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## Effects of Drought and Flooding Stresses on Growth and Photosynthetic Activity of Mungbean, *Vigna radiata* (L.) Wilczek, Cultivars

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The responses to drought and flooding stresses and the recovery from stress-induced damages were compared between three mungbean cultivars, Chinese (CN), and newly released cultivars in Myanmar, VC2991–112B–1B (VC) and KPS2 (KP). Growth, gas exchange rate and chlorophyll fluorescence quenching of these cultivars were investigated. The results were as follows: (1) CN was sensitive to both drought and flooding treatments compared to the other cultivars. VC and KP were less sensitive to drought and flooding, respectively. (2) The photosynthetic rate ( $P_N$ ) and stomatal conductance ( $G_s$ ) in VC were less affected by drought, with a quick recovery by re-watering. On the other hand, both parameters in KP were strongly depressed by drought, but less by flooding. (3) VC showed a higher value for the quantum yield of photosystem II ( $\Phi_e$ ) and a lower value for the photorespiration ratio ( $P_N/T_c$ ) than the other cultivars in the drought treatment. KP had a higher  $\Phi_e$  and lower  $P_N/T_c$  in the flooding treatment. (4) The stomatal behavior was closely related to the stress-tolerance of mungbean cultivars. A partial retainment of gas exchange under the stress conditions was essential to sustain electron transport in the photosystems and prevent functional damages caused by excessive accumulation of energy in leaves.

### INTRODUCTION

Plants grown in the field are frequently damaged by water stresses. Both drought and flooding have been regarded as the main adverse factors limiting plant photosynthesis, growth and yield (Chaves, 1991; Lawlor, 1995; Cornic and Massacci, 1996). Drought effects have been studied by many researchers such as Boyer (1976), Turner *et al.* (1984) and Lawlor (1995). The water status in leaves is well known to have a mutual interaction with stomatal movement or transpiration, and also a close correlation is observed between leaf water potential and stomatal movement (Flexas *et al.*, 1999). Stomatal movements are controlled by a signal from roots (Davies and Zhang, 1991), in the process of which abscisic acid is likely related to the turgor pressure variation in guard cells (Rashke, 1975; Collatz *et al.*, 1991). In the investigation of photosynthetic responses to droughts, the stomatal conductance ( $G_s$ ) is regarded as an integrative parameter reflecting the water stress situation of a plant (Medrano *et al.*, 2002).

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By flooding the growth and productivity of crops are often severely restricted. Flooding treatments induce several physiological impacts such as the reduction of leaf photosynthesis, stomatal closure and growth inhibition in mungbean cultivars (Ahmed *et al.*, 2002). A decrease in photosynthesis by flooding is likely due to the stomatal closure in sensitive species (Pezeshki and Chambers, 1985; Pezeshki, 1994).

Mungbean is not only an important crop providing the Myanmar people with a vegetable protein source but also an important export commodity. However, in Myanmar the production of mungbean is still low and unstable mainly due to various environmental constraints. The major constraints are flooding in the rain-fed lowland areas and droughts in the upland areas. For establishing better cropping systems of mungbean and its genetic improvements under the environments of Myanmar, it is fundamentally necessary to understand the cultivar responses to climatic conditions. In this study using mungbean cultivars newly released from Myanmar, we identified their eco-physiological features in growth, photosynthetic response and tolerance to drought and flooding stresses.

## MATERIALS AND METHODS

### **Experiment 1. Effects of drought stresses on growth and photosynthetic activity**

The experiment 1 was conducted during July to August, 2004 at Kyushu University, Japan, using three mungbean cultivars: Chinese (CN) from China and two newly released cultivars, VC2991-112B-1B (VC) and KPS2 (KP), in Myanmar. CN is a cultivar that has been long tested in our laboratory, then used here as a contrast cultivar. These three cultivars were sown separately at three points in an 8-liter pot filled with sandy loam soil. Thereafter, they were thinned to one plant per point for each cultivar and grown outdoors under adequate soil moisture conditions for 35 days until the beginning of drought treatments. The drought treatments were divided into three steps: (1) the first step; two-day drought stress imposition (2d-DS) (2) the second step; four-day drought stress imposition (4d-DS) and (3) the third step; recovery treatment after the droughts. The drought was imposed by gradually decreasing water supply to plants from the first to the second step, and then the plants were re-watered for three days to observe their recovery features in growth. Each treatment was arranged with three replications.

### **Experiment 2. Effects of flooding stresses on growth and photosynthetic activity**

The experiment 2 was carried out during May to June, 2004 using three mungbean cultivars: CN, VC and KP. The cultivation for 30 days before the flooding treatment was similar to that described in the experiment 1. The flooding treatment was continued for six days, during which pots were flooded up to 4 cm over the pot soil surface. After the end of the flooding, the growth recovery of plants was observed for six days.

### **Measurement of growth parameters**

Growth parameters such as plant height, stem diameter, number of leaf, leaf size and leaf area (LA) were measured at one week intervals before and after the drought or flooding treatments. The stem diameter was measured at the soil surface level using a digimatic caliper (CD-15C, Mitutoyo, Japan). The growth parameters were measured

with four plants for each cultivar. The crop growth rate (CGR) and net assimilation rate (NAR) was determined here as the value of a single plant.

### Measurement of photosynthetic parameters

The third-uppermost fully expanded leaves were used for determination of photosynthetic rate ( $P_N$ ). The  $\text{CO}_2$  concentration of reference air was about  $370 \mu\text{mol mol}^{-1}$ . During the measurement, the air humidity in the assimilation chamber was controlled at about 50%. The  $\text{O}_2$  concentration of reference air was adjusted at two levels of 21% or 2%. Leaf temperature was at  $30 \pm 1^\circ\text{C}$ , and the intensity of light supplied to a leaf was  $600 \mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD. The area of a leaf set in the assimilation chamber was  $6.25 \text{ cm}^2$  and the air flow rate was  $0.706 \text{ mmol s}^{-1}$ .

The  $\text{CO}_2$  concentration and vapour pressure in reference and sample air were monitored with an infrared  $\text{CO}_2$  analyzer (Li-6262, Li-COR, USA). The concentration of  $\text{O}_2$  was adjusted using a gas concentration controller (GM-3A, KOFLOC, Japan). From the monitored values,  $P_N$ , dark respiration rate ( $R_D$ ), gross photosynthetic rate ( $P_G$ ), stomatal conductance ( $G_s$ ) and mesophyll conductance ( $G_m$ ) were calculated. At the same time, soil and leaf water potentials were measured using a dew-point meter (WP4, Decagon Devices, USA).

The chlorophyll fluorescence of photosystem II (PSII) was monitored with a fluorescence probe (PAM-2000, Walz, Germany) equipped on the assimilation chamber. The initial fluorescence ( $F_0$ ) in the non-photosynthetic situation was measured with a dark-adapted leaf under a beam of  $3.2 \mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD, 4.8 kHz, and then the maximum fluorescence ( $F_m$ ) was determined by giving a 1.2 s pulse to the leaf.

After this, the time course of quenching of the fluorescence ( $F_s$ ) was monitored at an irradiance of  $600 \mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD, during which the fluorescence spike ( $F'_m$ ) was periodically measured by giving pulses of saturating light to the leaf.

Based on measurements of fluorescence, the quantum yield of PSII ( $\Phi_e$ ) and electron transport rate (ETR) were calculated from the equations (1) to (3) (Genty *et al.*, 1989).

$$F_v = F_m - F_0 \quad \dots\dots\dots (1)$$

$$\Phi_e = (F'_m - F'_s) / F'_m \quad \dots\dots\dots (2)$$

$$\text{ETR} = \Phi_e I a b \quad \dots\dots\dots (3)$$

where  $I$  is the intensity of irradiance supplied to a leaf. The symbol,  $a$ , is the ratio of leaf-absorbed photons to total incident photons; a measured value of 0.8 is used for the value of  $a$ . Assuming the supplied photons are evenly distributed to the photosystem I and II,  $b=0.5$  was used.

The parameter  $k_C$  is the number of electron equivalents required to reduce 1 mol  $\text{CO}_2$ , and calculated from the equation (4).

$$k_C = P_{G2\%} / \text{ETR}_{2\%} \quad \dots\dots\dots (4)$$

where  $P_{G2\%}$  and  $\text{ETR}_{2\%}$  are  $P_G$  and ETR determined, respectively, in the air of 2%  $\text{O}_2$  concentration.

Photorespiration rate ( $P_R$ ) was given by subtracting  $P_G$  from the total  $\text{CO}_2$  assimilation rate ( $T_C$ ) in the Calvin cycle as shown in the equation (5).

$$P_R = T_C - P_G \dots\dots\dots (5)$$

The equation (5) is based on CO<sub>2</sub> balance, and this is written as the equation (6) based on the electron transport rate.

$$ETR = k_C T_C + 2.06 k_C P_R \dots\dots\dots (6)$$

where  $k_C T_C$  and  $2.06 k_C P_R$  indicate the electron transport rates used for CO<sub>2</sub> fixation and photorespiratory CO<sub>2</sub> release, respectively. The number of electrons required to release 1 mol CO<sub>2</sub> in photorespiration is 2.06 times that required for reducing 1 mol CO<sub>2</sub> (Oliver, 1994). From the equations (5) and (6), the equation (7) is given.

$$T_C = (2.06 k_C P_G + ETR) / 3.06 k_C \dots\dots (7)$$

The photorespiration ratio ( $P_R/T_C$ ) is calculated by the equations (5) and (7).

## RESULTS

### Drought treatment

Effects of the drought treatment (4d-DS) on growth parameters are shown in Table 1. Plant height, leaf number, stem diameter and LA decreased by the treatment. The

**Table 1.** Effects of drought treatment on plant height, leaf number, stem diameter, LA, CGR and NAR.

Treatment	Cultivars	Plant height (cm)	Leaf (number plant <sup>-1</sup> )	Stem diameter (mm)	LA (m <sup>2</sup> plant <sup>-1</sup> )	CGR (g plant <sup>-1</sup> day <sup>-1</sup> )	NAR (g m <sup>-2</sup> day <sup>-1</sup> )
Control	CN	56.00	9.75	5.89	0.18	0.667	3.62
	KP	48.75	8.25	4.95	0.14	0.613	4.96
	VC	45.25	8.25	5.40	0.16	0.638	4.03
	mean	50.00	8.75	5.41	0.16	0.639	4.20
Drought	CN	37.25 <sup>a</sup> (66)	6.75 <sup>c</sup> (69)	4.06 <sup>b</sup> (69)	0.13 <sup>c</sup> (72)	0.317 <sup>a</sup> (48)	3.88 <sup>d</sup> (107)
	KP	35.50 <sup>b</sup> (73)	6.25 <sup>c</sup> (76)	3.58 <sup>c</sup> (72)	0.10 <sup>c</sup> (74)	0.381 <sup>b</sup> (62)	4.68 <sup>d</sup> (93)
	VC	38.75 <sup>b</sup> (86)	6.75 <sup>c</sup> (82)	4.50 <sup>c</sup> (83)	0.12 <sup>c</sup> (75)	0.554 <sup>d</sup> (87)	5.54 <sup>b</sup> (137)
	mean	37.00 (75)	6.25 (76)	3.95 (75)	0.12 (71)	0.417 (65)	4.70 (113)

The value in parentheses represents the percentage of treatment value to control. LA, leaf area per plant; CGR, crop growth rate; NAR, net assimilation rate; CN, Chinese; KP, KPS2; VC, VC-2991-112B-1B. The symbols, a, b, c and d represent 0.1%, 1%, 5% and not significant between control and treatment value, respectively.

decreasing ratios of these parameter values were 13–25% in VC, 24–28% in KP and 31–34% in CN. LA also decreased under the drought condition, but a significant cultivar difference was not found. The extent of CGR depression was different among the cultivars: 52% in CN, 38% in KP but only 13% in VC, and 37% increase was observed in NAR of VC.

Table 2 shows the parameters related to photosynthesis and PSII electron transport measured under the control, 2d-DS or 4d-DS and recovery conditions. The water potential of pot soil was -0.24, -1.62, -2.5 and -0.34 MPa, respectively, under these conditions. Also the average water potentials of leaves of three mungbean cultivars were -0.71, -1.34, -1.88 and -0.72 MPa, respectively.  $P_N$  and  $P_N/LA$  decreased by the drought

**Table 2.** Cultivar difference in parameter values observed under the control, drought treatments and recovery condition.

Cultivars	Treatment	SWP (- Mpa)	LWP (- Mpa)	$P_N$ ( $\mu\text{ mol m}^{-2}\text{ s}^{-1}$ )	$P_N/LA$ ( $\mu\text{ mol m}^{-2}\text{ s}^{-1}$ )	$G_s$ ( $\text{mol m}^{-2}\text{ s}^{-1}$ )	$G_m$ ( $\text{mol m}^{-2}\text{ s}^{-1}$ )	$P_N/T_c$ (%)	$\Phi_e$
CN	Control	0.24	0.55	14.44	2.60	0.169	0.066	20.70	0.54
	2d-DS	1.62	1.31	11.89 (82)	2.11 (81)	0.142 (84)	0.055 (83)	24.21 (117)	0.44 (81)
	4d-DS	2.50	1.98	7.77 (54)	1.32 (51)	0.077 (46)	0.044 (67)	37.90 (183)	0.40 (74)
	Recovery 4d-DS	0.34	0.69	11.62 (80)	1.53 (59)	0.160 (95)	0.051 (77)	31.49 (152)	0.45 (83)
KP	Control	0.24	0.63	13.88	1.87	0.170	0.052	22.56	0.47
	2d-DS	1.62	1.45	10.86 (78)	1.64 (88)	0.125 (74)	0.043 (83)	30.18 (134)	0.43 (91)
	4d-DS	2.50	1.88	7.80 (56)	1.15 (62)	0.087 (51)	0.041 (79)	35.65 (158)	0.38 (81)
	Recovery 4d-DS	0.34	0.72	10.81 (78)	1.27 (68)	0.160 (94)	0.043 (83)	22.98 (102)	0.48 (102)
VC	Control	0.24	0.96	12.63	1.94	0.163	0.052	20.99	0.46
	2d-DS	1.62	1.26	12.04 (95)	1.88 (97)	0.160 (97)	0.055 (106)	22.08 (105)	0.44 (96)
	4d-DS	2.50	1.78	9.47 (75)	1.52 (78)	0.127 (78)	0.049 (94)	24.03 (114)	0.42 (91)
	Recovery 4d-DS	0.34	0.75	12.59 (99)	1.56 (80)	0.166 (102)	0.050 (96)	20.60 (98)	0.46 (100)

The value in parentheses represents the percentage of treatment value to control. SWP, soil water potential; LWP, leaf water potential;  $P_N$ , net photosynthetic rate; LA, leaf area per plant;  $G_s$ , stomatal conductance;  $G_m$ , mesophyll conductance;  $P_N/T_c$ , ratio of photorespiration rate to total  $\text{CO}_2$  fixation rate;  $\Phi_e$ , photosystem II quantum yield; 2d-DS, 2-day drought treatment; 4d-DS, 4-day drought treatment. See Table 1 for the symbols CN, KP and VC.

(4d-DS) were not completely recovered by re-watering. The depression of both parameter values was lenient in VC in the drought compared to those of the other cultivars.

The values of  $P_N$ ,  $G_s$  and  $G_m$  in VC were almost unchanged in 2d-DS, but in 4d-DS the parameter values reduced by 25% in  $P_N$ , 22% in  $G_s$  and 6% in  $G_m$ . On the other hand, in CN and KP,  $P_N$  reduced by 18–22% in 2d-DS, and a further reduction (by 46–44%) was found in 4d-DS. The small reduction ratios of  $G_s$  and  $G_m$  measured in 4d-DS were 22% and 6% in VC, respectively, though they were large, 54% and 33%, in CN, respectively. As the cultivars were compared under the recovery condition, photosynthetic parameters in VC returned close to the control levels by re-watering, but those of CN and KP did not.

$P_N/T_C$  ratios were not different between the cultivars under the control condition, but a significant difference was found in 4d-DS (Table 2); particularly this ratio was low in VC. The value of  $\Phi_c$  in KP and CN was depressed by 19–26% in 4d DS, but the depression was lenient, 9%, in VC. By re-watering the values of  $\Phi_c$  and  $P_N/T_C$  in VC and KP returned close to the control levels while not so in CN.

### Flooding treatments

The growth parameters under the control and flooding conditions are shown in Table 3. Leaf number, stem diameter, CGR and NAR in KP were less affected by the flooding

**Table 3.** Effects of flooding treatment on plant height, leaf number, stem diameter, LA, CGR and NAR.

Treatment	Cultivars	Plant height (cm)	Leaf (number plant <sup>-1</sup> )	Stem diameter (mm)	LA (m <sup>2</sup> plant <sup>-1</sup> )	CGR (g plant <sup>-1</sup> day <sup>-1</sup> )	NAR (g m <sup>-2</sup> day <sup>-1</sup> )
Control	CN	53.75	9.50	5.65	0.23	0.775	3.87
	KP	49.50	9.25	5.95	0.16	0.625	4.33
	VC	44.50	8.50	5.80	0.22	0.668	3.40
	mean	49.25	9.08	5.80	0.20	0.689	3.87
Flooding	CN	35.50 <sup>b</sup> (66)	6.25 <sup>c</sup> (66)	4.06 <sup>c</sup> (72)	0.13 <sup>b</sup> (56)	0.368 <sup>b</sup> (47)	3.33 <sup>d</sup> (86)
	KP	44.50 <sup>c</sup> (90)	9.10 <sup>d</sup> (98)	5.10 <sup>d</sup> (86)	0.14 <sup>c</sup> (83)	0.541 <sup>d</sup> (87)	4.46 <sup>d</sup> (103)
	VC	36.75 <sup>c</sup> (83)	5.75 <sup>c</sup> (68)	4.50 <sup>c</sup> (78)	0.13 <sup>b</sup> (59)	0.411 <sup>b</sup> (62)	3.66 <sup>d</sup> (108)
	mean	38.92 (80)	7.03 (77)	4.55 (79)	0.13 (66)	0.440 (65)	3.82 (99)

The value in parentheses represents the percentage of treatment value to control. See Table 1 for the symbols LA, CGR, NAR, CN, KP and VC. The symbols, a, b, c and d represent 0.1%, 1%, 5% and not significant between control and treatment value, respectively.

treatment, but the effect was serious in CN and VC. A large cultivaral difference was observed in the response of growth parameters. The depression ratios in CGR were 13% in KP, 38% in VC and 53% in CN. NAR in KP and VC increased by 3% and 8% under the flooding, respectively.

Table 4 lists the parameters related to leaf photosynthesis and PSII electron transport measured under the control, flooding and recovery conditions. Under the flooding  $P_N$  in CN and VC were reduced by 68% and 62%, respectively; however, that of KP was 41%.  $P_N$  in CN and VC was not sufficiently returned to the control level at the recovery step; on the other hand, KP showed a quick recovery. The response of  $P_N LA$  to the flooding was similar in pattern to that of  $P_N$ . Also the effect of flooding on  $G_s$  and  $G_m$  were roughly similar in tendency to that of  $P_N$  in all the cultivars but this effect on these parameters was lenient in KP.

The ratio of  $P_N/T_C$  increased more than twice in CN and VC by flooding, but did not so greatly increase in KP. The value of  $\Phi_e$  in CN and VC decreased by 21 to 25% at the flooding step, but the depression was only 4% in KP. At the 6th day after the recovery

**Table 4.** Cultivaral difference in parameter values observed under the control, flooding and recovery condition.

Cultivar	Treatment	$P_N$ ( $\mu \text{ mol m}^{-2} \text{ s}^{-1}$ )	$P_N LA$ ( $\mu \text{ mol s}^{-1}$ )	$G_s$ ( $\text{mol m}^{-2} \text{ s}^{-1}$ )	$G_m$ ( $\text{mol m}^{-2} \text{ s}^{-1}$ )	$P_N/T_C$ (%)	$\Phi_e$
CN	Control	15.72	2.55	0.20	0.074	10.14	0.52
	Flooding	5.10 (32)	1.88 (50)	0.05 (24)	0.032 (44)	29.21 (288)	0.39 (75)
	Recovery	8.87 (56)	1.48 (58)	0.10 (50)	0.045 (60)	22.23 (219)	0.47 (82)
KP	Control	13.69	1.99	0.17	0.064	12.90	0.50
	Flooding	8.02 (59)	1.54 (77)	0.08 (44)	0.047 (73)	18.62 (144)	0.48 (96)
	Recovery	12.94 (95)	1.680 (84)	0.150 (87)	0.056 (88)	13.07 (101)	0.50 (100)
VC	Control	12.77	2.01	0.15	0.064	12.70	0.48
	Flooding	4.81 (38)	1.32 (65)	0.05 (33)	0.031 (48)	30.20 (238)	0.38 (79)
	Recovery	9.25 (72)	1.41 (70)	0.10 (70)	0.046 (75)	26.30 (207)	0.44 (91)

The value in parentheses represents the percentage of treatment value to control.  $P_N$ , net photosynthetic rate; LA, leaf area per plant;  $G_s$ , stomatal conductance;  $G_m$ , mesophyll conductance;  $P_N/T_C$ , ratio of photorespiration rate to total  $\text{CO}_2$  fixation rate;  $\Phi_e$ , photosystem II quantum yield. See Table 1 for the symbols CN, KP and VC.



treatment began, the value of  $\Phi_e$  in KP recovered up to the pre-treatment level, while did not in CN and VC.

## DISCUSSION

Leaf area production has been reported to have a close relationship with crop growth production in many experiments. Also in our study, LA and CGR of mungbean were sensitive to the drought stress, but the changing trend in LA of mungbean cultivars was different from that in CGR (Table 1). A large cultivaral difference was found in CGR, but not in LA. This demonstrates that the biomass production is more strongly restricted by leaf photosynthesis than leaf area per plant.

A leaf water potential of  $-1.32$  MPa has been regarded as a level at which sweet potato plants suffered a relatively severe stress (Kubota *et al.*, 1993). However, in our study with mungbean, a leaf water potential of  $-1.78$  MPa caused only 22% reduction in  $G_s$  and 6% in  $G_m$  in VC (Table 2). This means that the stomatal openness of VC is relatively large at such a low water potential, by which  $P_N$  is allowed to sustain a higher value in droughts. Yordanov *et al.* (2003) also reported that drought-resistant species were able to control a stomatal function, keeping carbon fixation under drought stresses, and their stomatal function was rapidly recovered after water deficits were relieved. The reduction of  $G_m$  is regarded as the evidence of a drought-induced damage in mesophyll due to loss of the turgor pressure (Cornic *et al.*, 1989; Renou *et al.*, 1990). Of the mungbean cultivars used here, VC was less affected by drought, and the  $G_m$  sustained a relatively high value at 4d-DS (Table 2). This functional feature may be predicted to depend on the osmotic potential adjustment, and the turgor pressure in leaves is maintained during the drought periods, by which the stomatal openness and carbon fixation are sustained.

Both  $P_N$  and  $P_N$  LA were depressed by drought in 4d-DS, and not completely recovered by re-watering, but the depression ratio of these parameters were lenient in VC (Table 2). For the reason of photosynthetic depression, Sharkey (1990) described that the down-regulation of photosynthesis depended more directly on stomatal closure and mesophyll resistance than on leaf water potential. Chaves *et al.* (2002) reported that there was a tight co-regulation between mesophyll photosynthesis and stomatal aperture under water stress conditions. In our study, as shown in Table 2, the variation ratio in  $G_s$  with treatment was larger than that of  $G_m$  and a better recovery of  $G_s$  was found in VC.  $G_s$  is regarded as a more powerful determinant of  $P_N$  than  $G_m$ .

The value of  $\Phi_e$  in CN decreased by 26% in 4d-DS, but the reduction ratio in VC was only 9% (Table 2). Keeping a higher  $\Phi_e$  means that the energy-dependent metabolism is actively functioning in leaves, by which photo-inhibition damage is prevented. On the other hand,  $P_r/T_c$  ratio was lower in VC under the drought conditions. A relatively large  $G_s$  in VC may increase  $CO_2$  concentration in the intercellular spaces of mesophyll, and decrease  $P_r/T_c$ .

Ahmed *et al.* (2002) reported that the physiological effects of flooding on the leaf photosynthesis, stomatal function and growth of mungbean cultivars and other bean species. Also in our study, the growth parameters of mungbean cultivars were significantly affected by flooding, but it was relatively lenient in KP (Table 3). Yadav and Saxena (1998) noted that growth damages by water-logging in mungbean were partially

alleviated by the large dry matter accumulation in tolerant genotypes. Both NAR and CGR in KP showed a higher value in the flooding treatment, which indicates that this cultivar has a strong moisture-tolerance in biomass production system. Such an understanding is also found in the report of Musgrave *et al.* (1989).

The decrease in photosynthesis by flooding is mainly caused by stomatal closure in sensitive species, and this phenomenon has been observed in a number of crop species (Pezeshki, 1994). In our study,  $P_N$  of mungbean decreased by the flooding treatment (Table 4), but KP showed a sufficient photosynthetic recovery. A similar fact is observed in the report by Ahmed *et al.* (2002), in which he pointed out that a quick recovery in photosynthesis effectively improved the growth of mungbean plants after the water-logging and prevented the reduction of seed yield. For mungbean cultivars used here, as shown in Table 4, the changing trend in  $G_s$  was similar to that in  $G_m$ , but the variation ratio in  $G_s$  was larger than that of  $G_m$ ; therefore,  $G_s$  may be considered to be a more effective factor of determining  $P_N$  than  $G_m$ .

A high value of  $P_N/T_C$  was observed in CN and VC in the flooding and recovery treatments (Table 4). This may predict that these cultivars shared more energy into photorespiration. In addition, roots of flooded plants are known to consume a larger amount of carbohydrate through the energetically inefficient anaerobic-respiration. Photorespiration has a role of dispersing the excessively accumulated energy to prevent functional damages in leaves, but it is unbeneficial to photosynthetic production. Of these three cultivars, KP was characterized by having a higher  $\Phi_e$  and lower  $P_N/T_C$  under the flooding and recovery conditions. The feature of this cultivar is considered to be effective in sustaining the production and lessening the photo-inhibition damage in flooding.

As mentioned above, mungbean cultivars differently responded and acclimated to both types of water stress, drought and flooding, and the genotypic variation was found in the acclimation process. The new released Myanmar cultivars, VC and KP, were characterized by having a higher tolerance against drought and flooding stresses, respectively. It may be considered that stomatal behavior is closely related to the cultivaral difference in stress-tolerance. A larger openness of stomata under drought conditions may cause much water loss; while the complete closure of stomata is also dangerous for photosynthetic organs due to the excessive accumulation of energy in leaves by the limited gas exchange. The sustainability of stomatal openness at a minimal level under stress conditions is essential for stressed plants to continue minimal gas exchange to disperse the excessive energy. But it may be difficult to define such a minimal level. For example, in the present study, VC plants decreased to  $0.129 \text{ molm}^{-2}\text{s}^{-1}$  in  $G_s$  in drought (Table 2) and KP plants  $0.08 \text{ molm}^{-2}\text{s}^{-1}$  in flooding (Table 4) were possible to have a sufficient recovery in photosynthesis. Therefore, this range of  $G_s$  might be predicted to be a minimal level for preventing stressed damages. Furthermore studies are necessary to identify this finding.

Mungbean cultivars having a mild-sensitivity in  $G_s$  or a lenient stomatal-response to growth environments are suggested to show a superior stress-tolerance. The improvement of stomatal behavior is an important criterion to enhance the stress-tolerance of mungbean cultivars. This may give a piece of information to the mungbean breeding program that aims to produce new cultivars highly suitable for the farming systems

unique to Myanmar.

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