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Drought resistance in an interspecific backcross population of rice (*Oryza* spp.) derived from the cross WAB56-104 (*O. sativa*) × CG14 (*O. glaberrima*)

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ABSTRACT

The ability to identify drought-resistant lines in all seasons would accelerate variety introduction. A total of 202 backcross-inbred lines of rice were subjected to drought during the 2006 and 2007 dry seasons at AfricaRice in Benin. Two irrigation regimes were applied: fully irrigated to maturity and 21 days of drought from 45 days after sowing. Plants were harvested at maturity. Increased canopy temperature under drought as compared to fully irrigated condition was observed. Delays were observed in plant flowering and maturity, with drought susceptibility index reaching 26.8 for flowering. Plant leaves were greener (2.9% increase) under drought than when fully irrigated. Drought negatively affected tiller number, plant height, number of leaves, leaf width and grain yield (16.9%, 13.7%, 6.7%, 14.1% and 26.7% respective reductions). Highly significant ($P \leq 0.01$) correlations were observed between traits measured under fully irrigated and drought conditions (r between 0.52 and 0.92), except for leaf greenness (SPAD), leaf width and canopy temperature ($r = 0.42$ ns, −0.03 ns and −0.30**, respectively). The study identified canopy temperature, SPAD, plant height and leaf number as possible traits that best correlated with grain yield. The performance of these traits under drought was a function of the rice line.

1. Introduction

Rice (*Oryza sativa* L.) is grown on more than 148 million ha in diverse agro-ecosystems under various temperatures and water regimes. It is the staple food of more than two-thirds of the world's population [1]. Twenty-eight percent of the world's rice is grown in rainfed lowlands [2] and around 13% under upland conditions without any surface water accumulation. In both cases, rice suffers from drought during part of the growing season due to uncertain and uneven rainfall distribution patterns, which induces significant reduction in yield [3,4]. Drought has been identified as one of the most important rice production constraints in West Africa [5], especially when it coincides with the reproductive stage of the plant [6]. Genetic analysis of drought resistance at the reproductive stage is therefore crucially important. Drought is also the major limiting factor for rice yield stability in rainfed lowland and upland environments [7]. Most high-yielding varieties of rice developed for irrigated conditions are usually highly susceptible to drought stress, thereby limiting their adoption in rainfed environments with their risk of water shortage during certain periods of the growing season.

To arrive at genetically improved varieties with drought resistance, it is important to generate backcross populations of rice and select superior lines in controlled-stress environments in order to evaluate which features of the selected lines differ from the recurrent parents. Pantuwan et al. [2] indicated that the susceptibility of rice to drought is related to crop genotype and to the characteristics of the drought-stress environment. A number of plant growth traits are associated with drought avoidance in rice, e.g. root thickness, length density, pulling force, penetration ability, depth of rooting, and osmotic adjustment [8]. The diversity of affected ecosystems, the variability of drought in terms of timing and severity, and the multiple traits involved in drought resistance require strategic research to prioritize and develop environment-specific approaches for drought-resistant rice varieties through

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genetic improvement. This is an important element in reducing risk, increasing productivity, and alleviating poverty in communities dependent on rainfed lowland and upland rice production [1].

Several drought-resistant rice genotypes have already been identified in West Africa. These include *O. glaberrima* accessions from AfricaRice's gene bank, *O. sativa* varieties – such as Morobérékan, IRAT109 and B 96-3 – and AfricaRice-bred interspecific lines derived from crosses between *O. glaberrima* and *O. sativa*. Although many of these accessions are drought-resistant [9,10], resistant to rice yellow mottle virus [11], nematodes and African rice gall midge (AfRGM) [12], they also have undesirable agronomic characteristics, such as lodging, grain shattering, long growth cycle and low yield potential. Their drought resistance could be transferred through hybridization into elite breeding lines and widely grown high-yielding varieties of rice. AfricaRice scientists followed this approach over two decades with a breeding program that led to a new plant type, NERICA (NEw RICe for Africa), which is well adapted to most of the major constraints of rice and takes into account farmers' needs. NERICA varieties were first developed for the upland ecology and 18 varieties have been released from among thousands of lines produced. Subsequently, 60 other NERICA varieties adapted to lowland conditions were named by AfricaRice.

The rustic characters of CG14 – an *O. glaberrima* from the Casamance in Senegal and adapted to both upland and lowland ecosystems – that confer high weed-competitiveness and resistance to several stresses, diseases and insect pests [13] were successfully combined with the high-yielding ability of two *O. sativa* lines: WAB56-104 to develop NERICAs 1–7 and WAB181-18 to develop NERICAs 8–18. However, the performance of NERICA varieties under drought condition is still largely unknown. In this study, the performance of NERICA sister progenies derived from a cross between CG14 as donor and WAB56-104 as recurrent parent was evaluated under drought conditions in 2006 and 2007.

2. Materials and methods

2.1. Genetic materials

A population of backcross-inbred lines developed from a cross between CG14 (*O. glaberrima*) as donor and WAB56-104 (*O. sativa* subsp. *japonica*) as recurrent parent, was used. CG14 is characterized by low yield potential (due to grain shattering and lodging susceptibility) but several useful traits, including high weed-competitiveness [14] as a result of early vigor and high tiller number. WAB56-104 is an improved upland line developed by AfricaRice, with important agronomic traits such as high yield and short growth duration. The population used in the current study comprised 202 interspecific lines randomly selected from 120 BC_2F_4 families. The families are indicated in Table 1. The two parents CG14 and WAB56-104 were included in the experiments for data comparisons.

2.2. Experimental site

Two separate field experiments were conducted in an upland environment at the AfricaRice Research Station (25 m above sea level; 6°25N latitude and 2°20E longitude) at Togoudo, southern Benin. The station is located in the coastal savanna zone, with a subequatorial climate and soil that is hydromorphic in nature [15]. The south of Benin is characterized by a long dry season (December–March) during which rice cannot be grown without supplementary irrigation as the available soil moisture during this period is below the total evapotranspiration needs of the rice crop. There is also a short, one-month dry season in southern Benin, usually experienced between mid-July and mid-August [15].

Table 1
Families of 202 interspecific backcross populations of rice evaluated for drought resistance potential at AfricaRice, 2006–2007 dry seasons.

Line family	Percentage lines
3	1.53
20	1.02
24	4.08
27	1.53
34	2.55
35	2.04
36	1.02
38	1.02
39	2.04
46	2.55
48	3.57
50	1.02
53	1.53
55	4.59
61	3.06
63	5.10
73	0.51
77	7.14
83	1.53
85	0.51
86	1.02
87	0.51
89	3.06
94	4.59
96	1.02
97	2.04
100	1.02
101	0.51
104	2.55
107	0.51
110	1.02
114	3.57
115	0.51
116	3.57
117	3.06
121	4.08
126	3.06
128	2.55
138	3.06
140	1.02
143	3.57
151	6.12
Total	100.00

2.3. Experimental details

An experiment was conducted during July–October 2006, and repeated during the long dry season of December 2006–March 2007. The experiments were direct-seeded with three seeds per hill, later thinned to one healthy plant per hill soon after emergence, at a spacing of 20 cm between and within rows. Plots were 1 m × 1.5 m in both experiments and were arranged in a split-plot design replicated two times with irrigation regime as the main plot factor and rice lines as the sub-plot factor. Within each sub-plot, the lines were randomized using an alpha lattice design. Two irrigation regimes were used: fully irrigated up to maturity and imposing 21 days of drought [16] from 45 days after sowing (DAS) onwards. Plants were sprinkler-irrigated using a pipe with water from a borehole to maintain the soil above field capacity until 45 DAS when the treatments were applied according to the experimental design. The irrigation continued in fully irrigated plots until the end of the experiments. Compound fertilizer (NPK 15-15-15) was applied at the rate of 200 kg/ha two weeks after sowing followed by 40 kg/ha N as urea (46% N) 40 DAS. Both experiments were kept weed-clean by regular hand weeding and bird damage was controlled using bird scares. Plants were harvested at maturity (four months after sowing).

2.4. Measurements

Data on rainfall, evapotranspiration, temperature and relative humidity during the experimental periods were recorded by the AfricaRice weather recording section. Soil moisture content at different depths (0–20, 20–40 and 40–60 cm) was measured after 20 days of drought in the repeat experiment using the gravimetric soil analysis method. A graduated soil auger was used for sampling the soil. Collected soil was weighed (fresh weight), oven dried for 48 h at 70 °C and re-weighed (dry weight). Percent moisture content was calculated as [(fresh weight − dry weight)/fresh weight] × 100 [16]. In both experiments, data for several above-ground agronomic traits of the plants were collected on a weekly basis following the reference manual of the Standard Evaluation System (SES) for rice [17]. Four plants were randomly selected and labeled in each experimental plot for plant growth measurement. During the vegetative stage, plant height was considered as the distance from the soil surface to the tip of the last developed leaf of the main tiller. During the reproductive stage, plant height was considered as the distance from the soil surface to the tip of the tallest panicle of each plant. Leaf (canopy) temperature was recorded using a handheld infrared thermometer (Model AG-42, Telatemp Corporation, Inc., Fullerton, CA, USA) placed in the middle (the widest part) of the last fully developed leaf. Greenness of leaves (SPAD) was recorded using a SPAD meter on the last fully developed leaf before flowering and on the panicle leaf during flowering. In both cases, the SPAD meter was placed in the middle of the widest part of the leaf. Leaf canopy temperature and SPAD were recorded between 9 and 10 am and environmental temperature every 30 min. Tiller number per plant, days when panicles were exerted in 100% of the plants in a plot, number of leaves per plant, grain yield per plant as determined after drying at 50 °C during three days with moisture content adjusted to 14%, and leaf width measured in the middle of the last developed leaf of each plant were also recorded. Flowering was recorded as the number of days from seeding to panicle initiation and the rice lines evaluated were classified into three groups, namely early (up to 70 DAS), intermediate (71–90 DAS) and late (more than 91 DAS) flowering [18]. Maturity was recorded as the number of days from seeding to grain ripening (85% of grains on panicle are mature) only in 2007. The lines evaluated were also classified for maturity into three groups, early (up to 100 DAS), intermediate (101–120 DAS) and late (more than 121 DAS) [18]. Drought susceptibility index (DSI) measured as percentage reduction of each trait (X) relative to irrigation conditions was calculated by the method suggested by Reyniers et al. [19] as: drought susceptibility index for trait $X = [(X$ fully irrigated condition $- X$ drought condition)/X fully irrigated condition] × 100.

2.5. Statistical analyses

Analysis of variance (ANOVA) and Pearson correlation analysis were performed using SAS (version 9.1) statistical software [20]. The Student–Newman–Keuhl test ($P \leq 0.05$) was used to test the difference between the lines and their parents (CG14 and WAB56-104) considered as controls. The nature of genotype by environment (G × E) interactions on evaluated characters was examined using Finlay and Wilkinson [21] and Eberhart and Russell's [22] models.

3. Results

During the imposed drought period, some rain was observed in both years: seven rains totaling 78.7 mm in August–September 2006 and a single 17.3 mm rainfall on February 9, 2007. Values for evapotranspiration and temperature were lower in the first experiment than in the repeat one; but the opposite was observed for relative humidity (Fig. 1). After 20 days of drought, soil moisture content at different depths of 0–20, 20–40 and 40–60 cm was higher in fully irrigated plots than in plots subjected to drought in the repeat experiment. Also, the deeper the soil was collected for analysis, the higher the moisture content under both conditions (Fig. 2). The results for the plant traits measured (Table 2) indicated that mean values for canopy temperature were similar under both conditions (means of 29.5 °C and 29.9 °C, respectively, under fully irrigated and drought conditions), though in 2006, significant differences were observed between the two temperatures

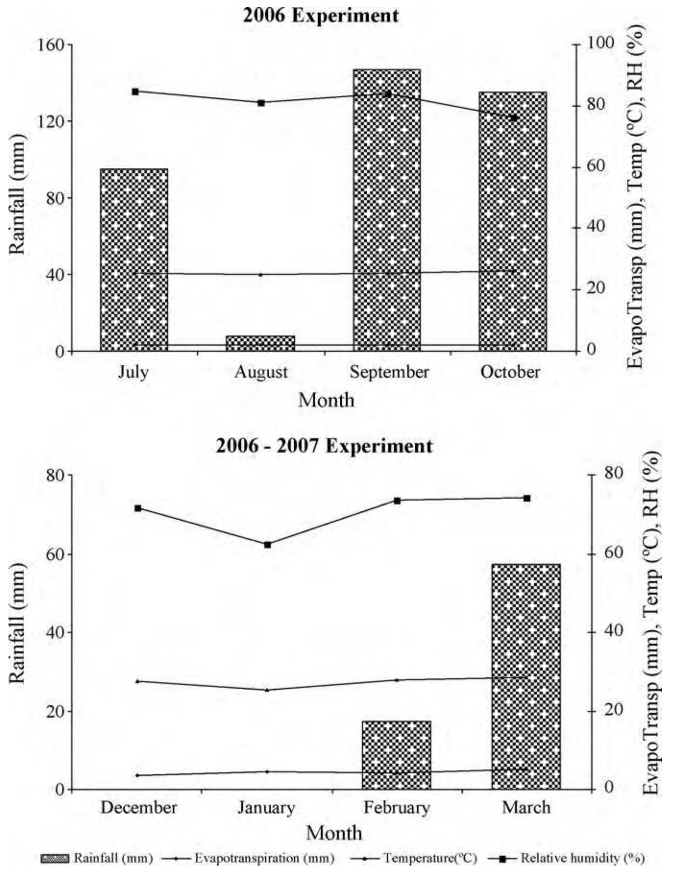

Fig. 1. Weather conditions during two consecutive experiments conducted at AfricaRice Research Station, Togoudo, Benin in 2006 and 2007.

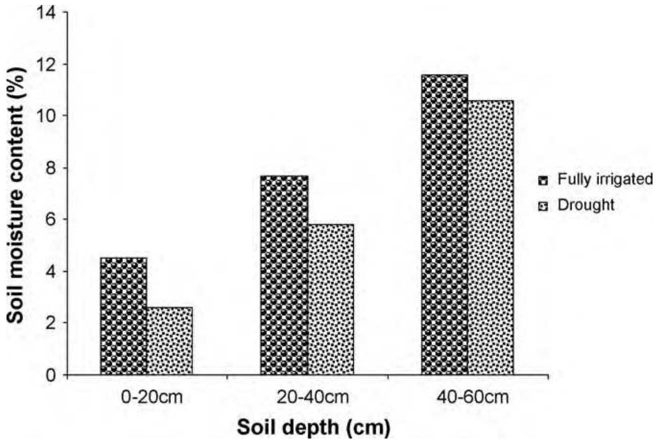

Fig. 2. Moisture of soil collected at different depths after 20 days of drought from fully irrigated and drought-stressed plots, AfricaRice, 2006–2007, Cotonou, Benin.

Table 2
Effect of 21 days of drought on 202 rice backcross-inbred lines' morphological traits: AfricaRice, 2006–2007 dry seasons.

	2006			2006–2007			Mean for the two experiments		Mean for parents for the 2 experiments		Percent increase/reduction for all lines and parents
	Fully rrigated	Drought	CV	Fully rrigated	Drought	CV	Fully rrigated	Drought	CG14	WAB56 -104	
Canopy temperature (°C)	30.1b	30.5a	11.2	29.0a	29.4a	5.5	29.5a	29.9a	29.9	29.4	−1.3
Days to 100% flowering	69.9b	73.1a	6.5	80.1b	83.7a	6.4	75.0b	78.5a	75.0	81.0	−4.6
Maturity (days after sowing)	–	–	–	105.5b	109.7a	4.5	105.5b	109.7a	101.0	103.5	−4.0
SPAD	41.0b	42.6a	9.3	37.4b	38.1a	13.6	39.2b	40.6a	32.7	40.8	−2.9
Tiller number/plant	2.2a	2.1b	11.0	6.3a	5.2b	25.2	5.5a	4.6b	8.0	3.5	16.9
Plant height (cm)	94.0a	77.1b	9.1	79.7a	69.7b	16.3	82.5a	71.2b	76.6	76.4	13.7
Number of leaves/plant	4.4a	4.1b	11.0	4.7a	4.3b	9.8	4.5a	4.2b	4.5	4.3	6.7
Leaf width/plant (cm)	1.8a	1.6b	21.7	1.0a	1.0b	14.4	1.8a	1.6b	1.6	1.6	14.1
Grain yield (kg/ha)	1520.3a	1140.6b	20.4	1063.6a	756.0b	26.4	1290.8a	946.8b	2048.5	1290.4	26.7

SPAD = leaf greenness. Each value represents mean for 202 lines. For each trait, values for irrigated and drought conditions with different letters are significantly different ($P \leq 0.05$) according to Student–Newman–Keuhl test. Percentage increase/reduction was calculated considering values for fully irrigated condition as 100%. "–" = data not evaluated. For traits not evaluated in a given year, mean value was considered as mean for the second year. CV = coefficient of variation.

(30.1 °C and 30.5 °C, respectively). Canopy temperature was 29.9 °C and 29.4 °C, respectively, for the parents CG14 and WAB56-104 (Table 2). The difference between the mean environment temperature and canopy temperature was 1.5 °C during the first experiment and 2.4 °C during the repeat one. A delay was observed in flowering and maturity of rice plants under drought as compared to the fully irrigated condition, considering the overall mean values for the trait (Table 2). Flowering value for the parent WAB56-104 was higher than the overall means in both irrigation conditions. But the maturity value was lower for the two parents as compared to the overall values in both irrigation conditions (Table 2). Grown under drought, plant leaves were greener than under fully irrigated condition. SPAD value for WAB56-104 leaves was inferior to that of CG14 and to the overall mean values in both irrigation conditions. Percentage increase of values for measured traits under drought ranged between 1.3% and 4.6% as compared to fully irrigated condition. Drought negatively affected the number of tillers, plant height, number and width of leaves, and grain yield. The traits most affected by drought were grain yield, tiller number, leaf width and plant height (26.7%, 16.9%, 14.1% and 13.7% reduction, respectively) (Table 2). In the first experiment, the coefficient of variation for the traits ranged between 6.5 and 21.7 and between 4.5 and 26.4 in the repeat experiment.

None of the lines evaluated flowered before the start of the drought period in either experiment and under both irrigation conditions. Flowering started 56 and 58.5 DAS, respectively, on irrigated and drought-subjected plots, i.e. during the drought period. The majority (63.5%) of the rice lines evaluated on fully irrigated plots had intermediate flowering with a mean value of 78.1 DAS. Evaluation showed that 32.5% and 3.9% of the lines had, respectively, early (mean of 67.3 DAS) and late flowering (mean of 94.3 DAS). The parents WAB54-106 and CG14 had intermediate (mean of 75.8 DAS) and early (mean of 70.3 DAS) flowering, respectively. The difference between minimal and maximal values for the different groups of flowering ranged between 4 and 19 DAS (Table 3a). Most of the rice lines (78.1%) showed intermediate maturity (mean of 107.5 DAS), while 20.9% of the lines showed early maturity (mean 97.1 DAS). Only 1.0% of the lines showed late maturity (121.5 DAS). The parents CG14 and WAB54-156 matured on almost the same day. The difference between minimal and maximal values for the different groups of maturity ranged between 1 and 57 (Table 3a).

On plots subjected to drought, almost all the rice lines (98.0%) had early flowering between 58.5 DAS and 96.5 DAS. Only 2.0% of the lines had intermediate flowering between 101.5 DAS and 106.0 DAS. No line showed late flowering. The parent CG14 and WAB54-106 flowered, respectively, at 83.0 and 86.0 DAS. Most lines (86.6%) had intermediate maturity while just 1.5% had early maturity. The parents CG14 and WAB56-104 matured at 103.0 and 107.0 DAS, respectively (Table 3b).

Of the traits evaluated, only tiller number and leaf width showed significant G × E interactions. These interactions were highly significant. No significant difference was observed between genotypes for canopy temperature, maturity, number of leaves and plant height. The difference between genotypes for other traits is highly significant ($P < 0.001$). Highly significant differences were observed between environments for all traits measured with the exception of the number of leaves (Table 4).

The correlation between leaf greenness (SPAD) and all other traits measured was negative ($P \leq 0.01$) under both fully irrigated and drought conditions (Table 5). Similar observations were made between grain yield and other traits, with the exception of leaf width (0.09 ns and 0.05 ns, respectively, under fully irrigated and drought conditions). Highest correlation coefficients were observed between canopy temperature and tiller number, plant height, grain yield and leaf width under fully irrigated condition ($r = 0.71^{**}$ and 0.93^{**}, 0.66 ns, 0.72^{**}, respectively); between days to

Table 3
Number of days from sowing to flowering and maturity of 202 interspecific lines and of two parent lines: CG14 and WAB56-104 evaluated under fully irrigated and drought conditions during two dry seasons of 2006 and 2007. AfricaRice, Cotonou, Benin.

	Flowering					Maturity				
	Percent lines	Minimum	Maximum	Difference	Mean	Percent lines	Minimum	Maximum	Difference	Mean
(a) Fully irrigated plots										
Early	32.5	56	70	14	67.3	20.9	93	99	6	97.1
Intermediate	63.5	71	90	19	78.1	78.1	100	157	57	107.5
Late	3.9	92	97	5	94.3	1.0	121	122	1	121.5
CG14	–	67	74	7	70.3	–	98	100	2	99.0
WAB54-106	–	74	78	4	75.8	–	96	104	8	100.0
(b) Plots subjected to drought										
Early	98.0	58.5	96.5	38	77.9	1.5	95	99	4	97.3
Intermediate	2.0	101.5	106.0	4.5	102.9	86.6	100	120	20	108.1
Late	0.0	–	–	–	–	11.9	121	125	4	122.3
CG14	–	80.0	86.0	6	83.0	–	100	106	3	103.0
WAB54-106	–	84.5	87.5	3	86.0	–	104	110	6	107.0

Each value represents mean from the two experiments for flowering. For maturity, each value represents mean from the second year experiment only.

100% flowering and number of leaves ($r = 0.55^{**}$ and 0.51^{**}, respectively, under fully irrigated and drought conditions); between tiller number and plant height and number of leaves (r ranging between 0.70^{**} and 0.76^{**}); and between plant height and number of leaves ($r = 0.95^{**}$ and 0.93^{**}, respectively, under fully irrigated and drought conditions). The relations among other traits were weak. Leaf width was very weakly associated with all other traits assessed (highest value of $r = 0.10$ ns) with the exception of the canopy temperature (0.72 ns and −0.14 ns, respectively, under fully irrigated and drought conditions (Table 5)).

For the traits: days to 100% flowering, tiller number, plant height, number of leaves and grain yield, the correlations under fully irrigated and drought conditions were strong ($r \geq 0.50$), highly significant ($P \leq 0.01$) and positive ($r = 0.85^{**}$, 0.81^{**}, 0.96^{**}, 0.96^{**} and 0.52^{**}, respectively) (Table 6). For canopy temperature, leaf greenness and leaf width, the correlation was weak ($r = -0.30^{**}$, 0.42^{**} and -0.03 ns, respectively). The correlation between leaf width under fully irrigated condition and all other traits under drought was very weak (maximum value of $r = 0.13$) and non-significant except for canopy temperature. Leaf greenness under fully irrigated conditions was significantly correlated with all other traits measured under drought except with leaf width ($r = 0.01$ ns). Grain yield under fully irrigated conditions was weakly and negatively correlated with all other traits measured under drought except with leaf greenness ($r = 0.20^{**}$). Interestingly, a relatively strong correlation was found between grain yield under fully irri-

Table 4
Analysis of variance performed on traits of 202 inbred lines evaluated under fully irrigated and drought conditions at AfricaRice, Cotonou, Benin, 2006–2007.

Source	DF	Type III SS	Mean square	*F*-value	*P* > *F*
Canopy temperature					
Genotype (G)	201	315.8749379	1.5715171	0.58	1.0000
Environment (E)	1	56.4091854	56.4091854	20.65	<.0001
G × E	200	304.6798680	1.5233993	0.56	1.0000
Tiller number					
Genotype (G)	201	4666.986409	23.218838	5.39	<.0001
Environment (E)	1	462.156277	462.156277	107.30	<.0001
G × E	201	1634.681626	8.132744	1.89	<.0001
Yield					
Genotype (G)	201	116,689,607.4	580,545.3	1.62	<.0001
Environment (E)	1	23,505,080.4	23,505,080.4	65.73	<.0001
G × E	201	51,991,864.3	258,666.0	0.72	0.9951
Flowering					
Genotype (G)	201	51,892.14652	258.16988	3.05	<.0001
Environment (E)	1	2480.75912	2480.75912	29.31	<.0001
G × E	200	4221.71753	21.10859	0.25	1.0000
SPAD					
Genotype (G)	201	8318.639131	41.386264	1.60	<.0001
Environment (E)	1	791.217371	791.217371	30.57	<.0001
G × E	201	2791.134193	13.886240	0.54	1.0000
Leaf width					
Genotype (G)	200	143.8014514	0.7190073	99.50	0.0090
Environment (E)	1	6.7546880	6.7546880	934.70	0.0011
G × E	200	150.7650777	0.7576135	104.84	0.0095
Maturity					
Genotype (G)	200	16,515.40417	82.57702	8.93	0.1059
Environment (E)	1	1792.17191	1792.17191	193.75	0.0051
G × E	200	2948.50000	14.89141	1.61	0.4616
Number of leaves					
Genotype (G)	201	54.52644030	0.27127582	0.05	1.0000
Environment (E)	1	12.83235757	12.83235757	2.44	0.1193
G × E	201	25.45087472	0.12662127	0.02	1.0000
Plant height					
Genotype (G)	201	346,317.2150	1722.9712	0.07	1.0000
Environment (E)	1	170,937.9807	170,937.9807	7.27	0.0073
G × E	201	97,573.0894	485.4383	0.02	1.0000

Table 5
Linear coefficients of correlation between traits evaluated in a collection of 202 backcross-inbred lines of rice during two consecutive years under fully irrigated and drought conditions: AfricaRice, 2006–2007.

Traits	Canopy temperature (°C)	Days to 100% flowering	Tiller number/plant	SPAD	Plant height (cm)	Number of leaves/plant	Grain yield (kg/ha)
Days to 100% flowering	0.20** 0.27**						
Tiller number/plant	0.71** 0.34**	0.52** 0.41**					
SPAD	−0.24** −0.14**	−0.32** −0.37**	−0.39** −0.44**				
Plant height (cm)	0.93** 0.11**	0.44** 0.40**	0.72** 0.76**	−0.43** −0.49**			
Number of leaves/plant	0.15** 0.34**	0.55** 0.51**	0.73** 0.70**	−0.46** −0.53**	0.95** 0.93**		
Grain yield (kg/ha)	−0.66** −0.12**	−0.19** −0.10 ns	−0.17** −0.11*	−0.26** −0.26**	−0.31** −0.34**	−0.31** −0.33**	
Leaf width/plant (cm)	0.72 ns −0.14 ns	0.07 ns 0.03 ns	−0.01 ns −0.00 ns	−0.08 ns −0.05 ns	0.06 ns −0.02 ns	0.10 ns −0.03 ns	0.09 ns 0.05 ns

SPAD = leaf greenness. For each trait, values on top and at the bottom represent, respectively, the coefficient of correlation under fully irrigated and drought-stress conditions. ns = non-significant.

[*] Significant at 5%.

[**] Significant at 1%.

gated and drought conditions (r = 0.52**). Canopy temperature under fully irrigated conditions was highly ($P \leq 0.01$) correlated with tiller number (r = 0.94**), number of leaves (r = 0.84**), and grain yield (r = −0.88**). Similar observations were made for days to 100% flowering under fully irrigated and drought conditions; between tiller number and canopy temperature, plant height and number of leaves (r = 0.81**, 0.75** and 0.80**, respectively) (Table 6).

Lines of the family 94 were the most represented among the 26 top yielding and stable lines selected from the population of lines evaluated (Table 7). In the 2006 experiment (first column of data for each trait in Table 7), the DSI varied with the measured traits and also with rice lines. Negative values of DSI for a given trait indicate for that trait a higher value under drought as compared to fully irrigated condition. In 2006 (Table 7), canopy temperature of 84.6% of the 26 selected rice lines was higher under drought than under fully irrigated conditions. The days to 100% flowering were delayed for 84.6% of rice lines (including the two parents, CG14 and WAB56-104) under drought as compared to fully irrigated condition. A contrary observation was made for lines 55-4-1 and 94-4-3A7; while drought did not affect flowering of lines 151-3-8 and 61-1-1. About 42.3% of selected lines produced fewer tillers under drought than under fully irrigated condition. For the majority of the selected lines (65.4% of total number), plant leaves were greener under drought as compared to under fully irrigated condition. Only two (117-2-6 and 94-5-10) of the selected lines had shorter plants under fully irrigated condition as compared to drought (DSI = −13.9% and −0.94%, respectively). Similar observations were made for leaf width and grain yield for which only 11.5% and 3.8%, respectively, of the lines performed better under drought than under fully irrigated condition. Grain yield was reduced by more than 50% for both parents and for line 77-2-4. More leaves under fully irrigated conditions than for drought were recorded for 65.4% of the selected rice lines (Table 7).

In the repeat experiment, (second column of data for each trait in Table 7), canopy temperature was higher under drought as compared to irrigated conditions for 80.8% of selected rice lines. Flowering was delayed for 73.1% of rice lines (including the two parents) under drought, whereas lines 0003-1-02, 104-3-5, 114-1-2A3, 61-1-1, 77-5-3 and 94-1-5 flowered with delay under fully irrigated conditions as compared to drought. The drought did not affect flowering of line 46-2-2. Most of the rice lines (65.4%) produced more tillers under fully irrigated as compared to under drought conditions. Plant leaves for 53.8% of lines were greener under drought than under fully irrigated conditions. For 76.9% of lines, plants were taller under fully irrigated than under drought condition. For all the rice lines, no effect of drought was observed on the number of leaves. Values for leaf width and grain yield were higher under fully

Table 6
Linear coefficients of correlation between traits of 202 backcross-inbred lines of rice evaluated under fully irrigated and drought conditions in two consecutive years: AfricaRice, 2006–2007.

Traits measured	Under fully irrigated condition							
	Canopy temperature (°C)	Days to 100% flowering	Tiller number/plant	SPAD	Plant height (cm)	Number of leaves/plant	Grain yield (kg/ha)	Leaf width/plant (cm)
Under drought condition								
Canopy temperature (°C)	−0.30**	0.51**	0.81**	−0.46**	0.97**	0.98**	−0.34**	−0.18*
Days to 100% flowering	0.24**	0.85**	0.49**	−0.31**	0.43**	0.52**	−0.18**	0.04 ns
Tiller number/plant	0.94**	0.48**	0.81**	−0.42**	0.73**	0.77**	−0.17**	−0.02 ns
SPAD	−0.09**	−0.39**	−0.47**	0.42**	−0.55**	−0.53**	0.20**	−0.02 ns
Plant height (cm)	0.11**	0.50**	0.75**	−0.46**	0.96**	0.95**	−0.34**	0.03 ns
Number of leaves/plant	0.84**	0.55**	0.80**	−0.45**	0.94**	0.96**	−0.30**	0.10 ns
Grain yield (kg/ha)	−0.88**	−0.67 ns	−0.18**	0.23**	−0.36**	−0.33**	0.52**	−0.01 ns
Leaf width/plant (cm)	0.13**	−0.05 ns	−012 ns	0.01 ns	−0.09 ns	−0.03 ns	−0.04 ns	−0.03 ns

SPAD = leaf greenness; ns = non-significant.

[*] Significant at 5%.

[**] Significant at 1%.

Table 7

Drought susceptibility index of 26 top yielding and stable lines selected from a population of 202 backcross-inbred lines of rice screened under fully irrigated and 21 days of imposed drought: AfricaRice, 2006.

Lines	Line family	Canopy temperature (°C)		Days to 100% flowering		Tiller number/plant		SPAD		Plant height (cm)		Number of leaves/plant		Leaf width/plant (cm)		Yield (kg/ha)		Days to maturity
0003-1-02	3	−4.02	−3.53	−5.69	26.83	−3.21	−58.82	0.08	−9.91	29.41	−12.16	5.91	20.00	−114.6	−40.00	29.47	−12.77	0.00
003-2-2	3	−2.86	−2.30	−10.00	−3.95	7.28	−18.52	−0.91	−13.21	19.03	11.21	9.38	0.00	11.76	0.00	43.10	−0.88	−8.08
104-3-5	104	−13.57	−2.33	−7.56	5.00	−2.59	32.26	−7.59	1.83	14.13	−0.99	−10.66	0.00	14.74	0.00	7.49	40.51	−4.76
107-2	107	−12.24	−2.35	−8.05	−6.98	30.18	−15.79	33.88	5.74	12.57	7.38	−3.58	0.00	6.82	16.67	22.41	11.97	−4.50
114-1-2A3	114	2.02	0.00	−6.82	3.75	−6.99	0.00	−11.86	12.39	19.57	10.68	10.38	0.00	25.95	-9.09	11.54	54.95	1.92
116-2-2	116	−9.48	−1.15	−9.04	−7.69	20.52	−12.00	0.82	6.31	15.28	15.52	16.88	0.00	15.38	10.00	46.17	−36.36	−2.59
116-2-4	116	−3.97	−4.71	−9.03	−15.85	−1.27	21.74	−10.56	−1.77	15.99	13.25	3.54	20.00	19.86	7.69	−0.13	46.34	−13.46
117-2-6	117	−4.76	−1.15	−8.18	−6.02	−26.85	35.21	−5.94	1.55	−13.89	11.42	−7.45	0.00	−24.14	25.00	8.75	47.33	−6.48
138-31-2	138	−0.67	−3.45	−0.6	−12.5	28.71	33.33	1.76	−3.45	23.51	18.28	17.40	0.00	74.81	38.46	21.15	42.11	−7.96
151-3-8	151	−3.70	−3.49	0.00	−5.95	2.68	15.00	−7.61	−2.48	5.33	1.35	−13.85	0.00	0.00	0.00	30.05	15.85	−4.46
46-2-2	46	−1.61	0.00	−3.68	0.00	−17.07	−47.06	−5.22	−8.85	9.75	−7.07	2.19	20.00	8.03	−8.33	43.99	16.08	−0.99
55-4-1	55	−3.66	0.00	9.03	−7.25	11.07	40.91	2.30	−0.87	24.07	18.89	30.22	20.00	39.78	28.57	18.45	47.44	−8.33
61-1-1	61	−1.20	−2.30	0.00	3.90	−11.38	30.77	−1.93	−2.61	28.89	12.88	8.36	0.00	13.28	16.67	36.69	−4.31	0.00
77-1-4A5	77	−3.77	−4.71	−7.32	−6.76	30.50	−6.67	−1.05	−22.22	20.87	−3.42	−10.91	40.00	11.30	11.11	11.90	50.00	0.97
77-2-4	77	−2.46	−2.33	−5.65	−9.59	18.66	32.00	−2.85	−11.71	22.06	14.20	15.12	20.00	13.60	25.00	54.44	2.17	−7.07
77-5-3	77	3.27	0.00	−5.69	1.25	9.73	12.00	−6.48	6.45	15.86	4.31	18.57	20.00	23.53	9.09	36.05	8.13	0.00
77-5-4	77	−3.00	−1.18	−19.57	−10.13	−13.48	18.75	−8.29	−0.88	10.35	32.53	−10.09	20.00	11.85	22.22	33.08	41.46	−4.81
94-1-1	94	−0.40	0.00	−1.30	−2.35	12.64	8.00	0.08	−9.62	21.69	−6.94	5.95	0.00	16.67	−10.00	26.22	50.29	−5.88
94-1-10	94	5.56	−1.15	−10.61	−8.97	16.28	17.39	1.11	4.20	8.84	20.74	−8.54	0.00	3.03	30.77	6.44	40.65	−3.88
94-1-5	94	−5.67	−2.33	−8.96	3.49	15.57	−50.00	0.05	−11.65	11.29	−14.66	2.33	0.00	9.30	23.08	26.17	−5.84	0.93
94-2-3	94	5.87	−1.14	−15.57	−8.82	7.94	−50.00	2.67	−5.93	18.47	11.34	30.88	20.00	16.23	−8.33	42.44	6.12	−8.74
94-4-3A7	94	−3.60	−3.41	1.41	−10.84	−9.85	30.43	−11.52	1.67	6.33	20.06	1.62	20.00	22.73	27.27	19.34	35.08	-2.83
94-5-10	94	−4.24	−2.35	−5.71	−2.63	13.07	12.50	−7.10	5.22	−0.94	2.93	−4.29	0.00	16.99	0.00	21.18	33.52	4.63
94-5-3	94	−3.70	−1.14	−9.03	−3.8	−9.78	45.16	−7.68	1.69	9.67	35.9	4.62	0.00	−37.31	38.46	18.27	37.43	1.89
CG14	–	−7.81	−4.71	−15.04	−12.16	−12.87	−29.79	−19.66	3.26	27.43	28.49	−11.58	20.00	0.00	21.43	50.73	19.82	−4.04
WAB56-104	–	−1.25	−2.35	−17.69	−10.26	19.92	62.07	−2.40	4.10	17.89	24.63	9.20	20.00	15.56	38.46	55.59	48.09	−7.00
% lines with nil or positive DSI[a]		15.4 (84.6)[b]	19.2 (80.8)[b]	15.4 (84.6)	26.9 (73.1)	57.7 (42.3)	65.4 (34.6)	34.6 (65.4)	46.2 (53.8)	92.3 (7.7)	76.9 (23.1)	65.4 (34.6)	100 (0.0)	88.5 (11.5)	80.8 (19.2)	96.2 (3.8)	80.8 (19.2)	30.8 (69.2)

For each trait, the first column (left) indicates values for the first experiment and the second column (right), values for the repeat experiment. Maturity was evaluated only in the repeat experiment.

[a] Drought susceptibility index.

[b] Values in parentheses represent the percentage of rice lines with negative DSI.

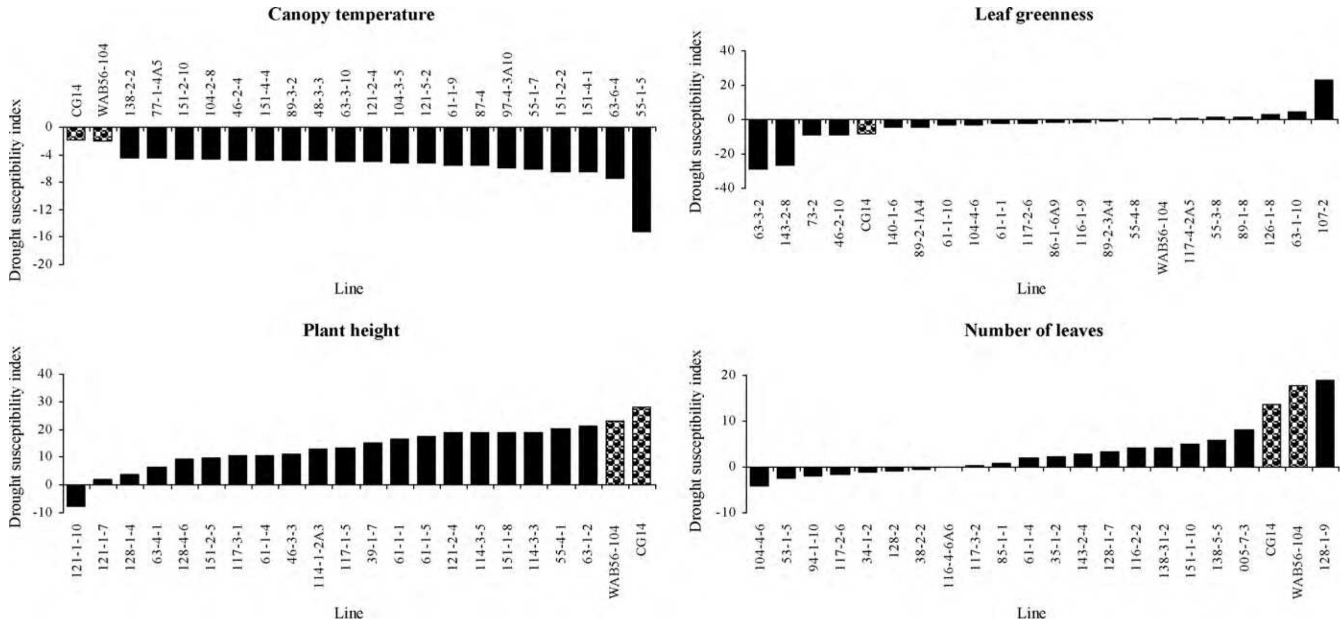

Fig. 3. Drought susceptibility index of four traits showing highest correlation coefficients with grain yield of 202 inbred lines screened under fully irrigated and 21 days of imposed drought conditions: AfricaRice, 2006–2007. Lines WAB56-104 and CG14 are parental lines.

irrigated than under drought condition for 80.8% of selected lines (for both traits). But the number of days to maturity was delayed by drought for 69.2% of selected lines. The maturity of lines 0003-1-02, 61-1-1 and 77-5-3 was not affected by drought (Table 7).

Tables 5 and 6 indicated that strongest correlations with grain yield were observed for such traits as canopy temperature, leaf greenness, plant height and number of leaves. These traits were selected and the 20 lines that performed the best for each of them were used to plot Fig. 3. Lines with best performance for the selected traits were considered as those with highest mean values for SPAD, plant height and number of leaves [23] and lowest value for canopy temperature [24]. Fig. 3 indicated that all the selected lines had canopy temperature higher under drought as compared to fully irrigated condition, with DSI values ranging between −15.27 (line 55-1-5) and −4.47 (line 138-2-2). The same observation was made for the parents WAB56-104 and CG14 with DSI values of −2.07 and −1.78, respectively. Negative DSI values for leaf greenness were observed for 63.6% of the selected lines, while the parent line CG14 had a DSI value of −8.44. The second parent WAB56-104 had greener leaves under fully irrigated than under drought conditions with a DSI value of 0.83. Of the lines with tallest plants, plants of line 121-1-10 were taller under drought than under fully irrigated conditions. The remaining lines gave taller plants under fully irrigated condition than under drought. The DSI of the two parents were higher than those of all other selected lines. Plants of most of the lines (54.5%), including the two parents, produced more leaves under fully irrigated condition than under drought. Drought did not have any influence on leaf production of line 116-4-6A6; while line 104-4-6 leaf production was the most affected by drought.

4. Discussion

This study showed differences in agronomic performance among rice lines screened under fully irrigated and drought conditions. It confirmed some results of previous research on the effects of drought on rice production, especially when drought coincides with the reproductive stage of development of rice plants [25].

The weather conditions observed during the course of the experiments were appropriate for rice production [26]. The differences observed between trait values under fully irrigated and drought conditions could be due to differences in soil moisture content observed under the two conditions. Rain was more frequent and intense, and the relative humidity higher during the first experiment than the repeat one, indicating that the drought conditions foreseen for the experiments (no rain/artificial irrigation during the imposed 21-day drought period) were more observed during the repeat experiment than the first. This could be one of the reasons for the better results obtained from drought-subjected plots in the first experiment as compared to the repeat one for flowering, SPAD, plant height and grain yield. Moormann and Von Breemen [27] reported that rice plants require high humidity for good development and production with their needs varying with the duration of the life cycle, the genotype and climate influences on plant transpiration. Temperature regime also influences growth duration and pattern of rice plants. Under high temperatures, depletion of the internal water status of plants is enhanced through high transpiration.

A delay was observed in the time to flowering and to maturity of the rice lines under drought as compared to fully irrigated condition. Arraudeau [26] reported that, as for the other stages of the reproductive phase of rice, flowering is affected by abiotic constraints such as water deficit and extreme temperature regimes. Under these constraints, dry matter production is reduced, panicle exsertion is delayed, and sometimes male sterility is induced, which results in uneven and delayed flowering [28]. Novero et al. [29] reported that the delay in time to flowering depends on intensity, time, and period of drought. Furthermore, Wopereis et al. [30] observed longer flowering delay when drought occurred during early tillering rather than the mid-tillering stage. Pantuwan et al. [2] made similar observations and concluded that under prolonged drought, flowering time is an important determinant of rice grain yield. This indicates large genotype by environment (G × E) interactions which have implications for plant breeding [25]. It is therefore important to consider the variations in drought patterns, flowering time and potential yield in the development of drought-resistant rice varieties.

The maturation stage, which is regarded as the period between anthesis and harvest, is also delayed as a result of delayed flowering or when drought appears after flowering. Significant variation exists among genotypes in response to drought stress during this period. When drought occurs at maturity, its effect on total grain yield is less severe as compared to the vegetative and reproduction stages [31]. In this study, the differences in the time to 100% flowering and to maturity for the various rice lines evaluated, the majority of which had intermediate flowering and maturity, indicated that the rice lines evaluated responded differently to the experimental conditions, possibly as a result of the differences in their developmental cycles [23] and ability to tolerate drought [32]. Under fully irrigated condition, first flowers appeared 56 DAS for early flowering lines and 92 DAS for late flowering ones. Even inside each group of flowering, differences were observed among lines. For example, 19 days separated the start and end of flowering for the group of lines with intermediate flowering. Similar observations were made for maturity.

Plant height, tiller number, number of leaves, leaf width and grain yield were negatively affected by drought in this study. These results corroborate previous observations of Efisue [16] who concluded that rice drought resistance ability is a complex trait that should be defined relative to several plant characters. Blum et al. [33] earlier reported significant differences for plant phenology and production traits under irrigated and drought conditions, and for indicators of plant drought stress among a subset of double haploid lines. Drought occurring at the vegetative stage causes leaf drying, leaf rolling, and reduction in leaf area index, plant height, tiller number and dry matter production, which may have direct effects on grain yield. This might be a result of reduced growth of plant root systems (not measured in this study) under drought. Plant roots play a key role in water and nutrient uptake for the development of plants and are responsible for resistance to many rice plant stresses, in particular drought and mineral deficiency [34]; they are significantly shorter and thinner under drought than under irrigated condition [35]. The depth, thickness and hydraulic resistance of the root system are highly implicated in the drought avoidance mechanism of rice plants [36]. Yield is affected when drought appears at both the vegetative and reproduction stages of rice development. In both experiments and at both irrigation conditions in the current study, the reproduction phase of some of the lines evaluated coincided with the drought period and appeared for some lines after that period. Ekanayake et al. [37] reported that when drought occurs during panicle developmental stages, panicle emergence from the flag leaf sheath fails and anthesis inhibits. Thus the spikelets left inside the leaf sheath are not fertilized, resulting in significant yield reduction [38]. Zinolabedin et al. [39] observed significantly higher grain yield reduction when drought was applied at flowering stage than during vegetative or grain-filling stages (50%, 21% and 21% on average as compared to the fully irrigated control, respectively). This may explain the significant difference (26.7% reduction in average) observed in this study between grain yields under fully irrigated and drought conditions and also the low percentages of rice lines with better performance under drought than under fully irrigated conditions. Dikshit et al. [40] reported significant correlation between maturity prolongation and yield reduction due to drought. In the current study, the parents WAB56-104 and CG14 and line 77-2-4 had DSI values of 55.59, 50.73 and 54.44, respectively, under drought condition in 2006. These yield reductions are considered critical (being higher than 50%) for the expression of drought resistance mechanism in rice [2]. However, the contrary observation made in 2007 (only 19.2% rice lines performing better under drought against 80.8% under fully irrigated conditions) confirmed the observations of Blum [41] according to which rice yield under drought, which is usually considered as a tool to evaluate drought susceptibility, may not always be reliable. The better performance observed for some rice lines (3.8% and 19.2% in 2006 and 2007, respectively) under drought than under fully irrigated condition corroborate those of Hounkpatin [23] who observed 25% of the screened material with higher grain yield under drought than under fully irrigated conditions. This study observed such performance mostly for lines with tall plants. The observed differences in the grain yield of the evaluated materials probably indicate genetic variability among them; and the variation in the results over the two years can be attributed to the degree of drought intensity and variation in the environment. The study identified lines 0003-1-02, 003-2-2, 116-2-2, 94-1-5, CG14 and 61-1-1 as genotypes with higher grain yield under drought condition than under fully irrigated condition, shown by their negative DSI in 2007. Contrary observations were made for the second parent WAB56-104. But these observations were not similar to those obtained in 2006, confirming the importance of genotype by environment interactions stated above for rice plant breeding [25]. The DSI calculated in this study helped evaluate the effect of drought effect on the lines relative to the fully irrigated condition. It indicated that the different lines tested had different abilities to support drought.

This study identified canopy temperature, leaf greenness, plant height and number of leaves as the traits most correlated with grain yield. The findings on canopy temperature corroborate those of Ingram et al. [42] who observed a significant correlation between canopy temperature and grain yield under drought. Garrity and O'Toole [43] further observed highly significant differences in canopy temperature among rice genotypes as is the case for this study. This trait was proposed as a good indicator of plant stress level for its association with plant water status under drought [24]. Turner et al. [32] reported negative correlation between canopy temperature under drought and midday leaf water potential and turgor pressure. As *ca.* 590 calories are lost by the plants following transpiration of every gram of water, the transpiration process tends to cool the plant canopy, while the water losses due to transpiration increase with the incidence of leaf surface area [26]. Maurya and O'Toole [44] reported canopy temperature as a good drought avoidance indicator, based on the principle of this cooling effect of transpiration, as high transpiration rate occurs in the canopy under lower temperatures. Genotypic variation exists within rice for canopy temperature and this variation is related to leaf water potential in rice [45]. Rice genotypes with high internal water potential maintenance would therefore yield well under drought condition. Fukai et al. [46] advised the use of early flowering rice genotypes when drought develops during the reproductive stage of plants (terminal drought) as such genotypes often escape from the drought and give higher yield than late-maturing genotypes. Genotypes which, additionally to early flowering potential, have the ability to maintain high amounts of leaf water under drought are advantageous to producing higher yield [2].

The present study indicated higher values of SPAD for stressed plants as compared to those for plants regularly irrigated following incidence of drought. These results corroborate those of Hounkpatin [23] but contradict those of Zinolabedin et al. [39] who reported that under drought, reduced uptake of water and nutrients by the plant root system normally induces reduction of chlorophyll concentration in plant leaves and therefore increases the yellowing of the leaves. The results for the leaf width and tiller number indicate that under fully irrigated condition rice plants develop wider leaves and more tillers as a result of better water and soil nutrient use by the plants as compared to under drought conditions. However, a very weak and non-significant correlation was observed between the two traits in this study. Hounkpatin [23] found that rice plant height has no physiological, but a morphological effect, on grain yield and that positive correlation between plant height and yield was probably due to other factors.

The significant correlation observed between traits under fully irrigated and drought conditions indicated that the performance of a line in a fully irrigated condition could be used to predict its performance under drought condition. So, in conditions where planting material is not limiting, screening for drought using off-season trials could be advised for rapid advancement. The selected genotypes from such trials could be evaluated for yield performance in the wet season. This is consistent with the finding of Fukai et al. [47].

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