

## Specific Feature in Photosynthetic Response of Kenaf (*Hibiscus cannabinus* L.) to Flooding Stress

Takuya ARAKI<sup>1</sup>, Mai Thi Phuong NGUYEN<sup>2</sup> and Fumitake KUBOTA<sup>3</sup>

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

<sup>2</sup> Faculty of Natural Resource and Environment, Hanoi University of Agriculture, Trau Quy, Gialam, Hanoi, Vietnam

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

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The response in gas exchange and photosystem II (PSII) functions to a flooding condition was characterized with kenaf (*Hibiscus cannabinus*) by comparing it with napiergrass (*Pennisetum purpureum*, C<sub>4</sub>-plant), corn (*Zea mays*, C<sub>4</sub>-plant) and mungbean (*Vigna radiata*, C<sub>3</sub>-plant). Pot-grown plants were subjected to a 1-week flooding and a 1-week recovery treatment. The flooding treatment had serious effects on the gas exchange of mungbean and corn, while the damages were lenient in kenaf and napiergrass. Kenaf and napiergrass were characterized by keeping a higher stomatal conductance ( $G_s$ ) and mesophyll conductance ( $G_m$ ), which resulted in sustaining the CO<sub>2</sub> assimilation under the flooding stress condition. As compared between these two high-yielding species, kenaf was superior in photosynthetic sustainment than napiergrass under the flooding and recovery treatments. The superiority in kenaf is attributable to the fact that this species keeps higher  $G_s$  under the flooding, by which photosynthesis was able to continue, and the photosynthetic apparatus prevents the excessive energy accumulation in the leaf. Also, kenaf showed the increase photorespiration and non-photochemical quenching (NPQ) during the treatments.

Keywords : flooding tolerance, gas exchange, kenaf, non-photochemical quenching, photochemical system II, photorespiration.

### INTRODUCTION

C<sub>4</sub> plants are known to be superior in photosynthetic and biomass productivity to C<sub>3</sub> plants when they are grown under the optimum growth conditions. But C<sub>3</sub> plants are not always inferior to C<sub>4</sub> species in growth and production. There are some C<sub>3</sub> plants having excellent productivity and stability to environments. Kenaf (*Hibiscus cannabinus* L.) is one of such C<sub>3</sub> plants. According to some previous studies, kenaf demonstrated a high and stable productivity: the dry matter weight was not less than that of C<sub>4</sub> plants such as sorghum (Muchow, 1992) and napiergrass (Nguyen et al., 2005). Also the high stability and adaptability of kenaf under the drought stresses was reported by Nguyen et al. (2005).

We are interested in the production and environmental adaptation system of kenaf, and have continued the study to clarify its specific feature in photosynthetic response to changing soil and climatic conditions. To understand the photosynthetic response to environmental stresses may be

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

come the fundamental information for improving the crop production sustainability under changing environments. It may be expected that the promising information related to the improvement of matter production and environmental adaptation in crops will be received by deepening the analyses of physiological and ecological features unique to kenaf. Of the various stresses onto crops, the flooding stress frequently causes a serious damage in the production of field-grown crops (Davis and Hillman, 1988; Sharma and Swarup, 1988; Lakitan et al., 1992; Nilsen and Orcutt, 1996). In this study, effects of flooding stress on gas exchange and photosystem functions were evaluated by comparing among four crops, which is two C<sub>3</sub>-plant, kenaf and mungbean, and two C<sub>4</sub>-plant, corn and napiergrass.

## MATERIALS AND METHODS

### *Materials and cultivation*

Experimental materials were selected by considering photosynthetic system and flooding sensitivity, that is, kenaf (*Hibiscus cannabinus* L., C<sub>3</sub>-plant and flooding tolerant), napiergrass (*Pennisetum purpureum* Schumacher, var. Markeron, C<sub>4</sub>-plant and flooding tolerant), mungbean (*Vigna radiata* (L.) Wilczek var. Chinese, C<sub>3</sub>-plant and flooding sensitive) and corn (*Zea mays* L. var. LCH9, C<sub>4</sub>-plant and flooding sensitive). The pot cultivation of these species was conducted in August, 2005 in the experimental field of Kyushu University (33°35'N, 130°23'E). The climatic condition of 28.4°C in temperature, 68% in relative humidity and 17.4 MJ m<sup>-2</sup> day<sup>-1</sup> in solar radiation during the growth period was favorable for growth of the four species.

One kenaf plant and one napiergrass plant were grown together in an 8 L pot filled with sandy soil sufficiently fertilized, and also one mungbean plant and one corn plant were combined and grown in the same condition.

### *Treatments*

Paired two species, kenaf — napiergrass or mungbean — corn, were grown in pots under the adequately watering condition for 30 days before the flooding treatment. For each combination, ten pots with vigorous growth plants were divided into two groups. One group, as a control, was continuously grown under the non-stressed condition, and the other group was subjected to the flooding treatment. During the flooding treatment, the pots were placed in water tanks: the soil surface of pots was submerged 4 cm below the water surface for 7 days. Directly after the flooding treatment, the pots were moved out from the water tanks and the excessive water was drained from the soil for 7 days to measure the photosynthetic recovery. Duration of these treatments was determined by preliminary experiments.

### *Measurement of CO<sub>2</sub> exchange rate (CER) and related parameters*

Gas exchange measurements were carried out with a sandwich-type assimilation chamber of an open system using the youngest fully expanded leaves for both species. During the measurement, the environment in the chamber was controlled at about 60% in humidity and 30°C in air temperature. Light applied by metal halide (LS-M210, SUMITA OPTICAL GLASS Inc., Saitama, Japan) was 1,000 μmol m<sup>-2</sup> s<sup>-1</sup> photosynthetic photon flux density (PPFD). The ambient air with about 350 μL L<sup>-1</sup> CO<sub>2</sub> and 21% O<sub>2</sub> was used for the measurement. The CO<sub>2</sub> concentration and water content in the used air were measured with an infrared CO<sub>2</sub>-H<sub>2</sub>O analyzer (Li-6262, LiCOR, USA). The assimilation chamber capacity was 4.38 mL. Leaf area enclosed in the chamber was 6.25 cm<sup>2</sup>, and the air flow rate through the chamber was adjusted at about 1.0 L min<sup>-1</sup>. CER, dark respiration (R<sub>d</sub>), transpiration rate (T<sub>r</sub>), stomatal conductance (G<sub>s</sub>), mesophyll conductance (G<sub>m</sub>), intercellular CO<sub>2</sub> concentration (C<sub>i</sub>) were calculated according to the method of Long and Hallgren (1985). The gross photosynthesis (P<sub>g</sub>) equaled the sum of CER and R<sub>d</sub>.

### *Measurement of chlorophyll fluorescence and calculation of related parameters*

Chlorophyll fluorescence was monitored with a fluorescence probe (PAM-2000, Walz,

Germany) attached on the assimilation chamber. The measurements of *CER* and chlorophyll fluorescence were carried out simultaneously. Chlorophyll fluorescence measurements were conducted with leaves dark-adapted for at least 20 minutes. The initial fluorescence ( $F_o$ ) was measured with a weak modulated irradiation ( $3.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  *PPFD*, 4.8 kHz). Next, a saturating flash ( $8,000 \mu\text{mol m}^{-2} \text{s}^{-1}$  *PPFD*) was applied to determine the maximum chlorophyll fluorescence ( $F_m$ ), and the time course of the fluorescence was monitored at  $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$  *PPFD*. After the fluorescence yield reached a steady state level ( $F_s$ ), the fluorescence spike ( $F_m'$ ) was periodically measured by giving pulses of the saturation light. Fluorescence parameters were calculated as follows (Genty et al., 1989). The quantum yield efficiency in PSII ( $\Phi_e$ ), non-photochemical quenching (*NPQ*) and PSII electron transport rate (*ETR*) were calculated from the equations below.

$$\Phi_e = (F_m' - F_s) / F_m' \quad (1)$$

$$NPQ = (F_m - F_m') / F_m' \quad (2)$$

$$ETR = \Phi_e I a b \quad (3)$$

where  $I$  is incident *PPFD*, ' $a$ ' is the fraction of absorbed quanta that used by PSII ( $a=0.5$  was used here) and ' $b$ ' is the light absorbance ratio in a leaf. According to Krall and Edwards (1992) non-succulent leaves typically have an absorbance of 0.8, therefore  $b=0.8$  was used here.

The value of photorespiration rate ( $P_r$ ) was estimated from  $P_g$ , total  $\text{CO}_2$  fixation rate ( $T_c$ ) and *ETR* using the equation below.

$$P_r = T_c - P_g \quad (4)$$

The equation (3) is rewritten as the equation (5) on the basis of electron transport rate

$$ETR = k \cdot T_c + 2.06 \cdot k \cdot P_r \quad (5)$$

where  $k$  is the number of electrons used for fixing 1 mol  $\text{CO}_2$  in assimilation ( $k=4$ ), then  $k \cdot T_c$  is the rate of electron transport that is equivalent to  $\text{CO}_2$  absorption rate in assimilation. The number of electrons required for releasing 1 mol  $\text{CO}_2$  by photorespiration is  $k_r$ , and the value of  $k_r$  is 2.06 times that of  $k$  (Oliver, 1994). Therefore,  $2.06 \cdot k \cdot P_r$  indicates the electron transport rate equivalent to  $\text{CO}_2$  releasing rate in photorespiration. By combining the equations (4) and (5), the equation (6) is given

$$T_c = (2.06 \cdot k \cdot P_g + ETR) / (3.06 \cdot k) \quad (6)$$

where  $P_g$  is a measured value. By substituting  $T_c$  given from the equation (6) into the equation (4), the value of  $P_r$  is estimated.

## RESULTS AND DISCUSSION

The parameters related to leaf gas exchange and PSII electron transport of four species determined under the control, flooding and recovery conditions are presented in Table 1. These measurements under control condition were conducted on the day before the starting of flooding treatment. *CER* values measured at *PPFD* of  $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$  under the control condition were  $19.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $25.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $16.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $25.8 \mu\text{mol m}^{-2} \text{s}^{-1}$  in kenaf, napiergrass, mungbean and corn, respectively. *CER* of the  $C_4$  species used here was little different between napiergrass and corn, and was higher than that of  $C_3$  species. As compared this parameter between two  $C_3$  plants, the superiority was found in kenaf.

The specific difference was found in the effect of 1-week flooding. Kenaf and napiergrass showed a higher tolerance to flooding than mungbean and corn. The *CER* values of the former two species kept at 87% and 71% of the control values, respectively, while those showed a sharp reduction to 3% of control values in the later two species. A quick recovery was also found in kenaf and

**Table 1** Responses of gas exchange, PSII parameters in kenaf, napiergrass, mungbean and corn to the flooding and their recovery treatments.

Species	Treatment	$CER$ $\mu\text{mol m}^{-2} \text{s}^{-1}$	$G_s$ $\text{mol m}^{-2} \text{s}^{-1}$	$G_m$ $\text{mmol m}^{-2} \text{s}^{-1}$	$ETR$ $\mu\text{mol m}^{-2} \text{s}^{-1}$	$NPQ$	$P/T_c$ %
Kenaf	Control	19.8(100)	0.21(100)	93.0(100)	162.9(100)	1.01(100)	23.8(100)
	Flooding	17.2(87)	0.18(85)	77.7(83)	154.6(95)	1.35(134)	35.2(148)
	Recovery	18.3(92)	0.19(91)	83.8(90)	146.0(90)	1.13(112)	26.4(111)
Napiergrass	Control	25.1(100)	0.19(100)	173.4(100)	135.0(100)	1.46(100)	
	Flooding	17.7(71)	0.12(65)	105.4(61)	68.0(50)	1.67(115)	
	Recovery	19.3(77)	0.16(83)	111.8(66)	96.0(67)	1.44(99)	
Mungbean	Control	16.7(100)	0.18(100)	77.8(100)	165.1(100)	1.20(100)	27.2(100)
	Flooding	0.5(3)	0.03(19)	1.7(2)	70.9(43)	2.50(203)	49.2(181)
	Recovery	—	—	—	—	—	—
Corn	Control	25.8(100)	0.19(100)	175.4(100)	138.6(100)	1.47(100)	
	Flooding	0.7(3)	0.06(32)	1.8(1)	14.4(10)	1.53(104)	
	Recovery	6.5(26)	0.07(39)	50.0(29)	34.7(25)	1.54(10.5)	

Values are the means of five replications.

napiergrass; they returned to 92% and 77% of the controls, respectively. The return in corn was 26%, and all mungbean plants died during the recovery treatment. The high flooding tolerance of kenaf and napiergrass was also known by comparing them with some other species. For example, Pezeshki and Chambers (1985) demonstrated that the photosynthesis of *Quercus falcata* seedlings depressed to zero after the 3-day flooding. Also, according to Bradford (1983), the assimilation rate of tomato reduced by 27% within 1-day flooding treatment. Like this, kenaf and napiergrass are plants having a higher tolerance to flooding than other species. However, when kenaf and napiergrass were compared, kenaf indicated a higher tolerance than napiergrass under the flooding and recovery conditions. It is interestingly predicted to obtain the suggestible information for the enforcement of plant production stability by clarifying the functional characteristics related photosynthetic system that allows kenaf to perform such superiority under inundation.

The photosynthetic regulation by stomata in relation to flooding conditions was reported in many previous studies (Else et al., 1996; Mielke et al., 2005; Pezeshki et al., 1996). One of the conspicuous responses of photosynthesis to root zone flooding was observed through stomatal closure in such sensitive species as tomato, wheat, pepper and bean (Else et al., 1996). This phenomenon was also found in mungbean and corn in our present study. After the 1-week flooding,  $G_s$  value of these species depressed to 19% and 31% of the controls, respectively; whereas  $G_s$  of kenaf and napiergrass kept at 85% and 65%, respectively (Table 1). Like this, the specific difference in stomatal action was regarded as one of the main causes of making a significant difference in their  $CER$  under the treatments. In accordance with a sharp reduction in  $G_s$ ,  $CER$  values of mungbean and corn dramatically decreased. On the other hand, because  $G_s$  was kept relatively high, the depression in  $CER$  of kenaf and napiergrass was not so large. This result is consistent with the result of Pezeshki et al. (1996) that showed a significant difference in the response of  $G_s$  to flooding between moisture-sensitive and -insensitive oaks species.

$G_m$ , another parameter causing  $CER$  to change, in the four species are shown in Table 1.  $G_m$  values of both flooded-sensitive species, mungbean and corn, dropped close to zero after the 1-week flooding. While those of kenaf and napiergrass kept at 83% and 61% of the controls, respectively. Lucia et al. (2003) reported that  $G_m$  regulated  $\text{CO}_2$  transfer in a leaf and varied with environments. But here,  $G_m$  values of both kenaf and napiergrass were not much affected by flooding, though relative value of  $G_m$  compared to control of kenaf was a little higher than that of napiergrass during the flooding and recovery treatments.

Plants show various patterns in adaptation to overcome the flooding damages. The adventitious root system is regarded as one of the adaptation responses. By observation, during the flooding period both kenaf and napiergrass emerged the adventitious roots from their flooded stems above the soil surface, while this phenomenon was not observed in both mungbean and corn. It is predicted that this root system may help kenaf and napiergrass effectively cope with the anaerobic condition. The physiological function of the adventitious root system in these species is an interesting subject to be examined.

The situation of electron transport in a leaf is also shown in Table 1. Unlike gas exchange parameters, the response of PSII parameters to flooding was significantly different between  $C_3$  and  $C_4$  species. It is clearly recognized that the reduction of  $ETR$  value in  $C_3$  plants was not parallel with decreasing  $CER$ . The depression level in  $CER$  of flooded corn was almost similar to that of flooded mungbean. But the reduction ratio of  $ETR$  was quite far different between them:  $ETR$  of flooded mungbean reduced to 43%, while that of corn greatly depressed to 10% of the control. Similarly, the difference between  $C_3$ -plant kenaf and  $C_4$ -plant napiergrass was found in the reduction ratio of  $ETR$ . The stability of  $ETR$  in  $C_3$  plants under changing environment are considered to be chiefly attributable to photorespiration. After the 1-week flooding,  $P_d/T_c$  ratios of kenaf and mungbean significantly increased to 148% and 181% of the controls, respectively.  $P_d/T_c$  ratio is an indicator for preventing excessive energy accumulation when  $CO_2$  assimilation is restricted in stressed in  $C_3$  leaves. This trend was also reported in some mungbean cultivars (Oo et al., 2005). We used here the same light absorption value ( $b=0.8$ ) in common for the four crop species. The value of  $b$  is strongly affected by leaf thickness, and is changeable in a certain extent with species and treatments. Flooding treatment in the present study may increased this value. Therefore, it may be considered that the specific feature in flooding response was able to be identified here on the basis of this calculation.

$NPQ$  showed a specific difference in response to high soil moisture stress in this study. As shown in Table 1, under the normal growth condition,  $NPQ$  of kenaf and mungbean were lower than that of napiergrass and corn. Yet, after the 1-week flooding was finished,  $NPQ$  of kenaf and mungbean greatly rose to 134% and 203% of the controls, respectively, while those of napiergrass and corn did not increased significantly.

As mentioned, as a whole, of the four species, kenaf showed considerable superiority to the other three species in photosynthetic stability and recovery under the treatments. Then, as the next step for deepening the understand of advantageous points in the photosynthetic system of kenaf, the changes in gas exchange parameter and PSII electron transport parameter values were discussed in relation to  $CER$  in the four species. The mutual relationships between the parameters measured through the control, flooding and recovery conditions are shown in Fig. 1.

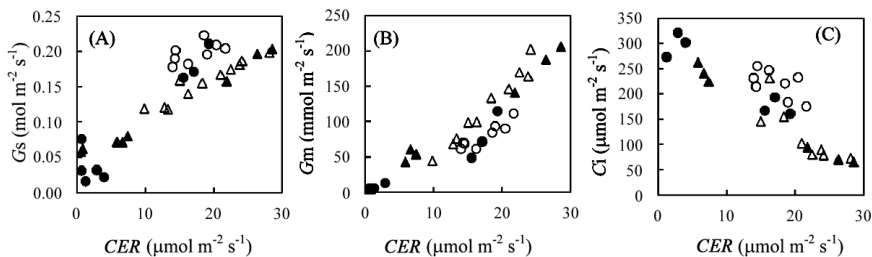
As shown in Fig. 1-A, at any given  $CER$  value,  $G_s$  of kenaf,  $C_3$  species, was always larger than those of  $C_4$  species, napiergrass and corn. It is frequently observed that  $G_s$  of  $C_3$  plants are higher than that of  $C_4$  plants (Edwards et al., 1983). However, when the  $C_3$  species used here are compared at the same  $CER$  level,  $G_s$  of kenaf was higher than that of mungbean. The high  $G_s$  may be considered to contribute to the high  $CER$  of kenaf. In Fig. 1-A, a close positive relationship in  $CER$ - $G_s$  was detected in napiergrass, mungbean and corn under flooding conditions. But it was not found in kenaf. The range of  $G_s$  fluctuation in the three species other than kenaf was large, which may mean that the stomata openness of kenaf is not strongly affected by soil moisture conditions, and this characteristic allows kenaf leaves to keep a certain level of  $CER$  under such a growth condition.

The relationship between  $CER$  and  $G_m$  is shown in Fig. 1-B.  $G_m$  was closely related with  $CER$  in all the species including kenaf. This fact suggested that  $G_m$  is likely a more powerful determinant regulating  $CER$  of kenaf.  $CER$  of the three species other than kenaf is considered to be affected or determined in parallel by  $G_s$  and  $G_m$  under flooding conditions. This finding is not in

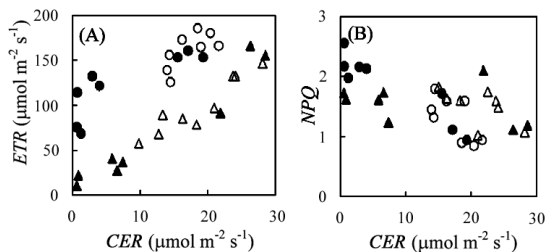
agreement with the result of Oo et al. (2005), in which the authors pointed out that  $G_s$  was considered to be a more effective determinant on  $CER$  than  $G_m$  in the mungbean cultivars used by them under flooding conditions.  $NPQ$  is an indicator for preventing excessive energy accumulation as well as  $P_i/T_c$  ratio.  $P_i/T_c$  ratio of mungbean under flooding condition in the present study was same level as that in Oo et al. (2005).  $NPQ$  of mungbean under flooding was the highest value among the used materials. However, this value was lower than the result of Oo et al. (2005). Mungbean leaves in the present study might be attacked by reactive oxygen species for accumulation of excessive energy in mesophyll tissues with low potential of  $NPQ$ , resulting in quite low value of  $G_m$  under flooding condition.

$C_i$ , a parameter having a close relation to stomata factor, was in a relationship to  $CER$  (Fig. 1-C). As shown here, a significant negative relationship was found between these two parameters in all the plant materials, except kenaf. A relatively large stomatal openness in leaves of flooded kenaf may contribute to sustain a  $C_i$  level; consequently  $CER$  of kenaf is not strongly depressed during the flooding period.

Next, the relationship between  $CER$  and two PSII parameters,  $ETR$  and  $NPQ$ , are given in Fig. 2-A and 2-B, respectively. As shown in Fig. 2-A, a close positive relationship was detected between  $CER$  and  $ETR$  in both  $C_4$  species. On the other hand, the relationship was insignificant or not tight in kenaf and mungbean. This means that when  $CER$  of  $C_3$  plants was depressed by flooding,  $ETR$  did not reduce sharply, i.e. the energy produced through photochemical pathway could not



**Fig. 1** Relationships between  $CO_2$  exchange rate ( $CER$ ) and stomatal conductance ( $G_s$ ) (A), mesophyll conductance ( $G_m$ ) (B) and intercellular  $CO_2$  concentration ( $C_i$ ) (C) in kenaf, napiergrass, mungbean and corn measured through the conditions of control, flooding and recovery treatments.  $\circ$ , kenaf;  $\triangle$ , napiergrass;  $\bullet$ , mungbean;  $\blacktriangle$ , corn. Regression coefficients of kenaf, napiergrass, mungbean and corn were 0.63\*, 0.98\*\*, 0.96\*\* and 0.99\*\* in  $G_s$ , 0.91\*\*, 0.99\*\*, 0.96\*\* and 0.99\*\* in  $G_m$ , and not significant,  $-0.85$ \*\*,  $-0.87$ \*\* and  $-0.93$ \*\* in  $C_i$ , respectively. \* and \*\* indicate significant 5% and 1% level, respectively.



**Fig. 2** Relationships between  $CO_2$  exchange rate ( $CER$ ) and electron transport rate ( $ETR$ ) (A), and non photochemical quenching ( $NPQ$ ) (B) in kenaf, napiergrass, mungbean and corn measured through the conditions of control, flooding and recovery treatments.  $\circ$ , kenaf;  $\triangle$ , napiergrass;  $\bullet$ , mungbean;  $\blacktriangle$ , corn. Regression coefficients of kenaf, napiergrass, mungbean and corn were not significant, 0.94\*\*, 0.97\*\* and 0.68\* in  $ETR$ , and  $-0.78$ \*\*, not significant,  $-0.94$ \*\* and not significant in  $NPQ$ , respectively. \* and \*\* indicate significant 5% and 1% level, respectively.



be consumed by CO<sub>2</sub> fixation but photorespiration and thermal dissipation. The energy used for the photorespiratory release of 1 mol CO<sub>2</sub> is almost double that of 1 mol CO<sub>2</sub> fixation. By being influenced by photorespiratory energy consumption, the relationship between *CER* and *ETR* may become lenient or unparallel in C<sub>3</sub> plants as described by Krall and Edwards (1992) and others. Such a trend is also found here in our result. Otherwise, in C<sub>4</sub> plant napiergrass and corn without photorespiration system, *ETR* directly connects with CO<sub>2</sub> fixation; accordingly, the close relationship between *ETR* and *CER* was found in both C<sub>4</sub> plants. The well photosynthetic recovery of kenaf from the flooding treatment may indicate that the stresses did not persistently impair the photosynthetic function in this species. We assume that photorespiration is an important photo-protective mechanism in kenaf grown under such a stress condition. Furthermore, the present study suggested that kenaf has high potential of the maintenance of stomatal opening under flooding condition to avoid the reduction of photosynthetic function in mesophyll tissues. These functions are considered to be the main reasons that kenaf is able to keep the photosynthetic stability against the water stress, and shows a quick recovery from the stress.

A close negative relationship between *NPQ* and *CER* was detected in kenaf and mungbean, but it was not significant in both C<sub>4</sub> species (Fig. 2-B). This means that in the case where CO<sub>2</sub> assimilation was restricted in kenaf and mungbean by flooding, the excessive energetic accumulation can be effectively dissipated by increasing *NPQ*. The positive relationship between *NPQ* and xanthophylls cycle was reported in many studies and the involvement of xanthophylls cycle in photo-protection under stress conditions was proven by Amy et al. (1997). Like this, C<sub>3</sub> plants may more avoid the damage of excessive energy by enhancing the function of xanthophylls cycle.

As mentioned through this paper, both kenaf and napiergrass presented a significantly high flooding tolerance compared with both mungbean and corn, and when the former two species were compared, kenaf was superior to napiergrass in the photosynthetic sustainability under the changing water conditions. It is concluded that the sustainment of stomatal openness in kenaf under the flooding and recovery condition is regarded as allowing this species to keep gas exchange and energy transport in the leaf, by which photosynthetic production and photo-damage prevention are realized. In addition, the increased *NPQ* and photorespiration is considered to have a role of dissipating the accumulated excessive energy in the leaf under the stress conditions.

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