J. Crop Sci. Biotech. 2019 (March) 22 (1) : 75 ~ 81
DOI No. 10.1007/s12892-019-0015-0

RESEARCH ARTICLE

Effect of Moderate Drought-Stress on Flowering Time of Interspecific Hybrid Progenies (*Oryza sativa* L. × *Oryza glaberrima* Steud.)

Dong-Jin Kang[1]*, **Koichi Futakuchi**[2]

[1] *Teaching and Research Center for Bio-coexistence, Faculty of Agriculture and Life Science, Hirosaki University, Gosyogawara 037-0202, Japan*
[2] *Africa Rice Center M'be Station, 01 B.P. 2551, Bouake 01, Cote d'Ivoire*

Received: January 08, 2019 / Revised: January 30, 2019 / Accepted: February 02, 2019

Abstract

We examined the effects of drought stress on flowering time, grain yield, and agronomic traits using 10 upland-adapted rice genotypes, i.e. eight interspecific *Oryza sativa* L. × *Oryza glaberrima* Steud. (NERICA) lines and two *Oryza sativa* varieties—WAB56-104, the *O. sativa* parent of eight interspecific lines and IRAT 109, a drought-resistant variety as a check—under wet control and moderate drought-stressed conditions. Analysis of variance results for the 10 rice genotypes indicated that the effects of genotype (G) and drought stress (environment, E) were highly significant for tiller number, spikelet fertility, grain yield, straw dry-matter weight, and harvest index. Flowering was delayed by 1.7–10.7 (4.5 on average) days under drought condition compared with that under the wet control condition. Genotype ($P < 0.001$), drought stress ($P < 0.001$), and G × E interaction ($P < 0.001$) were highly significant with respect to days from seeding to 50% flowering (DTF50). DTF50 was significantly and negatively correlated with grain yield, yield components, and harvest index under drought-stress conditions. Of these, panicle number, total spikelet number, spikelet fertility, grain yield, and harvest index in drought-stressed rice genotypes were significantly and negatively correlated with DTF50 compared with those under the wet control condition. In conclusion, drought during the early vegetative stage inhibits most of the major agronomic traits by delaying flowering in upland-adapted rice genotypes.

Key words : Drought, G × E interaction, grain yield, NERICA, upland rice, yield components

Introduction

Drought is one of the major factors limiting rice productivity, and it comes in various forms based on the timing and severity in rainfall in cultivation areas. Regarding drought types, timing (plant growth stages when drought occurs) and intensity of the drought play a vital role in determining specific plant traits (Kamoshita et al. 2008). The occurrence of drought during the vegetative stage in rice impedes leaf and tiller formation, which subsequently affects the development of panicles per plant, causing yield loss (Singh et al. 2017; Swain et al. 2017). A soil moisture tension of -20 kPa during the vegetative stage causes a 50% reduction in grain yield compared with wet control conditions (Swain et al. 2017). The numbers of leaves and tillers in rice is significantly reduced with the increased intensity of drought during the seedling stage (Singh et al. 2017). The first observed symptom in rice with drought imposed in the vegetative phase is a decline in the leaf expansion rate (Wopereis et al. 1996). In contrast, drought during the reproductive stage of the rice plant (the most critical stage) can cause substantial yield loss, particularly because of a reduction in filled grain number per panicle (Pantuwan et al. 2002a).

To evaluate the responses of agronomically important traits including phenology and grain yield to drought stress properly, precise water control using experimental tools such as pots, PVC pipe, sloping bed, and concrete tank in rainout greenhouse or a movable rainout shelter, and agri-

Dong-Jin Kang (✉)
Email: djkang@hirosaki-u.ac.jp
Fax: +81173525137

cultural land characterization have been implemented (Kameoka et al. 2015; Pantuwan et al. 2002b; Yue et al. 2006; Zu et al. 2017). Traits associated with yield generation that exhibit genotype (G, rice variety) × environment (E, drought) interaction under drought stress include flowering time, green-leaf area, root pressure, root length, and root biomass (Lafitte and Courtois 2002; Ndjiondjop et al. 2010).

In rainfed upland, rice is exposed to variable soil water conditions and unpredictable periods of drought stress (Alou et al. 2018). Compared with lowland rice, upland-adapted rice is widely recognized that it performs better regarding traits related to drought avoidance such as leaf rolling, root volume, leaf water-loss percentage, and relative conductivity (Ding et al. 2013). Drought stress between germination and flowering delays plant development in upland rice (Boojung and Fukai 1996). At the vegetative stage (seedling and tillering stages), drought hinders the development of leaf and tiller. The reduction of leaf area and the number of tillers subsequently affect the development of panicle, thus causing a yield loss (Pantuwan et al. 2002a).

NERICA (New Rice for Africa) lines were developed by the West Africa Rice Development Association (now Africa Rice Center) using interspecific hybridization between *Oryza sativa* L. and *O. glaberrima* Steud. (Africa Rice Center 2008; Ndjiondjop et al. 2010). As the male parent of the upland NERICA lines, CG 14, *O. glaberrima*, has several unique traits such as drought tolerance and weed competitiveness (Bocco et al. 2012). Matsumoto et al. (2014) show NERICA 4 and NERICA 10 are more tolerant than a Japanese upland variety (Yumenohatamochi). The drought tolerance of NERICA 4 is also recognized by Fofana et al. (2018). However, the performance of NERICA lines under drought stress is not fully discussed. Upland rice can be seen in the Guinea Savanna and Forest zones in West Africa and farmers do not seed just at the start of the rainy season but wait seeding until rainfall becomes to look like stable (personal communication). However, rainfall soon after the start of the rainy season in these climate zones can be highly unstable and farmers also cannot delay seeding for a long time since late seeding can bring another risk of terminal drought at the end of the rainy season. Thus, young plants of upland rice can always suffer from drought, at least moderate drought, more or less. Therefore, in this study, we evaluated the response of some NERICA lines to moderate drought during the early vegetative stage (tillering stage). We focused on associations between flowering time and grain yield or yield components. We hypothesized that drought affects flowering time according to the drought at the early vegetative stage and that grain yield and yield components, particularly spikelet fertility, is closely associated with flowering time.

Materials and Methods

Plant materials, cultivation, and drought-stress treatment

We used 10 upland-adapted rice genotypes: eight upland interspecific hybrid rice (NERICA) lines (NERICA 1–NERICA 8, respectively, coded as UN1–UN8 in this paper) and two *O. sativa* varieties—WAB56-104, which is the female parent of UN1–UN8 lines, and IRAT 109, a highly drought-resistant variety (Xu et al. 2017) (Table 1). The experiment was conducted in a rainout greenhouse in Goshogawara, Aomori Prefecture (40.5494N, 140.2743E), northern Japan.

In this study, three pots (replicates) per each different drought-stress conditions were used. Three grains of germinated seeds into 1/5000 a Wagner pots that was packed with 2.21 kg of dried soil were sown on May 24, 2017. A compound fertilizer, N–P–K (15–15–15), was applied as basal dressing at 1.0 g/pot, and N–P–K (10–0–15) was applied as top dressing before flowering at 0.5 g/pot. Figure 1 shows the experimental scheme and daytime air temperatures during the experiment. The maximum and minimum temperatures in the greenhouse were measured using a data logger (Temperature and Humidity USB Datalogger DL171, AS ONE Co. Ltd., Osaka, Japan) throughout the experiment (Fig. 1B).

Drought stress was imposed during tillering stage from 21 to 47 days after sowing (DAS) and was controlled by the time of watering the pots under two conditions: wet (control) and moderate drought (drought-stress) conditions (Table 1

Table 1. Genotype and adaptation of eight NERICA lines (UN1–UN8) and two Oryza sativa varieties (W104 and IRAT 109) used in the present study.

Label	Accession name	Type	Adaptation	Treatment
UN1	WAB450-IBP-2-1-1	Tropical *japonica* × *O. glaberrima*	Upland	Control, Drought
UN2	WAB450-IBP-51-2-1	Tropical *japonica* × *O. glaberrima*	Upland	Control, Drought
UN3	WAB450-IBP-57-3-1	Tropical *japonica* × *O. glaberrima*	Upland	Control, Drought
UN4	WAB450-IBP-82-1-1	Tropical *japonica* × *O. glaberrima*	Upland	Control, Drought
UN5	WAB450-IBP-91-HB	Tropical *japonica* × *O. glaberrima*	Upland	Control, Drought
UN6	WAB450-IBP-101-HB	Tropical *japonica* × *O. glaberrima*	Upland	Control, Drought
UN7	WAB450-IBP-163-3-1	Tropical *japonica* × *O. glaberrima*	Upland	Control, Drought
UN8	WAB450-16-2-BL2-DV2	Tropical *japonica* × *O. glaberrima*	Upland	Control, Drought
W104	WAB56-104	Tropical *japonica* (sativa parent)	Upland	Control, Drought
IRAT 109	IRAT 109	*Japonica*	Upland	Control, Drought

Upland NERICA lines were developed from crosses as follows: WAB56-104/CG14//2 × WAB56-104

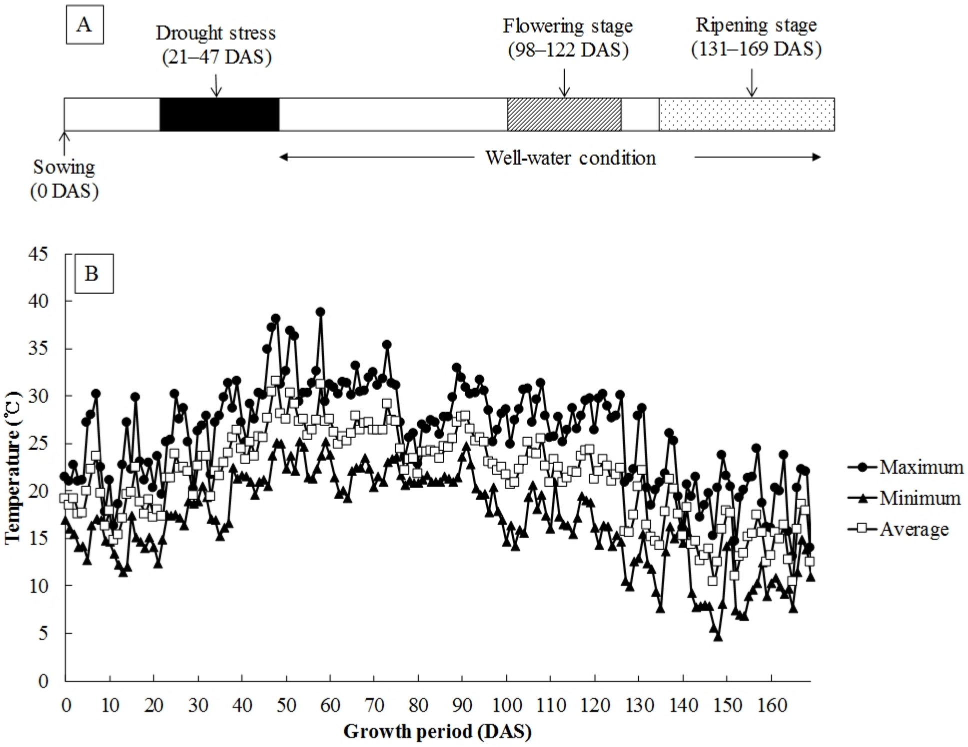

Fig. 1. Scheme of the present experiment (A) and daytime air temperature during the plant growth period (B). DAS = days after sowing.

and Fig. 1A). Before imposing drought stress at 21 DAS, all pots were watered in equal amounts to ensure similar soil moisture in all pots (total, 2010 mL water/pot). Soil tension at a depth of 20 cm in the pots was continuously assessed using a tension meter (DIK-8333, Daikirika Co. Ltd.,) during the drought-stress period (21–47 DAS). Pots were watered when soil tension reached the target value for each treatment during the drought-stress period (Table 2). During the early drought-stress period (26–37 DAS), pots were watered when soil tension ranged from −15 to −25 (ideally, −20) and −55 to −65 (ideally, −60) kPa under wet control and drought conditions, respectively, at a soil depth of 20 cm (Table 2). As the plants grew (38–47 DAS), the target soil tension in the pot was adjusted (because larger plants use more water for maintenance) to range from −5 to −10 and −45 to −55 kPa under wet control and drought conditions, respectively. The time of watering in each pot from 41 to 47 DAS was assessed based on a combination of targeted soil tension and leaf rolling in the vegetative stage when leaves folding was observed at scale 3 (deep V-shape; IRRI 2013).

Determination of days to flowering (DTF50), yield, and yield components

DTF50 was defined as DAS until 50% of the plants in a pot exhibited flowering tillers. Final plant height was measured as the plant length from the soil surface to the tip of the panicle at the harvest date. At harvesting, three individual plants (replicates) were collected to determine final dry-matter weight, grain yield, and yield components. Subsequently, aboveground parts were separated into straw and panicle parts, and then straw was dried at 80°C for 72 h in an oven and weighed. Grain yield was determined based on yield components and final dry-matter weight following the protocol reported by Itoh and Saigusa (2002). Harvest index was estimated as the ratio of grain weight to whole plant weight.

Statistical analysis

Data for all traits were subjected to analysis of variance (ANOVA) using the XLSTAT-Base software 2017 version (Addinsoft, New York, USA). Tukey's multiple range test and Fisher's least significant difference test were used to further analyze the difference between the mean values for their traits. Genotype by environment interactions (G × E) of all agronomic traits was evaluated using the model reported by Eberhart and Russell (1966). Correlation coefficients between DTF50 and agronomic traits were determined using simple linear correlations, and the results were analyzed using the Pearson's correlation coefficient (*r*) (Triola 2015).

Results and Discussion

Drought stress was imposed from 21 to 47 DAS; subsequently, well-watered conditions were kept until harvest. The flowering stage of all rice genotypes ranged from 98 to 122 DAS (Fig. 1A). The temperature during the flowering phase was 24.9–31.3°C (maximum; average = 28°C) and 14.2–20.9°C (minimum; average = 17.2°C) (Fig. 1B).

Table 2. Soil tension, timing (in days after sowing, DAS), and amount of watering under the wet control and drought conditions.

	Soil tension at 20-cm depth (-kPa)		Amounts applied water (g/pot)	
	Control	Drought	Control	Drought
0-20 DAS	0	0	2010	2010
			Start of water treatment (21 DAS)	
26 DAS	28 ± 1.0	-		-
27 DAS	-	-		-
28 DAS	-	63 ± 5.2		405
32 DAS	23 ± 2.4	-		-
33 DAS	-	-		-
35 DAS	-	54 ± 6.4		405
36 DAS	13 ± 1.8	-		-
37 DAS	-	-		-
40 DAS	-	50 ± 5.2		405
41 DAS	9 ± 2.0	-		-
44 DAS	-	-		-
45 DAS	4 ± 0.6	-		-
47 DAS	2 ± 0.0	49 ± 5.5	End of water treatment (47 DAS)	
Total amounts of water during stress period (g/pot)			2025	1215
Ratio of water amounts against to control condition (%)			100	60.0

Values of soil tension are presented as mean ± standard error (n = 3, individual pot).

Table 3. Agronomic traits, grain yield, yield components, and harvest index on the wet control and drought-stress conditions.

	Plant height (cm)		Tiller number (plant^{-1})		Panicle number (plant^{-1})		Spikelet number (panicle^{-1})		Spikelet fertility (%)		1000-grain weight (g)		Grain yield (g/plant)		Straw DW (g/plant)		Harvest index	
Line/var.	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought
UN1	120.3	115.5	8.3	8.0	8.0	7.7	83.3	79.5	80.0	65.1	28.2	29.3	14.8	11.5	32.5	29.5	0.31	0.28
UN2	100.3	96.3	11.7	10.0	9.7	9.0	62.7	68.9	53.5	38.4	30.5	30.7	9.7	7.3	32.2	29.8	0.23	0.20
UN3	99.3	105.0	10.7	10.7	9.0	10.0	83.8	96.8	43.9	42.9	26.1	25.8	8.7	10.8	27.5	31.1	0.24	0.26
UN4	114.0	111.7	10.3	8.7	9.3	8.0	55.5	58.4	55.1	47.3	35.7	32.3	10.2	7.1	34.8	30.3	0.22	0.19
UN5	100.3	98.3	11.3	9.3	8.0	8.3	82.9	78.3	15.0	5.7	28.3	29.5	2.8	1.1	29.3	28.0	0.09	0.04
UN6	109.3	109.8	12.5	10.0	9.5	6.7	87.7	82.8	33.4	10.6	27.8	27.8	7.8	1.8	39.6	32.8	0.16	0.05
UN7	110.7	111.2	9.7	9.3	8.0	7.7	59.8	62.2	59.5	50.1	34.9	32.7	9.9	7.6	33.6	32.8	0.23	0.19
UN8	114.2	110.5	10.7	9.0	10.0	8.7	94.1	92.6	43.3	38.9	28.2	28.0	11.3	8.7	28.2	25.5	0.29	0.25
W104	111.7	104.7	10.3	10.3	9.3	9.3	99.1	98.8	50.7	49.7	26.3	27.3	12.3	12.6	29.4	27.0	0.30	0.32
IRAT 109	89.5	92.3	11.0	10.3	10.3	10.0	70.5	76.0	45.7	33.7	35.6	37.5	11.7	9.6	28.3	25.9	0.29	0.27
Mean (genotype)	107.0	105.5	10.7	9.6	9.1	8.5	77.9	79.4	48.0	38.2	30.2	30.1	9.9	7.8	31.5	29.3	0.24	0.20
F-rations from ANOVA																		
G (genotype)	15.025 ***		2.559 *		2.153 *		27.222 ***		33.909 ***		96.678 ***		21.450 ***		5.336 ***		34.468 ***	
E (drought stress)	1.093 ns		9.592 **		2.729 ns		0.741 ns		27.716 ***		0.166 ns		21.164 ***		8.502 **		13.945 ***	
G × E	0.802 ns		0.661 ns		0.825 ns		1.087 ns		1.249 ns		5.166 ***		2.070 ns		1.083 ns		1.639 ns	

Straw DW = straw dry-matter weight.
*, **, and *** indicate significant correlation at 5, 1, and 0.1% levels, respectively; ns indicates no significant difference at 5% level.

Table 2 shows the soil tension at a depth of 20 cm and the time and amount of watering into the pot during the drought-stress period (21–47 DAS). Soil tension during the drought period ranged from −2 to −28 and −49 to −63 kPa under wet control and drought conditions, respectively. Total watering amount per pot during the drought stress period was 2025 mL/pot for wet control and 1215 mL/pot for drought (60% of that in wet control) stress conditions.

Agronomic traits under wet control and drought-stress conditions are summarized in Table 3. ANOVA revealed that the genotype effect was significant for all of the evaluated traits. Better performance of all traits, except for spikelet number per panicle, was observed in the wet control conditions. Drought stress had negative effects on all traits. Compared with the wet control, drought significantly decreased plant height (average, 1.5 cm), tiller number (average, 1.1), panicle number (average, 0.6), spikelet fertility (average, 9.8%), grain yield (average, 2.1 g/plant), straw dry-matter (average, 2.2 g/plant), and harvest index (average, 0.04). According to ANOVA, tiller number ($P < 0.05$), grain fertility ($P < 0.001$), grain yield ($P < 0.001$), straw dry-matter weight ($P < 0.01$), and harvest index ($P < 0.001$) were significantly affected by drought stress. The G × E interaction for 10 genotypes was significant only for 1000-grain weight as revealed by ANOVA (F-ratio = 5.166, $P < 0.001$). Of the yield components, 1000-grain weight was strongly related to both genotype and drought stress. Previous studies have reported that drought reduces the tiller number, plant height, leaf number and width, and

Table 4. Days to 50% flowering (DTF50) and flowering delays under the wet control and drought-stress conditions.

	DTF50		Flowering delay (d)†	
	Control	Drought	Control	Drought
UN1	99.7 ± 1.7	104.0 ± 0.0	0	4.3
UN2	106.0 ± 0.6	110.3 ± 0.9	0	4.3
UN3	105.0 ± 1.0	108.7 ± 0.7	0	3.7
UN4	107.3 ± 0.7	113.0 ± 1.0	0	5.7
UN5	115.7 ± 0.7	118.3 ± 0.3	0	2.7
UN6	109.7 ± 0.3	120.3 ± 1.2	0	10.7
UN7	108.0 ± 0.0	111.7 ± 1.2	0	3.7
UN8	105.0 ± 1.0	110.0 ± 0.6	0	5.0
W104	99.3 ± 0.3	102.3 ± 1.5	0	3.0
IRAT 109	106.3 ± 0.3	108.0 ± 0.0	0	1.7
Mean (genotype)	106.2	117.0	0.0	4.5
F-rations from ANOVA				
G (genotype)	72.349 ***			
E (drought stress)	142.508 ***			
G × E	4.342 ***			

†Flowering delay indicates days of delayed flowering under the drought conditions relative to that under wet control conditions.
DTF is presented as the mean ± standard error (n = 3, individual pots).
*** indicates significant correlations at the 0.1% level.

the grain yield of a population of introgression lines or interspecific backcross rice derived from *O. sativa* × *O. glaberrima* (Bocco et al. 2012; Ndjiondjop et al. 2010). Singh et al. (2017) reported that significant cultivar and treatment interactions ($P < 0.001$) were observed for most studied parameters such as tiller number, leaf area, dry weights (leaf and stem), and root traits (length, diameter, volume, number, and weight) when rice seedlings were subjected to soil moisture at 100, 66, and 33% of the field soil moisture capacity. In large-scale quantitative trait loci analysis (QTL), a QTL was identified that increased harvest index, biomass yield, and plant height under drought-stress conditions in upland-adapted rice (Bernier et al. 2007). A recent study identified that DTF and plant height were least affected by environmental factors such as drought, whereas spikelet fertility was most affected by environmental factors (Bhattarai and Subudhi 2018).

Drought stress was associated with a substantial delay in flowering time (Table 4). Flowering was delayed by 1.7–10.7 (average = 4.5) days under drought conditions compared with that under wet control conditions. The *F*-ratios obtained using ANOVA were 72.349 ($P < 0.001$) for G, 142.508 ($P < 0.001$) for E, and 4.342 ($P < 0.001$) for G × E interaction. Under drought conditions, flowering time in all NERICA lines, except for UN5, was delayed by drought compared with that in their sativa parent (W104). Among the NERICA lines (UN1–UN8), the shortest and longest flowering delays were observed in UN5 and UN6, respectively, despite these lines being derived from the same parents. Thus, flowering delay appears to be strongly affected by drought stress even within a genotype. Flowering delay due to drought stress is negatively associated with grain yield and appears to be governed by a lower plant-water status (Kumar et al. 2006). Similar to our study, another study also reported that delays in plant flowering during 21 days of drought stress at on an interspecific backcross population of *O. sativa* var. WAB56-104 × *O. glaberrima* var. CG14 (Ndjiondjop et al. 2010). Lafitte et al. (2004) reported that flowering delay under drought-stress conditions is associated with an apparent delay in floral development when stress is imposed between panicle initiation and pollen meiosis. Therefore, flowering time is an important determinant of grain yield under prolonged or severe drought-stress conditions (Pantuwan et al. 2002a). Moreover, genotypes that achieve higher plant dry matter at anthesis are desirable under less severe and prolonged drought conditions (Pantuwan et al. 2002b)

DTF50 under drought conditions was negatively correlated with all agronomic traits (Table 5). Spikelet fertility, grain yield, and harvest index were strongly and negatively correlated ($P < 0.001$) with DTF50 not only under drought condition but also under wet control condition. Panicle and total spikelet numbers per plant were significantly and negatively correlated with DTF50 under drought stress. From these results, flowering delay caused by drought stress imposed during the early vegetative stage (tillering stage) also negatively affects reproductive organ production, spikelet fertility, and grain yield. Saikumar et al. (2016) reported a significant negative correlation between DTF50 and grain yield under drought conditions in an interspecific population derived from a Swarna × *O. glaberrima* introgression line ($P < 0.05$–0.01). Reduction in dry matter accumulation by drought results in a delay in panicle exsertion, resulting in flowering delay (Saikumar et al. 2016). Peduncle elongation,

Table 5. Summary of correlation coefficients between days to 50% flowering (DTF50) after sowing and agronomic traits under the wet control and drought-stress conditions.

	DTF50	
Parameter	Control	Drought
Panicle number (plant^{-1})	-0.0970	-0.3985 *
Spikelet number (plant^{-1})	-0.3247	-0.3223
Total spikelet number (plant^{-1})	-0.3458	-0.4675 **
1000-grain weight (g)	0.2406	-0.0200
Spikelet fertility (%)	-0.7405 ***	-0.7877 ***
Grain yield (g/plant)	-0.8660 ***	-0.8998 ***
Harvest index	-0.8797 ***	-0.9228 ***

*, ** and *** indicates significant correlation at the 5, 1, and 0.1% levels, respectively.

which is closely associated with panicle exsertion, has a high and positive indirect effect on grain yield under drought-stress conditions through spikelet fertility in upland-adapted rice genotypes (He and Serraj 2012). Early maturation is advantageous under drought, even when stress is applied at specific developmental stages in rice plants (Lafitte and Courtois 2002). Furthermore, using a large-scale hybrid transcription factor approach in rice, drought-inducible transcription factors such as ABA-responsive element binding factor (OsABF1) were found to act as suppressor of floral transition in a photoperiod-independent manner (Zhang et al. 2016).

Conclusion

We found that drought stress, as expected, negatively affected all evaluated agronomic traits of upland-adapted NERICA lines and two *O. sativa* check varieties. In terms of yield loss, all NERICA lines except UN3 showed lower yield (23-78%) under moderate drought stress condition compared with that under the wet control condition. Among the NERICA lines (UN1-UN8), UN1 was found to have the highest yield performance under drought conditions; this was similar to that observed in its female parent variety, WAB56-104. In conclusion, moderate drought stress at the early vegetative stage negatively affects many agronomic traits (particularly panicle number per plant, total spikelet number per plant, and spikelet fertility), grain yield, and harvest index probably because of its close relationship with flowering delay. Further studies are warranted to investigate the morphological and anatomical traits of roots in these upland-adapted NERICA lines.

Acknowledgements

This work was partly supported by Grant-in-Aid for Scientific Research Grant Number 17K08163. We thank Dr. Y. Kato for kindly providing the IRAT109 seed used in this study, and Mr. Kaneaki Kimura and Ms. Wako Sutou for the assistance in this study.

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