya Araki, fax: +81-89-946-9526,  
e-mail address : araki@agr.ehime-u.ac.jp

the difference in flooding-tolerance and adaptability among greengram cultivars. Wondimagegne et al. (1992) stated that the reduction of growth was caused by flooding varied with crop species and genotypes. Although numerous studies have described the effect of flooding on growth and photosynthetic rate, little attention has been paid to the varietal difference in photosynthetic response of greengram cultivars.

In this study, differences in the response of flooding and recovery treatment to CO<sub>2</sub> exchange rate and chlorophyll fluorescence of greengram cultivars in Myanmar to flooding and recovery treatment were investigated.

## MATERIALS AND METHODS

### *Plant materials and treatments*

Eight greengram cultivars were included, five cultivars [cvs. Yezin-4, Yezin-5, Kanti, KPS2 (KP), VC 1973A (VC)] are released from Central Agriculture Research Institute (CARI), Myanmar, two landraces (cvs. Magwe and Nyaungoo) and Chinese (cv. CN) from China, which has been tested in Laboratory of Plant Production Physiology, Kyushu University, Japan. The experiment was carried out in greenhouse under natural light at the Kyushu University, Fukuoka, Japan from June to July in 2005. In order to make a comparison in the same conditions, the eight cultivars were divided into two groups; One group is Yezin-4, Yezin-5, Magwe and Nyaungoo, and another is CN, KP, VC and Kanti. Four cultivars in each group were grown together in an 8-liter pot filled with sandy loam soil. Sterilized soil was used to minimize the effect of soil microorganisms on plant. Insecticide was applied when needed.

Before the flooding treatment was imposed, the pots with vigorously growing plants were divided into two groups at 30 d old; one group was continuously flooded at 4 cm above the soil surface by putting 2 pots per container (60 × 40 × 30 cm), and the other was normally irrigated. Water supply was carried out every day to keep the water level. At the end of flooding treatment, the pots were taken up from the containers to drain the flooded water from the drainage holes of the pots to check the recovery response.

### *Measurement of CO<sub>2</sub> exchange rate and chlorophyll fluorescence*

Measurements were conducted at 6 d after flooding and 6 d after recovery. The fully expanded top leaves at 6 d after flooding were used for the determination of gas exchange rate and chlorophyll fluorescence measurements and the leaves were also used for the measurements at the recovery. *CER* was measured using a sandwich type assimilation chamber. During the measurements, the environmental condition in the chamber was controlled at 380 μL L<sup>-1</sup> of CO<sub>2</sub> concentration, 21% of O<sub>2</sub> concentration, 30 ± 1°C of leaf temperature, 60% of relative humidity, and 600 μmol m<sup>-2</sup> s<sup>-1</sup>, photosynthetic photon flux density (*PPFD*). The leaf area enclosed in the assimilation chamber was 6.25 cm<sup>2</sup>, and the air flow rate was adjusted to 0.706 mmol s<sup>-1</sup>. The CO<sub>2</sub> concentration and vapour pressure in the reference and sample air were monitored with an

infrared CO<sub>2</sub> analyzer (Li-6262, Li-COR, USA). Based on the gas exchange measurement, *CER*, *Gs*, *Gm*, ratio of photorespiration rate to total CO<sub>2</sub> fixation ratio (*Pr/Tc*) and water use efficiency (*WUE*) were calculated from the monitored value (Long and Hällgeren, 1993).

The chlorophyll fluorescence of PSII was monitored with a fluorescence probe (PAM-2000, Walz, Germany) equipped on the assimilation chamber and the gas exchange rate and chlorophyll fluorescence in a leaf were simultaneously measured. The initial fluorescence (*F<sub>o</sub>*) was measured by using a 20 min dark adapted leaf under a measuring beam (3.2 μmol m<sup>-2</sup> s<sup>-1</sup>, 4.8 kHz) and then the maximum chlorophyll fluorescence (*F<sub>m</sub>*) was determined by giving a saturating flash 8,000 μmol m<sup>-2</sup> s<sup>-1</sup> to the leaf. The time course of the fluorescence quenching (*F<sub>s</sub>*) was monitored at 600 μmol m<sup>-2</sup> s<sup>-1</sup>, during which the fluorescence spike (*F<sub>m</sub>'*) was periodically measured by giving pulses of saturating light. Based on measurements of fluorescence, the maximum quantum yield (*F<sub>v</sub>/F<sub>m</sub>*), electron transport rate (*ETR*), non-photochemical quenching (*NPQ*) were calculated by the equation described by Genty et al. (1989).

### *Statistical analysis*

One-way ANOVA was applied to assess the varietal difference of each parameter.

## RESULTS

Table 1 showed the parameters related to leaf photosynthesis and water use efficiency in the eight cultivars measured under the control, flooding and recovery conditions. *CER* was decreased sharply by the flooding treatment in all the cultivars. There was a statistically significant between the *CER* of these cultivars. The decline in *CER* of cvs. CN, VC, Kanti, Yezin-4, Yezin-5, Magwe and Nyaungoo were larger (45–63%) than that of KP (41%). In addition *CER* values in the formers were not sufficiently returned back to the control level at the recovery step but that in the latter showed a quick recovery (i.e. 95% of the control level). The response of *Gs* to the flooding treatment was roughly similar in tendency to that of *CER* in all the cultivars. However, *Gm* is relatively sustained in cv. KP during flooding. The values of *WUE* in KP and Kanti were not much affected by the flooding. However, the response patterns were different among the cultivars in control, flooding and recovery steps. *WUE* in cvs. KP and Yezin-4 were almost returned back to the control level while that in the other cultivars were not at the 6 d after rewatering.

The situation of electron transport in a leaf is shown in Table 2. *F<sub>v</sub>/F<sub>m</sub>* is a parameter reflecting the potential quantum efficiency of PSII, and is used as a sensitive indicator for the photosynthetic performance of a leaf. This parameter was not largely affected by the flooding treatment and cultivar difference in this parameter was observed only at the recovery step. *ETR* values in all cultivars were significantly difference and decreased under flooding, but the decreasing ratio was only 4% in cv. KP. At the 6 d after the recovery treatment began, the value of *ETR* in cv. KP

EFFECT OF FLOODING ON PHOTOSYNTHESIS OF GREENGRAM

**Table 1** Varietal differences in photosynthetic rate (*CER*), stomatal conductance (*Gs*), mesophyll conductance (*Gm*) and water use efficiency (*WUE*) under the control, the flooding and recovery.

Treatment	<i>CER</i> ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	<i>Gs</i> ( $\text{mol m}^{-2} \text{s}^{-1}$ )	<i>Gm</i> ( $\text{mol m}^{-2} \text{s}^{-1}$ )	<i>WUE</i> ( $\text{mmol mol}^{-1}$ )	
Yezin-4	Control	12.8±1.6	0.151±0.028	0.059±0.001	6.0±1.1
Yezin-5		12.7±1.5	0.149±0.013	0.057±0.002	6.2±1.3
Nyaungoo		13.9±1.2	0.170±0.018	0.064±0.005	7.0±0.7
Magwe		12.9±1.1	0.157±0.019	0.061±0.002	6.5±0.9
CN		13.7±1.1	0.170±0.014	0.060±0.003	6.8±0.4
KP		13.7±1.8	0.170±0.027	0.064±0.002	6.8±0.8
VC		12.8±0.9	0.150±0.022	0.064±0.004	6.4±0.3
Kanti		13.0±1.0	0.149±0.032	0.066±0.001	6.1±0.7
		ns	ns	ns	*
Yezin-4	Flooding	7.1±0.4(55)	0.077±0.011(51)	0.039±0.001(66)	3.9±0.1(64)
Yezin-5		6.5±1.1(51)	0.080±0.012(54)	0.030±0.001(53)	4.1±0.6(66)
Nyaungoo		6.7±0.9(48)	0.075±0.014(44)	0.041±0.002(64)	3.7±0.2(53)
Magwe		6.5±0.6(50)	0.086±0.02(55)	0.034±0.001(56)	3.5±0.0(53)
CN		5.1±0.5(37)	0.050±0.003(29)	0.032±0.001(53)	3.7±0.5(55)
KP		8.0±1.2(59)	0.088±0.006(52)	0.047±0.001(73)	4.8±0.9(71)
VC		4.8±0.9(38)	0.050±0.007(33)	0.031±0.002(48)	3.7±0.2(57)
Kanti		7.0±0.5(54)	0.071±0.013(48)	0.035±0.003(53)	4.8±0.4(78)
		**	**	**	*
Yezin-4	Recovery	9.6±2.1(75)	0.13±0.001(81)	0.052±0.001(82)	5.9±1.0(92)
Yezin-5		8.9±1.8(70)	0.11±0.001(74)	0.041±0.001(71)	3.8±1.1(61)
Nyaungoo		10.8±1.4(77)	0.13±0.002(76)	0.045±0.002(70)	5.6±0.4(80)
Magwe		9.9±0.8(77)	0.12±0.005(77)	0.038±0.002(78)	5.1±0.6(77)
CN		8.9±0.8(65)	0.10±0.008(56)	0.045±0.003(73)	5.0±0.7(73)
KP		13.0±0.4(95)	0.15±0.012(87)	0.053±0.004(82)	6.5±0.4(94)
VC		9.3±1.0(72)	0.10±0.015(64)	0.046±0.001(69)	5.2±0.8(78)
Kanti		9.9±1.1(76)	0.10±0.003(61)	0.057±0.004(81)	4.8±1.0(73)
		**	*	*	*

Values in the parentheses are percent of treatment to control.

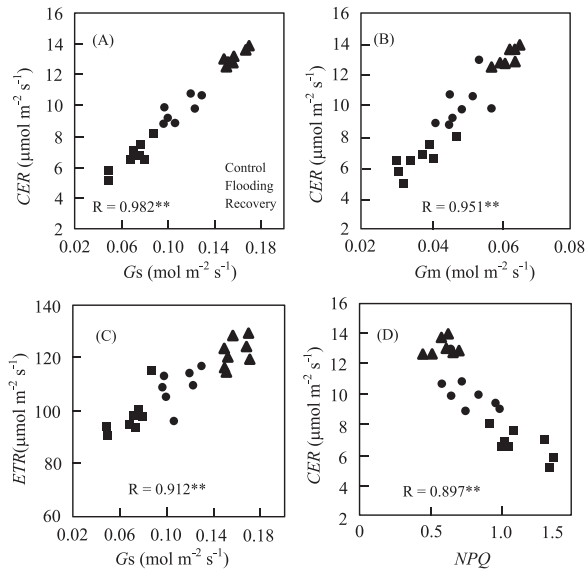
\*\*, \* and ns represent significant varietal differences and not significant at 1%, 5% level, respectively.

**Table 2** Varietal differences in maximum quantum yield of photosystem II (*Fv/Fm*), electrontransport rate (*ETR*), non-photochemical quenching (*NPQ*) and the percentage of photorespiration to total carboxylation rate under the control, the flooding and recovery.

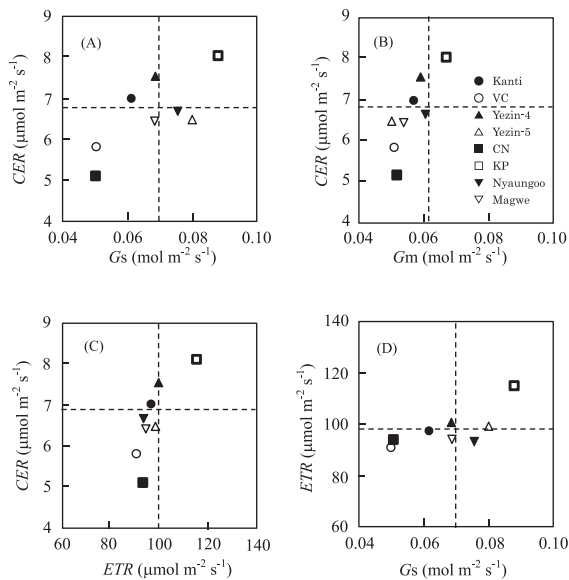
Treatment	<i>Fv/Fm</i>	<i>ETR</i> ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	<i>NPQ</i>	<i>Pr/Tc</i> (%)	
Yezin-4	Control	0.820±0.00	121.0±5.9	0.52±0.04	21.5±5.4
Yezin-5		0.831±0.00	123.5±15.9	0.45±0.23	20.0±2.3
Nyaungoo		0.823±0.10	150.0±2.8	0.62±0.08	23.4±6.2
Magwe		0.829±0.00	138.6±11.5	0.69±0.03	24.2±5.1
CN		0.870±0.03	124.8±15.0	0.58±0.15	18.1±4.8
KP		0.851±0.01	120.0±12.3	0.58±0.17	20.9±1.8
VC		0.818±0.00	115.2±9.9	0.66±0.22	19.7±2.0
Kanti		0.832±0.00	117.6±9.1	0.60±0.07	19.0±7.6
		ns	*	*	*
Yezin-4	Flooding	0.791±0.00(96)	70.3±13.6(58)	0.92±0.12(177)	38.6±2.2(180)
Yezin-5		0.807±0.02(97)	78.7±13.2(64)	1.01±0.08(224)	39.3±24.1(197)
Nyaungoo		0.810±0.01(98)	93.4±32.0(63)	1.03±0.12(166)	37.7±10.2(161)
Magwe		0.801±0.00(97)	84.9±5.2(61)	1.07±0.13(155)	36.9±9.1(152)
CN		0.823±0.04(95)	93.6±11.3(75)	1.35±0.03(233)	33.2±6.5(183)
KP		0.842±0.03(99)	115.2±20.1(96)	0.89±0.09(153)	29.6±3.8(142)
VC		0.814±0.00(100)	91.2±8.8(79)	1.37±0.17(208)	35.2±2.8(179)
Kanti		0.812±0.01(98)	87.3±5.5(74)	1.32±0.41(200)	38.2±4.2(201)
		ns	**	*	*
Yezin-4	Recovery	0.794±0.04(97)	111.4±10.2(92)	0.58±0.06(112)	21.7±3.2(101)
Yezin-5		0.803±0.06(97)	95.8±11.1(78)	0.76±0.04(169)	20.9±2.0(105)
Nyaungoo		0.815±0.00(99)	114.5±13.0(76)	0.73±0.10(118)	27.1±3.2(116)
Magwe		0.819±0.01(99)	109.9±16.0(79)	0.78±0.11(113)	26.0±4.1(107)
CN		0.821±0.12(94)	112.8±8.2(90)	1.01±0.09(174)	22.2±3.1(123)
KP		0.841±0.10(99)	120.0±14.5(100)	0.65±0.03(112)	19.1±2.6(91)
VC		0.804±0.06(98)	105.6±21.1(92)	0.98±0.18(148)	26.3±2.8(134)
Kanti		0.821±0.05(99)	108.3±17.0(92)	0.85±0.09(142)	25.1±3.0(132)
		*	*	*	*

Values in the parentheses are percent of treatment to control.

\*\*, \* and ns represent significant varietal differences and not significant at 1%, 5% level, respectively.



**Fig. 1** Relationships between *CER* and *Gs*, *CER* and *Gm*, *ETR* and *Gs*, and *CER* and *NPQ* (A, B, C and D) under the control, flooding and recovery condition. Values are means of three replicates.  $** (P < 0.01)$



**Fig. 2** The relationships between *CER* and *Gs* (A), *Gm* (B), *ETR* (C) and between *ETR* and *Gs* (D) under flooding. Broken lines show means of the cultivars for each parameter.

returned back to the pre-treatment level, while that in other cultivars were not recovered yet. *NPQ* and *Pr/Tc* ratios were significantly different between cultivars and increased greatly in cvs. Yezin-4, Yezin-5, CN, VC and Kanti under the flooded condition, but not so greatly increase in cvs. KP, Nyaungoo and Magwe. The increasing trends of *NPQ* were almost the same with those of *Pr/Tc* in all the cultivars under the flooded condition. The values of these parameters were still increased in all the cultivars at the recovery stage.

In order to examine the factors limiting *CER* in a greengram leaf, the relationships between *CER* and the

other parameters such as *Gs*, *Gm*, *ETR* and *NPQ* were shown in Fig. 1, using all the data obtained through the whole treatment series including the control, flooding and recovery treatments. The positive relationships were observed in *CER-Gs*, *CER-Gm* and *ETR-Gs*, but a negative relationship in *CER-NPQ*. Of these parameters, *Gs*, *Gm*, *ETR* and *NPQ* were recognized as dominant determinants for *CER* in all soil moisture conditions.

After examining the relationships between the photosynthetic parameters, the author tried to classify the distributing data obtained in the flooding treatment into four divisions of the quadrant I to IV (Fig. 2). The cultivars included in the quadrant I were judged to have a larger value in *CER*, *Gs*, *Gm* and *ETR* than the average values. The parameter values of cv. KP were included in the quadrant I, showing highest values in the flooding treatment. The cultivars, Kanti and Yezin-4, were found in the quadrant II but cvs. CN, VC, Yezin-5, Nyaungoo and Magwe were located in quadrant III, showing low values in *CER*, *Gs* and *Gm*.

## DISCUSSION

The flooding treatment induced several physiological disturbances including the reduction of leaf photosynthesis, stomatal closure and growth inhibition of leaves, stems and roots in greengram species similar to that observed in other bean species (Ahmed et al., 2002). In flooded situations, the decrease in photosynthesis is likely due to the stomatal closure in sensitive species, and this phenomenon has been observed in a number of crop species (Pezeshki, 1994). Lakitan et al. (1992) observed that net photosynthetic rate fell to zero in snap bean in a four-d flooding and returned back to the level of control plants at the 10th d after the flooding stopped. In our experiment,  $\text{CO}_2$  exchange rates sharply decreased by the flooding treatment in the eight greengram cultivars (Table 1). Among these cultivars, cv. KP showed a sufficient photosynthetic recovery at the 6th d of recovery step. A similar fact is observed in the report by Ahmed et al. (2002), in which author pointed out that a quick recovery in photosynthesis effectively improved the growth of greengram after the water-logging, and prevented the reduction of seed yield.

Waterloggings reduced the net photosynthetic rate and decreased the stomatal conductance in field-grown cowpea plants (Takely and McDavid, 1994). Also it was described that flooded greengram plants were reduced in photosynthesis as compared with control plants (Islam, 1994). A similar result was obtained in this experiment:  $\text{CO}_2$  exchange rates of greengram cultivars were reduced by the flooding and the reduction of *CER* was probably due to stomata closure. The reduction in stomatal conductance in flooded plants was reported in many previous studies (Joseph and Yelenosky, 1991; Pezeshki et al., 1996). A sharp decrease in stomata conductance was observed in Kidney bean (*Phaseolus vulgaris*) under flooding (Moldau, 1973). For greengram cultivars used here, the changing trend in *Gs* was similar to that observed in *CER*, and therefore, *Gs* may be more effective in determining *CER* under

flooding.

The increase in  $G_m$  by flooding is considered to depend on depletion in  $G_s$ , limiting the carbon uptake of leaves. The tight mutual-regulation between mesophyll photosynthesis and stomatal aperture was observed (Chaves et al., 2002). In this study,  $G_m$  of greengram was affected by flooding, and a cultivar difference was found in  $G_m$  reduction ratios. The reduction of  $G_m$  in flooded cv. KP was more lenient and this showed a better recovery of  $CER$  among the eight cultivars. Thus, the improvement of mesophyll behavior is an important criterion to enhance the flood resistance of greengram cultivars.

The value of  $F_v/F_m$  was slightly affected by the flooding. This may suggest that the light catching apparatus in PSII of greengram was not damaged by the 6-d flooding stress imposed here. A low decline in  $ETR$  was observed in cv. KP (4%) under flooding while the decline in that value was larger in others cultivars, ranging from 21 to 42%. This may suggest that a less decline in  $ETR$  in cv.KP is due to a stable action of  $G_s$  which is effective in preventing physiological inhibitions caused by an excessive accumulation of photon energy supplied from PSII. This fact can be clearly understood by the relationship between  $ETR$  and  $G_s$  shown in Fig. 2D.

$Pr/Tc$  ratio was different among cultivars and increased in cvs. Yezin-5, CN, VC and Kanti under the flooded condition, but not so much increased in cv. KP (Table 2). This may be pointed out that the former cultivars share more energy into photorespiration than the latter ones. In addition, roots of flooded plants are known to consume a larger amount of carbohydrate through the energetically inefficient anaerobic-respiration (Nelsen and Orcutt, 1996). Photorespiration has a role of dispersing the excessively accumulated energy to prevent functional damages in leaves, but it is unbeneficial to photosynthetic production. Thus, the smaller ratio in  $Pr/Tc$  of cv. KP represents a better performance under flooded condition.

A negative relationship was observed between  $CER$  and  $NPQ$  (Fig 1D). That indicated that when  $CO_2$  exchange rate was limiting under a high soil moisture condition, greengram leaves induced higher  $NPQ$  by excessive energy dissipation of the photosynthetic apparatus. On the other hand, combined effects of increased  $NPQ$  and  $Pr/Tc$  ratios are able to effectively protect to the photosynthetic apparatus from photo-damage in cv. KP, which cause a higher resistance to flooding and quick recovery. Of these eight cultivars, cv. KP was characterized by having higher  $G_s$ ,  $G_m$  and  $ETR$  and lower  $Pr/Tc$  and  $NPQ$  under the recovery condition. The feature of this cultivar is considered to be effective in sustaining the production and lessening the photo-inhibition damage in flooding.

According to Fig. 2A-D, cvs. Kanti and Yezin-4, were found in the quadrant II but cvs. CN, VC, Yezin-5, Nyaungoo and Magwe were located in quadrant III, showing low values in  $CER$ ,  $G_s$  and  $G_m$ . The order of flooding resistance from high to low is cvs.KP, Yezin4, Kanti, Magwe, Nyaungoo, VC, Yezin-5, CN.

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