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## Heterosis for Photosynthesis and Dry Matter Accumulation in F<sub>1</sub> Hybrid Rice (*Oryza sativa* L.) Produced from Thermo-sensitive Male Sterile Line under Drought Stress at Heading Stage

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Heterosis is defined as increased vigour of hybrids in comparison to their parents. In this study, seven cultivars of upland inbred rice (male parents) and their F<sub>1</sub> hybrids generated by crossing with a thermo-sensitive genic male sterile (TGMS) 103<sup>s</sup> line (female parent). The cultivars were examined for characters of photosynthesis and dry matter production under drought stress at flowering stage and recovery at ripening stage. The results showed that under drought, all F<sub>1</sub> hybrids exhibited very low negative heterosis for CO<sub>2</sub> exchange rate, stomatal conductance, mesophyll conductance and transpiration rate, but high positive heterosis for intercellular CO<sub>2</sub> concentration. The heterosis value increased much more in the F<sub>1</sub> hybrids under drought recovery than under well-water conditions. During drought stress, heterosis value decreased slightly for dry matter accumulation compared to well-irrigated conditions. Although CO<sub>2</sub> exchange rate significantly decreased, dry matter accumulation was maintained in all F<sub>1</sub> hybrids after drought recovery, which suggests the potential for using upland rice as male parent to produce F<sub>1</sub> hybrids from TGMS lines for drought tolerance.

**Key words:** drought stress, F<sub>1</sub> hybrid, photosynthesis, TGMS line, upland rice

### INTRODUCTION

In Asia, drought is a major abiotic stress, affecting over 20% of the total rice- (*Oryza sativa* L.) cultivated areas (Pandey and Bhandari, 2008). In Vietnam, over 100,000 hectares of rice in the central provinces are affected by severe drought, and an equivalent to 500,000 tons of paddy has been lost (MARD, 2010). Uncertain patterns of drought stress occur in most prime rainfed rice environments (Serraj *et al.*, 2009). Under prolonged or severe drought conditions, flowering time is an important determinant of grain yield. The limitation of plant growth imposed by low water availability is mainly due to reduction of plant carbon balance, which is largely dependent on photosynthesis. For this reason, plant photosynthesis responses to water stress have been the subject of study for decades, (Flexas and Medrano, 2002; Lawlor and Cornic, 2002). Moreover, recent reports have indicated that drought stress can cause a series of physiological and biochemical responses, such as stomatal clo-

sure, suppression of cell division and elongation, and inhibition of photosynthesis (Shinozaki and Yamaguichi, 2007).

Higher yield of hybrid rice over inbred rice and the parent under unfavorable environments has been investigated, including rainfed drought-prone lowland fields and soil problems (Virmani, 2003). Previously, a positive heterosis for photosynthesis was obtained under high temperature condition and radiation, due to the higher stomatal conductance and also the higher non-photochemical quenching (Pham *et al.*, 2005). Some recent studies have shown that hybrid rice shows more adaptability to stressful environments over conventional inbred rice (Li *et al.*, 2009). Villa *et al.* (2012) has evaluated hybrid rice produced from cytoplasmic male sterility (CMS) female lines under well-watered lowland, drought conditions, and the relative performance of hybrids which were not systematically compared with that of inbred parents. Thermo-sensitive male sterile line (TGMS), which exposed pollen sterility under high temperature but fertility under low temperature, has been used efficiently as a female parent to produce F<sub>1</sub> hybrid rice in tropical areas (Pham *et al.*, 2004). Drought tolerance of inbred parents is considered as a crucial factor for development of drought-tolerant hybrids (Luo, 2010). Therefore, the objectives of this study were to evaluate heterosis for photosynthetic characters and dry matter accumulation of hybrids produced from TGMS line, compared to their male parents (upland rice) under drought stress at flowering stage.

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## MATERIALS AND METHODS

### Plant materials

Seven cultivars of inbred upland rice were used as male parents, a thermo-sensitive genic male sterile line TGMS 103<sup>s</sup> (released from Vietnam) as female parent and their 7 F<sub>1</sub> hybrids (Table 1).

**Table 1.** Plant materials, male parents and F<sub>1</sub> hybrids, used in this research

Name	Male parent		F <sub>1</sub> hybrids
	Code	Original	Code
Beo Dien	TN2	Viet Nam Upland rice	103 <sup>s</sup> /TN2
Ep hat tron	TN11	Viet Nam Upland rice	103 <sup>s</sup> /TN11
IR71525	TN13	IRRI Upland rice	103 <sup>s</sup> /TN13
CT6510-24-1-2	TN15	IRRI Upland rice I	103 <sup>s</sup> /TN15
WAB96-1-1	TN17	IRRI Upland rice	103 <sup>s</sup> /TN17
ULPI-7	TN19	IRRI Upland rice	103 <sup>s</sup> /TN19
Nep Bao lac	TN23	Viet Nam Upland rice	103 <sup>s</sup> /TN23

### Rice Planting

Seeds of the F<sub>1</sub> hybrid and parent cultivars were incubated and sown at different time for synchronizing heading time in the seedling bed (60×35×8 cm). Seedlings at the 3–4 leaf stage were transplanted singly into Wager pot (0.03 m<sup>2</sup>) containing 5 kg of dry foaming soil, one seedling per pot. The experiment was laid out in randomly complete block design (Gomez and Gomez, 1984) in autumn season in 2010 in greenhouse at faculty of Agronomy, Hanoi University of Agriculture.

### Fertilization

Total fertilizer was applied with N, P<sub>2</sub>O<sub>5</sub> and K<sub>2</sub>O at the rate of 0.48, 0.36 and 0.36 (g per pot), respectively. Basal dressing for one pot with N, P<sub>2</sub>O<sub>5</sub> and K<sub>2</sub>O was at the rate of 0.16, 0.18 and 0.12 g, respectively. Top dressing at 7 days after transplanting (DAT) and 14 DAT with N, P<sub>2</sub>O<sub>5</sub> and K<sub>2</sub>O at the rate of 0.08, 0.18 and 0.08 g per pot, respectively. Final dressing at the panicle initiation stage (20–18 days before heading) was applied with N and K<sub>2</sub>O at the same rate of 0.06 g per pot.

### Drought treatment

At booting stage (five to three days before flowering), 20 plants of each F<sub>1</sub> hybrid and the respective parent were randomly selected for water withdrawn (drought treatment) in compared to other twenty well-watering (control). Tension meter was installed into the pots to measure soil potential. When the soil water potential reached –60 kPa, photosynthetic characteristics were measured. After that, water was re-applied in the drought treatment pots, photosynthetic parameters were measured after 5 days of recovery.

### Measuring

At flowering (under drought treatment) and ripening stage (drought recovery), four plants of each F<sub>1</sub> hybrid

and the respective parent under both drought and control conditions were selected for specific photosynthetic characters. For each plant, two top–fully flag leaves were selected for measuring CO<sub>2</sub> exchange rate (*CER*), transpiration rate (*Tr*), inter cellular CO<sub>2</sub> concentration (*Ci*) and stomatal conductance (*Gs*) using a portable photosynthesis gas exchange system (LICOR 6400, the USA) at temperature of 30°C, photosynthetic photon flux density (*PPFD*) of 1500 μmol m<sup>–2</sup> s<sup>–1</sup>, CO<sub>2</sub> concentration of 370 μmol mol<sup>–1</sup> and relative humidity of 60%. The plants on which photosynthesis was measured were also selected for drying at 80°C in 48 h to constant weight for total dry matter accumulation.

### Analyses consisted of photosynthesis–derived calculations and statistical comparisons

Water use efficiency was calculated as:  $WUE = CER/Tr$  (μmol CO<sub>2</sub>/mmol H<sub>2</sub>O).

Heterosis over the best parent (*Hb*) and that over the mean of parents (abbreviated to mid–parent) (*Ht*) were calculated according to the following formula;

$$Ht (\%) = \frac{F_1 - \text{Mid-parent}}{\text{Mid-parent}} \times 100$$

$$Hb (\%) = \frac{F_1 - \text{best parent}}{\text{best parent}} \times 100$$

Data were analyzed by SAS (Full name of software manufacturer, 1990). The *t*–test procedure was used to examine the difference between F<sub>1</sub> hybrid and the respective male parent and mid–parent at different stage under both drought and control conditions. Best parent was considered as the parent with the higher value of each parameter.

## RESULTS

Under well–watering condition (control), the average value of CO<sub>2</sub> exchange rate (*CER*) was higher in the F<sub>1</sub> hybrids than that in male parents at flowering stage, but the significant difference was not obtained at ripening stage (Table 2). In contrary, the average value of *CER* was higher in the male parents (7.6 μmol m<sup>–2</sup> s<sup>–1</sup>) than that in the F<sub>1</sub> hybrids (2.5 μmol m<sup>–2</sup> s<sup>–1</sup>) under drought condition at flowering stage, but that value was higher in F<sub>1</sub> hybrids under recovery condition. At flowering stage, all F<sub>1</sub> hybrid rice showed significantly negative heterosis for *CER* under drought condition with the heterosis over mid–parent (*Ht*) value ranged from –83.7% in 103<sup>s</sup>/TN13 to –30.1% in 103<sup>s</sup>/TN19, but which was not found in well–watered conditions (Table 3). At ripening stage, all F<sub>1</sub> hybrids showed positive heterosis for *CER* over both mid–parent (average *Ht*=23.0%) and best parent (average *Hb*=18%) under recovery condition, whereas it was not observed under control condition.

At the flowering stage, a significant and positive correlation was found between *CER* and stomatal conductance in F<sub>1</sub> hybrids ( $r=0.85^{**}$ ) and male parents ( $r=0.89^{**}$ )

under drought condition. In contrast, *CER* was negatively correlated with inter cellular CO<sub>2</sub> concentration (*C<sub>i</sub>*) in all F<sub>1</sub> hybrids and their parents ( $r=-0.52^*$ ) (Fig. 1). When data was calculate separately, the *CER* was

significantly and positively correlated with transpiration rate in male parents ( $r=0.86^{**}$ ), but the correlation was not significant in the F<sub>1</sub> hybrids ( $r=0.27$ ).

At the ripening stage, a significant and positive cor-

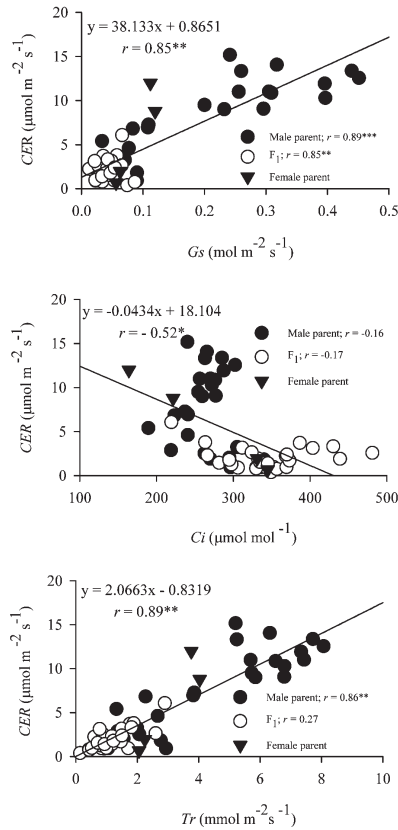
**Table 2.** The CO<sub>2</sub> exchange rate (*CER*;  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) in F<sub>1</sub> hybrid and parent rice under drought and recovery conditions

F <sub>1</sub> hybrids and parents		Flowering		Ripening	
		Drought	Control	Recovery	Control
F <sub>1</sub> hybrids	103 <sup>s</sup> /TN2	2.1	15.8	14.2	7.1
	103 <sup>s</sup> /TN11	2.5	20.3	9.8	8.1
	103 <sup>s</sup> /TN13	1.7	22.1	14.0	8.4
	103 <sup>s</sup> /TN15	1.2	22.6	13.0	10.3
	103 <sup>s</sup> /TN17	1.4	15.4	14.0	14.2
	103 <sup>s</sup> /TN19	3.4	17.9	11.3	10.3
	103 <sup>s</sup> /TN23	1.8	19.7	9.9	8.2
	Average	2.0	19.1	12.3	9.5
Male parents	TN2	7.2	16.0	11.9	10.2
	TN11	9.7	16.2	9.8	10.4
	TN13	12.4	15.7	12.2	6.5
	TN15	6.5	14.2	11.0	11.2
	TN17	12.0	15.3	10.6	9.2
	TN19	3.9	13.8	10.3	10.7
	TN23	1.8	15.3	7.5	7.0
	Average	7.6	15.2	10.5	9.3
Female parent	103 <sup>s</sup>	5.9	21.8	9.5	11.1
LSD <sub>0.05</sub>		3.63	2.80	2.69	3.02

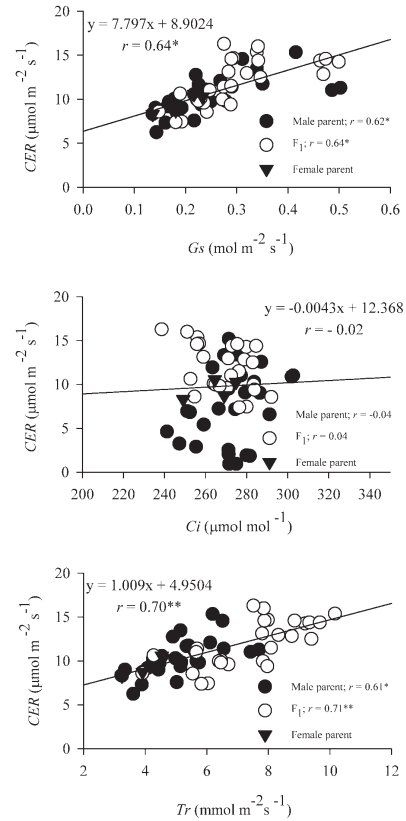
**Table 3.** Heterosis for *CER* in F<sub>1</sub> hybrid rice under drought and recovery conditions

F <sub>1</sub> hybrids	Heterosis (%)	Flowering		Ripening	
		Drought	Control	Recovery	Control
103 <sup>s</sup> /TN2	Ht	-68.0*	-16.4*	32.4*	-33.2*
	Hb	-70.9*	-27.4*	18.8*	-35.7*
103 <sup>s</sup> /TN11	Ht	-68.3*	6.8	1.8	-25.0*
	Hb	-74.5*	-6.8	0.4	-27.3*
103 <sup>s</sup> /TN13	Ht	-83.7*	18.0*	29.3*	-4.2
	Hb	-88.7*	1.7	14.8*	-23.8*
103 <sup>s</sup> /TN15	Ht	-80.0*	25.5*	26.8*	-7.3
	Hb	-81.0*	3.7	18.2*	-7.9
103 <sup>s</sup> /TN17	Ht	-85.9*	-16.7*	39.5*	39.7*
	Hb	-90.0*	1.0	32.2*	27.7*
103 <sup>s</sup> /TN19	Ht	-30.1*	0.7	15.0*	-5.0
	Hb	-42.0*	-17.7*	10.6*	-6.8
103 <sup>s</sup> /TN23	Ht	-52.2*	6.5	16.3*	-8.8
	Hb	-68.9*	-9.3	4.4	-25.8*
Average	Ht	-66.9	3.5	23.0	-6.3
	Hb	-73.7	-7.8	14.2	-14.2

Note: Ht: heterosis over mid-parent; Hb: heterosis over best parent; \*: Significant at the probability of 0.05 by t-test.



**Fig. 1.** Correlation of  $\text{CO}_2$  exchange rate ( $\text{CER}$ ) with stomatal conductance ( $G_s$ ), inter cellular  $\text{CO}_2$  concentration ( $C_i$ ) and transpiration rate ( $T_r$ ) in  $F_1$  hybrids (black round symbol), male parents (white round symbol) and female parent (black angle symbol) under drought condition. Note: \*, \*\*, Significant at the probability of 0.05 and 0.01 levels, respectively.



**Fig. 2.** Correlation of  $\text{CO}_2$  exchange rate ( $\text{CER}$ ) with stomatal conductance ( $G_s$ ), inter cellular  $\text{CO}_2$  concentration ( $C_i$ ) and transpiration rate ( $T_r$ ) in  $F_1$  hybrids (black round symbol), male parents (white round symbol) and female parent (black angle symbol) under recovery condition. Note: \*, \*\*, Significant at the probability of 0.05 and 0.01 levels, respectively.

**Table 4.** The water use efficiency (WUE;  $\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ H}_2\text{O}$ ) in  $F_1$  hybrid and parent rice under drought and recovery conditions

$F_1$ hybrids and parents		Flowering		Ripening	
		Drought	Control	Recovery	Control
$F_1$ hybrids	103 <sup>s</sup> /TN2	2.5	1.8	1.6	1.3
	103 <sup>s</sup> /TN11	2.0	2.9	1.5	1.2
	103 <sup>s</sup> /TN13	2.4	2.5	1.6	1.2
	103 <sup>s</sup> /TN15	2.0	2.7	1.4	1.4
	103 <sup>s</sup> /TN17	2.5	2.1	1.8	2.1
	103 <sup>s</sup> /TN19	2.3	2.0	1.6	1.4
	103 <sup>s</sup> /TN23	1.6	2.2	1.5	1.3
	Average	2.2	2.3	1.6	1.4
Male parents	TN2	1.9	2.5	2.1	1.7
	TN11	1.5	3.0	1.8	1.6
	TN13	2.0	2.3	2.5	2.1
	TN15	2.1	2.7	2.0	1.8
	TN17	2.0	2.2	1.9	2.1
	TN19	2.6	2.9	2.5	1.9
	TN23	1.2	2.6	1.8	1.4
	Average	1.9	2.6	2.1	1.8
Female parent	103 <sup>s</sup>	1.7	2.7	2.1	1.4
LSD <sub>0.05</sub>		0.27	0.31	0.27	0.20

relation was found between *CER* and stomatal conductance in all F<sub>1</sub> hybrids and male parents ( $r=0.64^*$ ) under drought recovery (Fig. 2). In contrast, the *CER* was negatively correlated with *Ci* in all F<sub>1</sub> hybrids and their parents ( $r=-0.52^*$ ) (Fig. 2). *CER* was significantly and pos-

itively correlated with transpiration rate in all F<sub>1</sub> hybrids and male parents ( $r=0.70^*$ ).

At flowering stage, the average value of water use efficiency (*WUE*) in F<sub>1</sub> hybrids was higher than that in the male parents under drought condition. In contrary,

**Table 5.** Heterosis for WUE in F<sub>1</sub> hybrid rice under drought and recovery conditions

F <sub>1</sub> hybrids	Heterosis (%)	Flowering		Ripening	
		Drought	Control	Recovery	Control
103 <sup>s</sup> /TN2	Ht	40.5*	-31.0*	-21.4*	-18.1*
	Hb	32.8*	-28.7*	-22.4*	-23.7*
103 <sup>s</sup> /TN11	Ht	29.2*	-0.2	-23.0*	-22.8*
	Hb	-20.4*	-6.4	-17.4*	-26.6*
103 <sup>s</sup> /TN13	Ht	23.7*	-0.7	-29.9*	-33.8*
	Hb	8.0	6.8	-35.6*	-44.7*
103 <sup>s</sup> /TN15	Ht	7.6	2.1	-32.0*	-13.3
	Hb	-3.4	2.4	-31.8*	-23.2*
103 <sup>s</sup> /TN17	Ht	25.6*	-15.4*	-7.9	19.7*
	Hb	9.1	-7.2	-3.8	-0.4
103 <sup>s</sup> /TN19	Ht	10.2	-27.8*	-30.0*	-12.9
	Hb	-9.4	-30.2*	-35.9*	-23.6*
103 <sup>s</sup> /TN23	Ht	13.7	-17.1*	-20.0*	-5.3
	Hb	-2.3	-16.2*	-14.0*	-4.0
Average	Ht	21.5	-12.9	-23.5	-12.4
	Hb	2.1	-11.4	-23.0	-20.9

Note: Ht: heterosis over mid-parent; Hb: heterosis over best parent; \*: Significant at the probability of 0.05 by t-test.

**Table 6.** Dry matter accumulation (g hill<sup>-1</sup>) in F<sub>1</sub> hybrid and parent rice under drought and recovery conditions

F <sub>1</sub> hybrids and parents		Flowering		Ripening	
		Drought	Control	Recovery	Control
F <sub>1</sub> hybrids	103 <sup>s</sup> /TN2	22.4	28.3	33.0	31.8
	103 <sup>s</sup> /TN11	20.9	24.4	29.7	31.3
	103 <sup>s</sup> /TN13	20.9	26.7	30.4	27.4
	103 <sup>s</sup> /TN15	23.9	26.3	30.1	30.8
	103 <sup>s</sup> /TN17	23.3	27.4	32.7	35.9
	103 <sup>s</sup> /TN19	20.9	28.5	34.8	25.4
	103 <sup>s</sup> /TN23	24.5	33.4	33.6	36.1
	Average	22.4	27.9	32.0	31.2
Male parents	TN2	18.8	21.7	25.1	27.1
	TN11	20.5	23.7	29.9	29.5
	TN13	23.6	26.4	30.7	38.2
	TN15	18.7	20.3	26.1	27.1
	TN17	17.1	18.9	28.7	31.9
	TN19	18.3	21.2	26.8	35.6
	TN23	26.4	31.3	31.8	35.2
	Average	20.5	23.4	28.4	32.1
Female parent	103 <sup>s</sup>	22.0	23.3	26.0	25.6
LSD <sub>0.05</sub>		1.65	3.09	2.98	2.68

**Table 7.** Heterosis for dry matter accumulation in F<sub>1</sub> hybrid rice under drought and recovery conditions

F <sub>1</sub> hybrids	Heterosis (%)	Flowering		Ripening	
		Drought	Control	Recovery	Control
103 <sup>s</sup> /TN2	Ht	9.8	25.8*	29.3*	20.8*
	Hb	1.9	21.4*	27.0*	17.3
103 <sup>s</sup> /TN11	Ht	-1.6	4.0	6.1	13.7
	Hb	-5.0	3.3	-0.9	6.1
103 <sup>s</sup> /TN13	Ht	-8.3	7.3	7.3	-14.1
	Hb	-11.4*	1.1	-0.9	-28.3*
103 <sup>s</sup> /TN15	Ht	17.6	20.6*	15.5*	17.0
	Hb	8.7	12.8	15.4*	13.6
103 <sup>s</sup> /TN17	Ht	19.4*	29.5*	19.4*	24.9*
	Hb	6.0	17.3	13.8	12.4
103 <sup>s</sup> /TN19	Ht	3.7	28.0*	31.7*	-16.8
	Hb	-5.0	22.3*	29.8*	-28.6*
103 <sup>s</sup> /TN23	Ht	1.1	22.1*	16.1*	18.9*
	Hb	-7.4	6.6	5.5	2.6
Average	Ht	6.0	19.6	17.9	9.2
	Hb	-1.7	12.1	12.8	-0.7

Note: Ht: heterosis over mid-parent; Hb: heterosis over best parent; \*: Significant at the probability of 0.05 by t-test.

the value was higher in male parents under well-watering condition (Table 4). At ripening stage, the average value of *WUE* was lower in the F<sub>1</sub> hybrids than that in male parents under both conditions.

At the flowering stage, a significant and positive heterosis over mid-parent (mean *Ht*=21.5%) for *WUE* was observed in all F<sub>1</sub> hybrids under drought condition, whereas the heterosis value was negative under control conditions (mean *Ht*=-11.4%) (Table 5). The significant and positive heterosis for *WUE* under drought treatment was observed in four F<sub>1</sub> hybrids (103<sup>s</sup>/TN2, 103<sup>s</sup>/TN11, 103<sup>s</sup>/TN13 and 103<sup>s</sup>/TN17). At ripening stage, a negative heterosis for *WUE* was observed in all F<sub>1</sub> hybrids.

At flowering stage, the average value of dry matter accumulation (*DM*) was higher in F<sub>1</sub> hybrids and in male parents under both drought and control conditions (Table 6). At ripening stage, that value was higher in F<sub>1</sub> hybrids under drought recovery condition, whereas the difference was not observed under well-watering condition. None of F<sub>1</sub> hybrids showed significant and positive heterosis over the best parent (*Hb*) for *DM* under drought treatment (Table 7). However, three of them (103<sup>s</sup>/TN2, 103<sup>s</sup>/TN15 and 103<sup>s</sup>/TN19) showed significant and positive *Hb* for this traits under drought recovery (*Hb*=15.4%–29.8%). The mean *Ht* value for this parameter in F<sub>1</sub> hybrids was lower under drought (6.0%) than that under control condition (19.6%) at flowering stage. In contrary, the heterosis value was higher in the recovery condition (17.9%) than that in the control condition (9.2%).

## DISCUSSION

To survive under drought stress, plants have evolved a series of intricate mechanisms to trigger a suite of physiological, cellular, and photosynthetic responses governed by genotype interacting with environment (Shinozaki and Yamaguchi, 2007; Fujita *et al.*, 2006). This study to examined responses of photosynthesis and dry matter production to a drought environment at heading for the hybrid progeny of drought tolerant male parent (upland cultivars) and female parent paddy rice (TGMS 103<sup>s</sup> line). The findings showed much lower photosynthetic rate in all F<sub>1</sub> hybrids than that in the respective male parents under drought conditions. This is in agreement with Flexas *et al.* (2002) regarding reduced photosynthesis to compare with those in the parental lines. Drought influences photosynthesis through either pathway regulation by stomatal closure and decreasing flow of CO<sub>2</sub> into mesophyll tissue (Chaves, 1991; Chaves *et al.*, 2003; Ort *et al.*, 1994; Flexas *et al.*, 2004) or by directly impairing metabolic activities (non-stomatal inhibition) (Farquhar *et al.*, 1989). In this study, non-stomatal inhibition may occurred first in the F<sub>1</sub> hybrid rice, compared to diffusive limitation through stomatal closure in male parent lines, which showed decreased in *Ci* during drought stress. It also has been shown that non-stomatal inhibition (metabolic activities) may occur first, causing a temporary increase in internal CO<sub>2</sub> concentration, which generates stomata to close (Briggs *et al.*, 1986). In addition, it has been reported that drought stress causes an increase in *Ci* (Siddique *et al.*, 1999; Kicheva *et al.*, 1994). During onset of drought, stomatal conductivity declines before



reduction in photosynthesis and the suppression of photosynthesis during the stress is mainly due to the reduction of CO<sub>2</sub> diffusion (Lawlor, 2002). In our F<sub>1</sub> hybrid rice, non-stomatal limitation such as oxidative damage to chloroplast may be responsible for the decline in photosynthesis as was also claimed in the previous reports (Zhou *et al.*, 2007; Ji *et al.*, 2012).

The similarity in performance of heterosis for CO<sub>2</sub> exchange rate and mesophyll conductance in F<sub>1</sub> hybrid rice in both well-irrigated and drought-stress conditions partly disclosed the important contribution of mesophyll conductance over stomatal conductance in the regulation of photosynthesis. In the research of Flexas *et al.* (2002) on grapevines under drought stress, it was found that during early water stress, stomatal conductance played a predominant role and later contributed equally to mesophyll conductance after acclimation. In this study, it appears that in F<sub>1</sub> hybrid rice, mesophyll conductance may be governing CO<sub>2</sub> exchange rate from the beginning point. Greater stomatal closure led to strong reduction in transpiration rate in F<sub>1</sub> hybrid rice compared to male parent lines. The decrease in CO<sub>2</sub> exchange rate combined with strong reduction in transpiration rate caused a change in the heterosis value for water use efficiency under drought, but there was no difference under well-watered conditions. Although CO<sub>2</sub> exchange rate significantly decreased, dry matter accumulation still could be maintained during recovery. Strong recovery of dry matter accumulation may be due to the ability of F<sub>1</sub> hybrid rice to use CO<sub>2</sub> more effectively during drought stress.

Thus, using upland male parents to produce F<sub>1</sub> hybrids with the decrease in photosynthesis during drought, but much better performance in recovery stage appears to be an effective approach to produce drought tolerant rice hybrids.

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