



Agro-morphological characterization of a population of introgression lines derived from crosses between IR 64 (*Oryza sativa indica*) and TOG 5681 (*Oryza glaberrima*) for drought tolerance

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ABSTRACT

The study evaluated effects of drought on some agro-morphological traits of 60 rice genotypes comprising 54 introgression lines with their parents, IR 64 (*Oryza sativa*) and TOG 5681 (*Oryza glaberrima*) and four NERICA-L varieties developed from the same parents for comparison. The genotypes were subjected either to full irrigation from sowing to maturity (control) or to 21-day drought applied by stopping irrigation from the 45th day after sowing (DAS) onward (drought) in the dry seasons of 2006 and 2007–2008. Plant height, spikelet fertility, grain yield and leaf area at harvesting were consistently reduced by drought in both seasons. Values of leaf temperature, leaf rolling, leaf tip drying, leaf blast, days from seeding to flowering and maturity were higher under drought. The results on SPAD and number of tillers were not consistent. Significant relationship ($P < 0.05$) was observed between all traits evaluated and grain yield under drought. Introgression lines, SEN-L13-2, MPL-15-3, SEN-L10-1, SEN-L26-3 and SEN-L21-2 showed significantly higher yield than the highest yield NERICA-L variety (all of them had higher yield than the parents). Among them, SEN-L13-2 showed the lowest yield loss by drought and MPL-15-3 had high yield potential and considerably low yield loss by drought.

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1. Introduction

Rice (*Oryza* spp.) has the largest cultivation area of 150 million hectares among field crops [54]. Being a key food crop for more than the half of the humanity [1], rice contributes for more than 20% of calorie consumption, represents 27% of energetic supply of inhabitants of developing countries and 24% of food proteins [2]. Paddy rice production in Sub-Saharan Africa (SSA) has increased and was estimated at 14.6 million tones in 2006 [3]. However, rice consumption has also increased at a higher rate than the production in SSA (total consumption of 17 million tones in 2009; USD Foreign Agriculture Service) and been outstripping the production since mid-1970s. The estimated rice import of Africa in 2008 accounted for 10 million tones on a milled rice basis, which required about 3.6

billion US dollars [4]. Thus, increase of rice production at a higher rate than before is a crucial issue to contribute to food security of SSA. The loss of rice production due to biotic (blast, *Rice yellow mottle virus*, African rice gall midge, etc.) and abiotic (water deficit, submergence, salinity, extreme temperatures and deficiencies of P and Zn, etc.) constraints was estimated at more than 200 million tons [5]. To improve rice production in SSA, therefore, it is crucial to mitigate yield reduction by the biotic and abiotic constraints. This situation complicates the food security equation in many SSA countries. One of the main challenges of Africa Rice Center (AfricaRice) to contribute to poverty reduction in SSA, has been the development of effective countermeasures overcoming those major constraints that undermine rice production.

Among abiotic constraints undermining rice production, drought, defined as the occurrence of a rainfall shortage relative to the expected (average) amount for a target region [6], is the most important source of climate-related risk in rainfed areas [7]. It is a major challenge for all agricultural crops, particularly for rice because of its semi-aquatic origins and the diversity of its ecosystems and growing conditions [8]. Makara et al. [5] observed 12–46% yield loss due to drought in lowland rice production. In 2002, the catastrophic drought that occurred in India affected 55% of the

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country's area and 300 million people leading to production decline by 20% from the trend values [7]. Similarly, the 2004 drought in Thailand affected more than eight million people in almost all provinces. The consequences of such severe drought are starvation and impoverishment of affected populations with dramatic socio-economic impacts [9].

One of the approaches to mitigate drought problems is to expand irrigated areas. However, that is not affordable for rainfed upland rice farmers. Moreover, the increased scarcity of water, projected risks related to climate change [10] and varying degrees and duration of drought during the crop growing cycle [11] render scope limited for further expansion of irrigation in rainfed lowland rice production areas. Serraj and Atlin [12] have reported that both agronomic and genetic options need to be developed to manage rice in water deficit environments. The authors advised the identification of rice varieties and breeding lines with high levels of drought tolerance for use as donors in breeding and gene discovery as one of the important challenges for rice research. Serraj et al. [6] have further indicated that rice cultivars that combine improved drought tolerance with high yield potential under favorable conditions are the most promising and deliverable technology for increasing productivity in water deficit areas. Direct empirical selection for grain yield under managed drought was more successful recently in rice [13,14] than secondary trait-based and marker-assisted selection for increasing drought resistance in rice [15,16]. Rice producers have empirically been selecting those genotypes that survived drought events for centuries, and there could be a wealth of genetic variation for response to drought among traditional cultivars [17]. There are also a few examples, however, of improved cultivars that combine acceptable yield potential and drought tolerance. The challenges that the empirical selection needs to face are the large-scale and reliable protocols' application for managed-stress screening in rice-breeding programs and the resolution of genotype by environment ($G \times E$) interactions in the various drought-prone target environments [18]. Pinheiro [19] has advised the inclusion of tolerant parents in crossings and Fischer et al. [20] have suggested the use of managed environments and multi-location testing to facilitate a progress in breeding for drought tolerance in rice. Rice researchers are currently seeking QTLs that are stable across environments and that co-segregate with improved yield. Lafitte et al. [21] have reported co-segregation between QTLs for rice yield and its component under drought and for traits such as leaf rolling and leaf tip drying.

In the logic of identifying improved varieties that combine higher yield potential and drought tolerance, the current study was initiated to screen, under field conditions, introgression lines or a set of overlapping chromosome segment substitution lines (CSSLs) developed by Institut de la Recherche pour le Développement (IRD) and available at AfricaRice. The approach of developing such lines involved a systematic introduction of foreign alleles from an *Oryza glaberrima* (African cultivated rice species) line (TOG 5681) into one elite, highly productive *Oryza sativa* indica type variety (IR64). The IRD geneticists have utilized natural genetic diversity to develop whole-genome libraries of introgression lines as a permanent genetic resource for both breeding and genomics-based research. Plant geneticists have long recognized the value of introgression lines. The introgression lines between *O. sativa* and *O. glaberrima*, *Oryza rufipogon* (wild rice species indigenous in Asian) have demonstrated the utility of targeted introgressions as a basis for gene identification and plant improvement. *O. glaberrima* and *O. rufipogon* are known to be rich resources of genes for tolerance to biotic and abiotic stresses, and transgressive behavior of progeny derived from interspecific crosses has been demonstrated in several studies.

In this study, the performance of some agronomic and morphological traits of introgression lines, which are also interspecific

lines developed by crossing rice genotypes IR 64 and TOG 5681 at the IRD, was evaluated under fully irrigated and drought conditions to identify tolerant genotypes among the introgression lines. Additionally, some lowland NERICA (New Rice for Africa) varieties developed from the same parental combination (IR 46 and TOG 5681) by AfricaRice were included in the entry as checks together with the parents.

2. Materials and methods

2.1. The experimental site

The study was carried out on the experimental farm of the AfricaRice research station (06°25.415N, 02°19.684E and 21 m altitude, 12 km north-west from Cotonou) at its temporary headquarters at Togoudo in Southern Benin. The station is located in the coastal savannah zone, with a subequatorial climate and hydromorphic soil [22].

2.2. Genetic materials

Sixty rice genotypes including two parents (IR 64 and TOG 5681), 54 introgression lines of BC_3F_6 obtained from the cross of the parents, and four NERICA-L varieties adapted to lowland ecology (NERICA-L 19, NERICA-L 20, NERICA-L 41 and NERICA-L 42) were used. IR 64 was the female parent belonging to *O. sativa*, sub-species indica and TOG 5681 the male parent belonging to *O. glaberrima*. TOG 5681 possesses a resistant gene to *Rice yellow mottle virus*. The four NERICA-L varieties used in the study as checks were also developed from the same parents, i.e. NERICA-L 19 and NERICA-L 20 from TOG 5681/3 \times IR 64 and NERICA-L 41 and NERICA-L 42 from TOG 5681/4 \times IR 64.

2.3. Field management

An experiment was conducted between September and December 2006 and repeated between November 2007 and February 2008. The two periods coincided with dry seasons [22]. In both experiments, a split-plot design was used with three replicates in which the blocks were arranged in an Alpha lattice design. The main factor was the irrigation regime at two levels: fully irrigated from sowing to maturity and drought by stopping irrigation for 21 days from the 45th day after sowing (DAS) onward. Growth durations of the parents IR 64 and TOG 5681 were similar and large differences would not be anticipated in the growth durations among their progenies (personal communication with Matus). Therefore, drought treatment was imposed to all materials on the same day. For drought subjected plants, irrigation was recommenced after the imposed drought period and continued until maturity. The secondary factor comprised the 60 genotypes indicated above. Each replicate was composed of two blocks (one subjected to drought and the other fully irrigated—control). Each bloc comprised six incomplete blocs with 10 elementary plots each; therefore 60 elementary plots were generated as a total. Elementary plots were 1 m \times 1 m. Hills were arranged in square planting with a 20 cm distance.

In the first experiment, rice seeds were directly sown (three seeds per hill) on September 14th, 2006. Twenty-eight DAS, the number of plants per hill was thinned into one with the healthiest plant remaining. For the repeated experiment, seed were sown on a nursery on June 30th, 2007 and 21 days old seedlings were transplanted at a rate of one per hill. Plots were fertilized with the basal dressing of 40–40–40 kg ha⁻¹ of N–P–K (15–15–15) and urea (46% nitrogen) was top-dressed at a rate of 30 kg N ha⁻¹ at 20 and 30 DAS in the first experiment and 20 and 30 days after transplanting in the repeated experiment. In both experiments, Deltaméthrine

(40 ml was diluted by 15 l of water) and Dithiocarbamate (80 g was dissolved with 15 l of water) were applied, as insecticide and fungicide, respectively. To minimize the attack of stem borers (*Sesamia calamistis*) on the plants, each experimental plot was surrounded by maize (*Zea mays* L.) used as a trap crop for stem borers. In both experiments, the fields were kept weed-free by regular hand weeding and bird damage was controlled using bird scares during maturity.

2.4. Measurements

Experimental data were recorded on the following traits: plant height, number of tillers, leaf rolling, leaf tip drying, leaf temperature, leaf greenness (SPAD reading), days from sowing to the start, 50% and 100% of flowering and to maturity, dry weight of fertile spikelets per plant, spikelet fertility, grain yield, harvest index (HI), leaf length and width at harvesting (this was to estimate leaf area), and leaf blast damage. In each plot, four plants were selected at random from the central area excluding border plants and labeled; these plants were subjected to the measurements of plant height, number of tillers, leaf temperature, leaf greenness, dry weight of fertile spikelets per plant, spikelet fertility, HI and leaf length and width at harvesting. Leaf temperature was recorded at 70 DAS under non-windy conditions and clear skies during 09:00–10:00 AM using a hand-held infrared thermometer (Sato Keiryoki MFG, Co., Ltd.) placed to the middle (the widest part) of the last fully developed leaf of the main stem. Leaf greenness was recorded on the fully developed leaf of the main stem using a SPAD meter (SPAD-502, Konica Minolta). SPAD readings were recorded at 54, 74 and 89 DAS and harvest. The number of tillers per plant was determined at 54, 74 and 89 DAS and harvest. Plant height was considered as the distance from soil surface to the tip of the last developed leaf of the main tiller during the vegetative stage or to the tip of the tallest panicle of each plant after heading. Plant height was determined at 54, 74 and 89 DAS and harvest. Dates of the start, 50% and 100% of flowering were recorded for each plot. Dates of maturity (85% of grains were mature) were also recorded. Days from sowing to the start, 50% and 100% of flowering and maturity were used as phenology data. Plants were harvested at maturity, which was about 4 months after sowing. At harvesting, above ground parts of the four plants, which were used for the non-destructive measurements of some traits, were sampled from each plot. Grains were manually threshed and separated into fertile and unfertile spikelets according to the Standard Evaluation System (SES) for Rice [23]. All grains (fertile and unfertile) and the remaining stems and leaves were dried in an oven at 50 °C for 72 h. Dried grains and the other parts were separately weighed. Harvest index was calculated as the ratio of fertile spikelets to the total above ground parts on a dry weight basis. For each plant, the numbers of both fertile and unfertile spikelets were counted and spikelet fertility (percentage ratio of fertile spikelet number to total spikelet number) was calculated. For the determination of grain yield, all remaining plants (other than four plants used for the measurements of other traits) in the plot were harvested as bulk and threshed manually. After the removal of unfertile spikelets, fertile spikelets were dried in an oven at 50 °C for 72 h and weighed. Dry weights fertile spikelets of the four plants and remaining plants were both used to determine the grain yield of the plot. Grain yield (kg ha^{-1}) was expressed as paddy weight with moisture content adjusted to 14%. The modified scale of Raemaekers [24] was used to evaluate the flowering and maturity types of the genotypes. Early, intermediate and late flowering were considered as flowering occurring before 70 DAS, between 71 and 90 DAS, and after 90 DAS, respectively. Meanwhile, early, intermediate and late maturities were considered as maturity occurring before 100 DAS, between 101 and 120 DAS, and after 120 DAS, respectively. Leaf length was recorded at harvest as the

length of the longest leaf of each of the four plants used for the measurements of some other traits and leaf width was measured at harvest in the middle of the same leaf used for the measurement of leaf length. Leaf length and width and the number of leaves were used to estimate leaf area per plant at harvest according to the formula: $0.74 \times \text{leaf length} \times \text{leaf width} \times \text{number of leaves per plant}$ [25]. Leaf blast damage was evaluated only in the first experiment at 59 and 76 DAS using a scale of 0–9 as described in SES ([23]: 0 = no lesions observed; 1 = small pinpoint brown specks or larger brown specks without sporulating centre, mostly on lower leaves; 2 = small roundish to slightly elongated necrotic grey spots, about 1–2 mm in diameter with a distinct brown margin, mostly on lower leaves; 3 = lesion type as for 2, but a substantial number of lesions on the upper leaves; 4 = typical susceptible blast lesions 3 mm or larger, affecting less than 4% of the leaf area; 5 = typical blast lesions affecting 4–10% of the leaf area; 6 = typical blast lesions affecting 11–25% of the leaf area; 7 = typical blast lesions affecting 26–50% of the leaf area; 8 = typical blast lesions affecting 51–75% of the leaf area and many leaves dead; 9 = more than 75% leaf area affected). Leaf rolling and leaf tip drying were evaluated at 51, 59 and 94 DAS using a scale of 0–9 as described in SES [23]. For leaf rolling, 0 = leaves healthy; 1 = leaves starting to fold (shallow V-shape); 3 = leaves folding (deep V-shape); 5 = leaves fully cupped (U-shape); 7 = leaf margins touching (O-shape); 9 = leaves tightly rolled. For leaf tip drying, 0 = no symptoms; 1 = slight tip drying; 3 = tip drying extended up to 1/4 length in most leaves; 5 = 1/4–1/2 of all leaves fully dried; 7 = more than 2/3 of all leaves fully dried; 9 = all plants apparently dead. Drought susceptibility index (DSI) was calculated by the method suggested by Reyniers et al. [26] as:

$$\text{DSI} = \frac{(X \text{ in fully irrigated condition} - X \text{ in drought condition})}{X \text{ in fully irrigated condition}} \times 100,$$

where X is a value of one of the traits evaluated.

2.5. Data analyses

Analysis of variance (ANOVA) and correlation analyses were performed using SAS (version 9.1) statistical software (SAS Institute, 1999). Least significant difference (LSD) test ($P=0.05$) was used to test the differences between means, where significant differences were detected by ANOVA. The Gupta test was used to separate genotypes that performed best in terms of grain yield under drought. Percentage data were transformed into arcsine prior to the statistical analysis of data and back-transformed data are presented in the tables.

3. Results

Weather data during the first and the repeat experiments are indicated in Fig. 1. Average temperature was same ($P<0.05$) between the two experiments. However, plants were grown under higher ($P<0.05$) evaporation demanding environments (higher evapotranspiration) and lower relative humidity in the repeated experiment than the first one. Average relative humidity and rainfall were higher ($P<0.05$) in the first experiment than the in repeat (Fig. 1). During the drought treatment of 21 days, in the two experiments, only little rainfall was recorded, i.e. mean of 1.2 and 3.3 mm day^{-1} in the first and repeated experiments, respectively (Fig. 2a and b). Evapotranspiration and temperature were higher in the first experiment than in the repeat experiment. The contrary observation was made for the relative humidity (Fig. 2a and b).

The results of the first experiment in the 2006 dry season are summarized in Table 1a. At each evaluation date, SPAD values for fully irrigated plants and for plants subjected to drought were

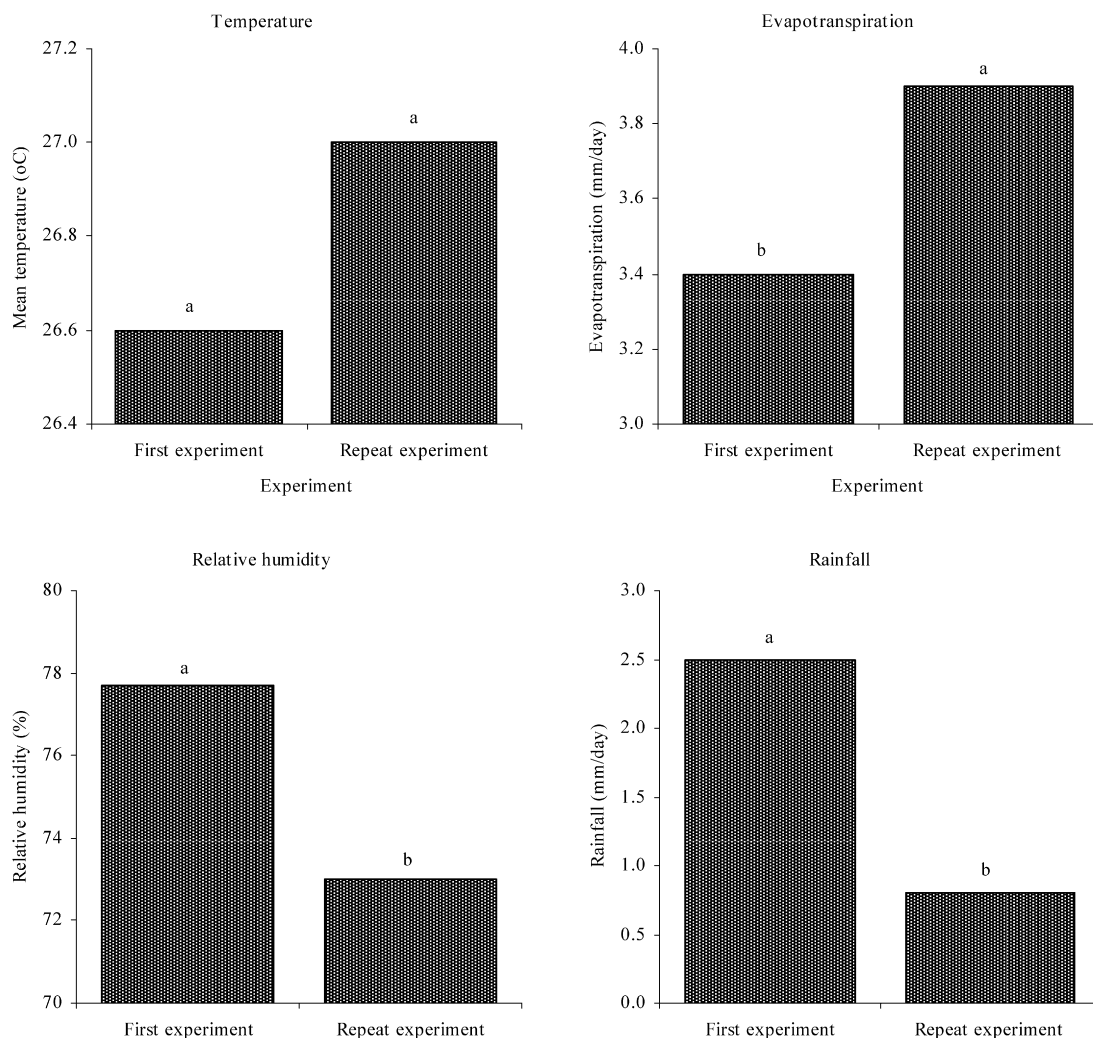


Fig. 1. Meteorological data during the first (2006) and repeated (2007–2008).

similar ($P < 0.05$) for the two parents (Table 1a). For the introgression lines and for NERICA-L varieties, however, SPAD values were significantly higher under drought than under fully irrigated condition with the exception of the SPAD values at 54 DAS for NERICA-L varieties. For all genotype groups, fully irrigated plants were significantly taller than plants subjected to drought. At 54 and 74 DAS, however, plants of IR 64 had similar height under both irrigation conditions. The number of tillers was not significantly affected by drought in the NERICA-L varieties and the two parents but was significantly higher under fully irrigated condition than under drought at 54 and 89 DAS and harvest in the introgression lines. No leaf rolling or leaf tip drying was observed on plants in fully irrigated plots for all genotype groups, while all the genotype groups had leaf rolled and leaf tip dried under drought. Severity of leaf rolling increased with the time on all genotype groups and plant leaves touched (O-shape) or tightly rolled at 94 DAS. Similarly, severity of leaf tip drying increased with the time on all genotype groups with slight tip drying or tip drying extended up to 1/4 length or slightly more in most leaves at 94 DAS. Flowering (start, 50% and 100%) was retarded for all genotype groups under drought as compared to under fully irrigated condition. Under both irrigation conditions, TOG 5681 was in the early flowering category, while the other genotype groups were in the intermediate or late flowering. Maturity was retarded for all genotype groups by drought. Earliest maturity was recorded in TOG 5681 under both irrigation

conditions. Under fully irrigated condition, IR 64 had early maturity, and intermediate maturity under drought. For the NERICA-L varieties and introgression lines, plants had intermediate flowering in both irrigation conditions. Leaf temperature was higher under drought than under fully irrigation condition for the NERICA-L varieties and introgression lines but was similar between the two irrigation regimes for the two parents. Dry weight of fertile spikelets per plant and spikelet fertility was reduced by drought for the NERICA-L varieties and introgression lines but were similar between both irrigation conditions for the two parents, with the exception of TOG 5681 in spikelets fertility. Harvest index and grain yield were lower under drought compared to fully irrigated condition for all genotype groups. Grain yield of TOG 5681 was very low (437 kg ha^{-1} and 56 kg ha^{-1} under fully irrigated and drought conditions, respectively) but yield ranged between 1522 and 3577 kg ha^{-1} for the other genotype groups and IR 64. Leaf area at harvest was significantly higher under fully irrigated condition than under drought for all genotype groups. Leaf blast symptoms were observed on all genotypes at both evaluation dates and under both irrigation regimes. The disease was severer under drought than under fully irrigated condition in the introgression lines but the disease severity was similar under both irrigation conditions for the other genotypes (Table 1a).

In the repeated experiment in the dry season of 2007–2008, SPAD value was not significantly different between drought and

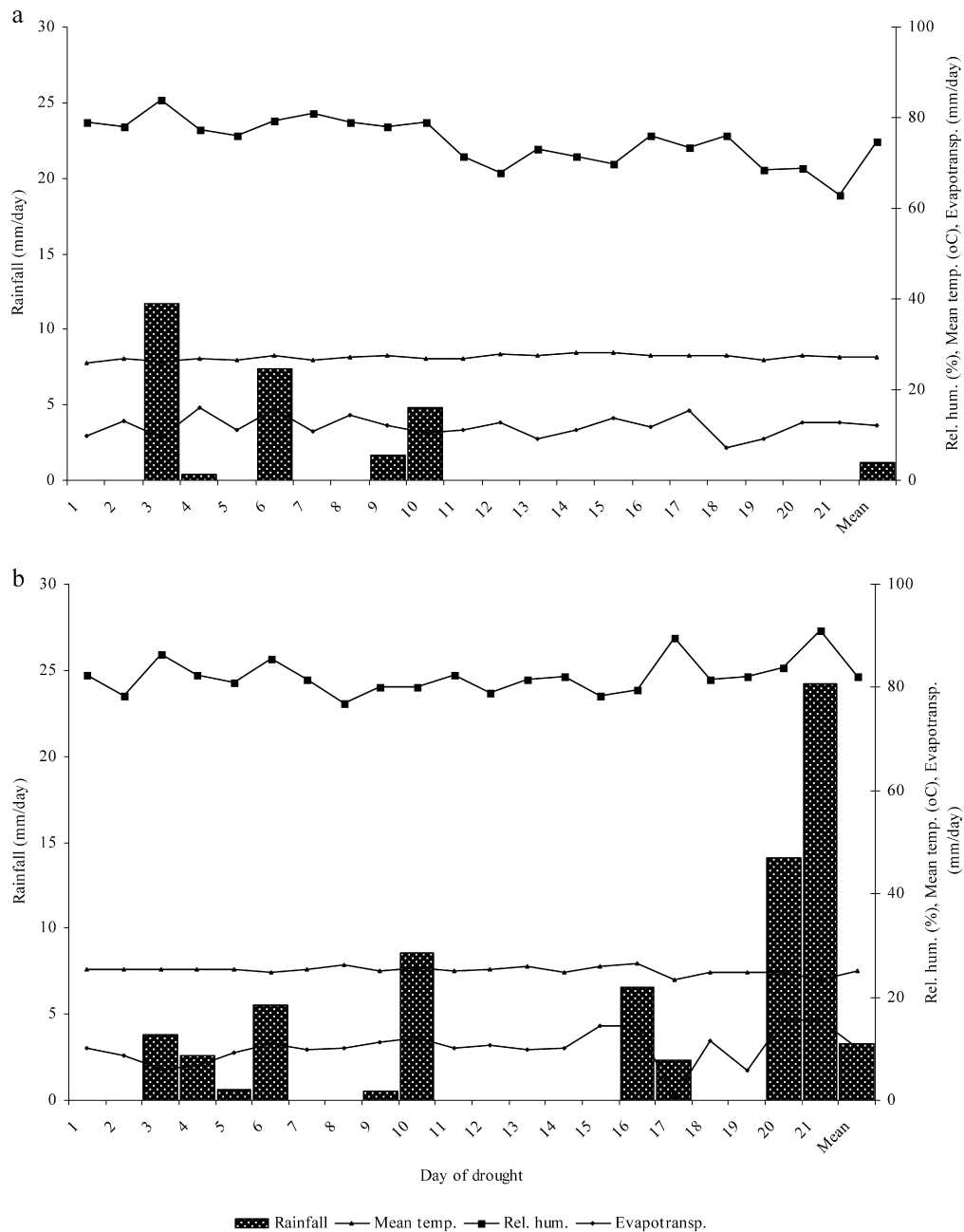


Fig. 2. Meteorological data during the 21 drought period of the first (2006) and repeated (2007–2008) experiments.

fully irrigated conditions in most cases, except TOG 5681 at 89 DAS and harvesting (Table 1b). Plants were shorter under drought than under fully irrigated condition for all genotype groups with the exception of TOG 5681 which had similar height under both irrigation regimes at 54 DAS. The number of tillers was similar across irrigation regimes and at each evaluation date for all genotype groups. As in 2006, for all genotype groups, no plant showed leaf rolling or leaf tip drying in fully irrigated condition in 2007–2008 (Table 1b). Plant leaves had deep U-shape in the introgression lines and NERICA-L varieties at 51 DAS and O-shape or tightly rolled in the other cases. In both genotype groups (introgression lines and NERICA-L varieties) under drought, leaf tip of some plants dried slightly while for some plants drying extended up to 1/4 length in most leaves or 1/4–1/2 of all leaves fully dried. At 94 DAS, IR 64 depicted the severest drying, i.e. more than 2/3 of all leaves fully dried under drought. The number of days from sowing to the

start, 50% and 100% of flowering were retarded by drought for all genotype groups. A similar observation was made in the days from sowing to maturity for the NERICA-L varieties, introgression lines and TOG 5681. Leaf temperature was lower under fully irrigated than under drought for the introgression lines and TOG 5681 and similar under both irrigation conditions for NERICA-L varieties and IR 64. Dry weight of fertile spikelets per plant, spikelet fertility, harvest index, grain yield and leaf area at harvest were significantly reduced by drought in all genotype groups (Table 1b).

Fig. 3 depicts *P* values calculated in ANOVA for differences between the two irrigation regimes and DSI for all traits. In the introgression lines, all traits were affected ($P < 0.05$) by drought (there was a significant difference in each of all traits), whereas number of tillers and leaf temperature were not influenced ($P < 0.05$) by drought in the NERICA-L varieties. In IR 64, only plant height, flowering (all types) and grain yield were affected by

Table 1
Effect of drought on agronomic and morphological traits in the 60 rice genotypes at Africa Rice Center, Togoudo, Benin, in the 2006 and 2007–2008 dry seasons.

Genotype group	Introgression lines		NERICA-L varieties		IR 64		TOG 5681	
	Fully irrig.	Drought	Fully irrig.	Drought	Fully irrig.	Drought	Fully irrig.	Drought
<i>(a) Experiment in the 2006 dry season</i>								
SPAD at 54 DAS	39.9b	40.7a	39.7a	41.1a	40.3a	41.7a	39.3a	40.0a
SPAD at 74 DAS	33.8b	36.4a	33.7b	37.3a	35.2a	35.4a	36.0a	35.1a
SPAD at 89 DAS	34.0b	36.4a	34.1b	37.6a	34.1a	34.7a	33.8a	35.1a
SPAD at harvest	29.8b	40.4a	31.2b	40.9a	26.3a	38.3a	34.2a	38.0a
Plant height at 54 DAS (cm)	58.7a	53.9b	66.6a	57.5b	65.0a	53.7a	90.3a	52.0b
Plant height at 74 DAS (cm)	67.5a	56.7b	76.9a	60.2b	70.7a	56.3a	90.7a	54.3b
Plant height at 89 DAS (cm)	72.3a	59.4b	85.7a	63.3b	77.7a	57.3b	90.9a	55.7b
Plant height at harvest (cm)	74.4a	65.1b	89.8a	75.9b	79.7a	63.3b	82.0a	60.4b
Number of tillers at 54 DAS	18.7a	16.9b	16.5a	14.9a	18.3a	16.3a	18.6a	16.3a
Number of tillers at 74 DAS	27.3a	20.3a	22.8a	22.5a	26.7a	20.0a	20.3a	18.0a
Number of tillers at 89 DAS	28.1a	20.9b	23.3a	23.2a	29.7a	20.1a	20.7a	19.3a
Number of tillers at harvest	30.4a	27.3b	24.1a	23.3a	35.7a	21.0a	21.0a	19.3a
Leaf rolling at 51 DAS	0.0b	7.5a	0.0b	7.8a	0.0b	7.0a	0.0b	6.3a
Leaf rolling at 59 DAS	0.0b	8.5a	0.0b	8.7a	0.0b	9.0a	0.0b	7.0a
Leaf rolling at 94 DAS	0.0b	8.9a	0.0b	8.8a	0.0b	9.0a	0.0b	8.3a
Leaf tip drying at 51 DAS	0.0b	2.5a	0.0b	2.7a	0.0b	3.0a	0.0a	1.3a
Leaf tip drying at 59 DAS	0.0b	3.1a	0.0b	3.0a	0.0b	3.0a	0.0b	2.3a
Leaf tip drying at 94 DAS	0.0b	3.7a	0.0b	3.3a	0.0b	3.7a	0.0b	3.0a
Start of flowering (days)	72.4b	84.3a	73.1b	86.8a	71.0b	81.3a	55.7b	57.0a
50% flowering (days)	75.6b	86.9a	79.8b	90.8a	72.7b	85.7a	61.7b	62.7a
100% flowering 100% (days)	79.6b	89.6a	84.5b	93.0a	76.0b	88.3a	60.0b	67.7a
Maturity (days)	100.8b	110.1a	102.9b	112.7a	95.3b	110.0a	77.0b	77.7a
Leaf temperature (°C)	32.4b	33.6a	32.5b	34.3a	32.7a	32.3a	30.7a	32.7a
Dry weight of fertile spikelets per plant (g)	12.1a	8.6b	14.6a	7.9b	12.4a	8.7a	0.2a	0.2a
Spikelets fertility (%)	88.3a	82.2b	91.0a	89.3b	91.0a	89.3a	88.4a	81.2b
Harvest index	0.2a	0.1b	0.5a	0.3b	0.2a	0.1b	0.4a	0.1b
Grain yield (kg ha ⁻¹)	2.897a	2.083b	3.438a	1.522b	3.577a	2.176b	437a	56b
Leaf area at harvest (cm ²)	4.677a	4.161b	4.851a	4.168b	4.570a	4.315b	3.787a	2.659b
Leaf blast damage at 59 DAS	1.4b	1.7a	2.5a	3.0a	1.7a	1.0a	5.0a	5.0a
Leaf blast damage at 76 DAS	2.0b	2.7a	2.8a	3.5a	2.3a	2.3a	4.3a	5.7a
<i>(b) Experiment in the 2007–2008 dry season</i>								
SPAD at 54 DAS	42.1a	42.5a	42.2a	42.6a	42.2a	41.3a	39.9a	41.5a
SPAD at 74 DAS	34.3a	34.6a	36.1a	35.8a	37.1a	30.7a	36.4a	35.4a
SPAD at 89 DAS	35.3a	35.9a	34.9a	35.5a	37.8a	29.8a	31.5b	37.6a
SPAD at harvest	27.9a	28.1a	28.5a	29.4a	29.0a	21.4a	26.0b	30.7a
Plant height at 54 DAS (cm)	48.7a	46.3b	53.8a	50.0b	46.0a	44.8b	81.9a	80.9a
Plant height at 74 DAS (cm)	67.4a	59.1b	80.2a	68.9b	68.9a	56.6b	119.0a	108.9b
Plant height at 89 DAS (cm)	82.7a	65.3b	97.4a	72.9b	84.2a	61.7b	132.4a	111.8b
Plant height at harvest (cm)	83.3a	65.9b	99.7a	76.4b	78.9a	61.8b	133.4a	120.9b
Number of tillers at 54 DAS	22.3a	22.1a	18.6a	16.6a	22.4a	22.9a	18.8a	10.7a
Number of tillers at 74 DAS	20.8a	19.41a	15.9a	15.6a	20.5a	20.3a	10.4a	10.3a
Number of tillers at 89 DAS	14.4a	13.92a	13.1a	12.4a	13.9a	12.3a	8.8a	8.3a
Number of tillers at harvest	26.5a	26.0a	29.3a	26.7a	24.2a	24.6a	40.3a	41.4a
Leaf rolling at 51 DAS	0.0b	4.3a	0.0b	4.7a	0.0b	4.3a	0.0b	7.0a
Leaf rolling at 59 DAS	0.0b	8.9a	0.0b	9.0a	0.0b	9.0a	0.0b	9.0a
Leaf rolling at 94 DAS	0.0b	9.0a	0.0b	9.0a	0.0b	9.0a	0.0b	9.0a
Leaf tip drying at 51 DAS	0.0b	0.9a	0.0b	0.9a	0.0b	1.0a	0.0b	1.0a
Leaf tip drying at 59 DAS	0.0b	1.1a	0.0b	1.0a	0.0b	1.0a	0.0b	2.3a
Leaf tip drying at 94 DAS	0.0b	5.4a	0.0b	5.0a	0.0b	7.0a	0.0b	5.0a
Start of flowering (days)	82.1b	85.1a	82.0b	86.4a	79.3b	81.3a	88.3b	95.3a
50% flowering (days)	84.9b	88.4a	86.3b	91.2a	83.0b	84.7a	92.0b	97.7a
100% flowering 100% (days)	88.6b	93.6a	90.4b	113.a	86.0b	89.0a	95.3b	162.3a
Maturity (days)	111.6b	121.3a	116.5b	129.4a	109.3a	111.0a	111.7b	129.0a
Leaf temperature (°C)	29.0b	30.0a	28.9a	29.9a	28.3a	30.2a	28.1b	29.8a
Dry weight of fertile spikelets per plant (g)	10.7a	2.7b	16.3a	4.6b	8.4a	2.3b	8.0a	2.4b
Spikelets fertility (%)	71.9a	35.9b	89.9a	57.2b	49.0a	42.2b	89.2a	72.0b
Harvest index	0.5a	0.1b	0.6a	0.2b	0.4a	0.1b	0.3a	0.1b
Grain yield (kg ha ⁻¹)	2701a	563b	4324a	914b	2493a	710b	2392a	816b
Leaf area at harvest (cm ²)	4677a	4161b	4851a	4168b	4570a	3648b	3787a	2659b

Means followed by different letters are significantly different ($P < 0.05$) between the two irrigation regimes for a given genotype group. Four NERICA-L varieties, 54 introgression lines and two parents (IR 64 and TOG 5681) were used in the experiments. DAS = days after sowing. Fully irrig. = fully irrigated.

drought, whereas in TOG 5681, only number of tillers was affected by drought. For all genotype groups, DSI was negative for SPAD, leaf temperature, the start, 50% and 100% of flowering, maturity, and blast damage and positive for the other traits. Leaf rolling and leaf tip burning were not recorded under fully irrigated condition for all genotype groups and therefore their DSI not calculated (Fig. 3). Pearson's correlation coefficient was calculated between grain yield and all the other traits under drought using all data

collected in all genotypes. All traits showed significant correlations to grain yield under drought (Fig. 4). A negative correlation was observed between grain yield and leaf tip drying, flowering (all types), maturity and leaf blast damage under drought (Fig. 4).

In all genotype groups, significant interactive $G \times E$ effects ($P < 0.05$) were observed in the traits of phenology (start, 50% and 100% of flowering and maturity), except maturity of NERICA-L varieties (Table 2). Similar observation was made for leaf rolling and leaf

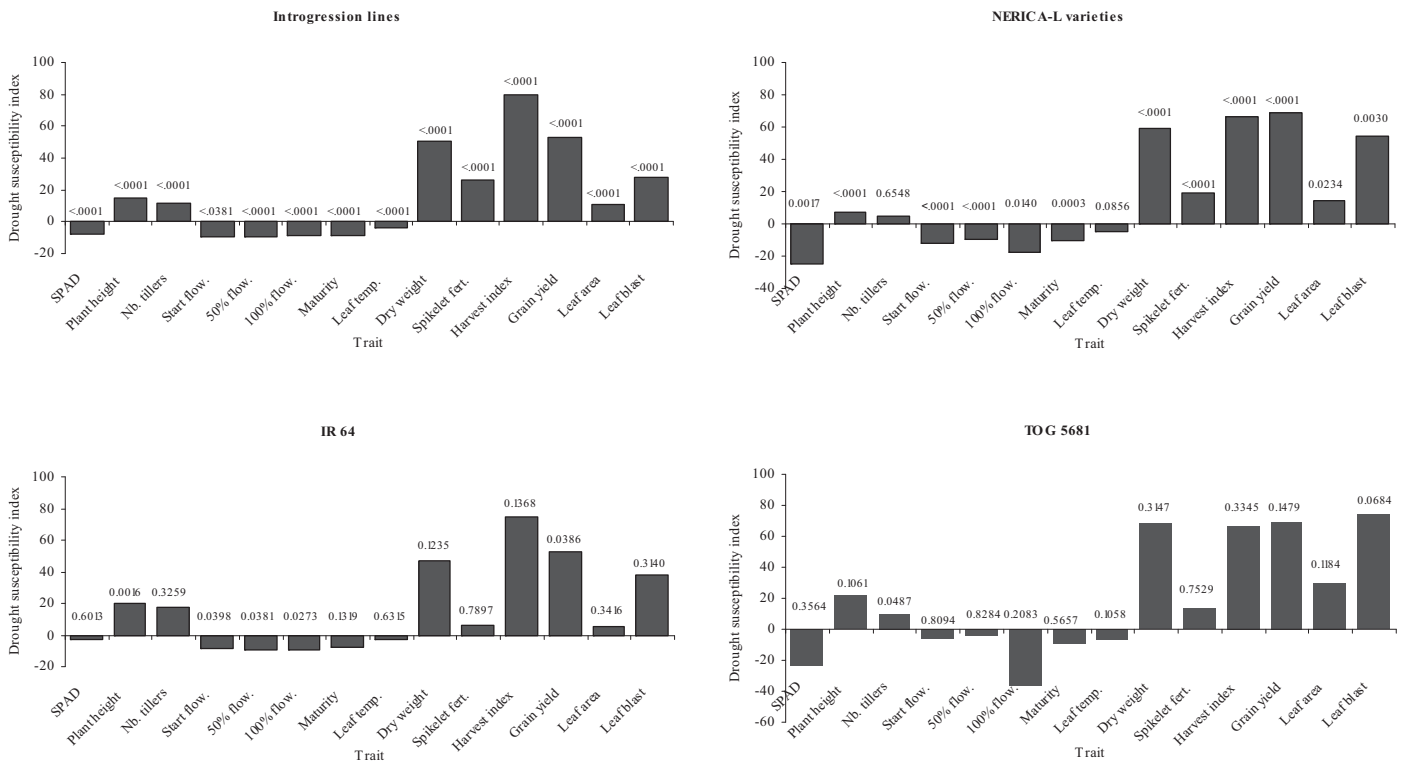


Fig. 3. Drought susceptibility index (bars) for 14 traits and P values (values on top of bars) for the difference between two irrigation regimes (fully irrigated and drought) in ANOVA.

tip burning. Harvest index and leaf area at harvest showed significant interactive $G \times E$ effects in the introgression lines and parents. Only the parents depicted $G \times E$ interactions in SPAD, number of tillers and blast damage. In all genotype groups, no significant interactive $G \times E$ effects were observed in plant height, leaf temperature, dry weight, spikelet fertility and grain yield (Table 2).

Three main groups of genotypes were identified for their grain yield under drought and for the percentage of their yield loss (Fig. 5). The first, second and third groups comprised 14, 39 and 7 of genotypes, respectively. Thirteen introgression lines and NERICA-L 42 constituted the first group of genotypes with grain yield under

drought ranging between 402 and 516 kg ha⁻¹. Grain yield of the second group genotypes ranged between 1223 and 1733 kg ha⁻¹. IR 64, NERICA-L41 and NERICA-L19 belonged to this group with yields of 1443, 1655 and 1409 kg ha⁻¹, respectively. All genotypes of this group had grain yield higher than that of the *O. glaberrima* parent, TOG 5681. Some of the genotypes (NERICA-L 20, for instance) had grain yield higher than the *O. sativa* parent, IR 64. The third group was made up of the best performing genotypes in terms of grain yield under drought which ranged between 2192 and 3308 kg ha⁻¹, surpassing yields of the two parents. Yield loss due to drought ranged between 62% and 88% for the first group. TOG

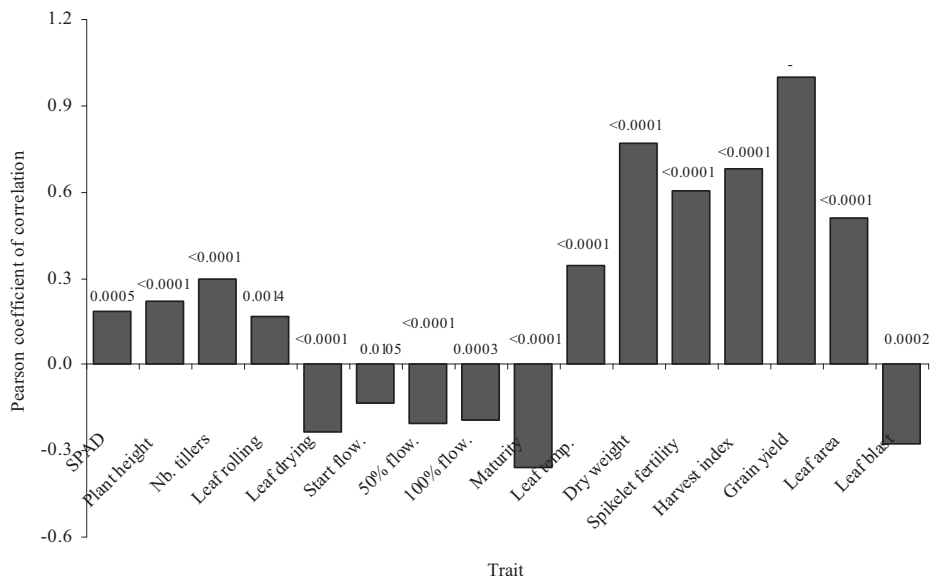


Fig. 4. Pearson's correlation coefficient between grain yield and the other 16 traits in the 60 rice genotypes evaluated under drought.

Table 2

P-values for genotype (60 genotypes), environment (fully irrigated and drought conditions) and their interaction (G × E) in the 17 traits evaluated.

Trait	Introgression lines			NERICA-L varieties			Parents (TOG 5681 and IR 64)		
	Genotype	Environment	G × E	Genotype	Environment	G × E	Genotype	Environment	G × E
SPAD	<0.0001***	<0.0001***	0.1000	0.3454	0.0019**	0.0521	0.0178*	0.6791	0.0285*
Plant height	<0.0001***	<0.0001***	0.0998	0.0038**	<0.0001***	0.0789	0.0003***	0.0070**	0.0687
Number of tillers	<0.0001***	<0.0001***	0.0964	0.2999	0.6603	0.0875	0.0140*	0.9602	0.0075**
Leaf rolling	0.4344	<0.0001***	0.0434*	0.2429	<0.0001***	0.0242*	0.7776	<0.0001***	0.0377*
Leaf tip drying	0.0778	<0.0001***	0.0078**	0.3465	<0.0001***	0.0346*	0.1566	<0.0001***	0.0156*
Flowering (start)	<0.0001***	<0.0001***	0.0458*	0.0002***	<0.0001***	0.0085**	0.4850	0.4512	0.0378*
Flowering (50%)	<0.0001***	<0.0001***	0.0400*	<0.0001***	<0.0001***	0.0187*	0.5866	0.3839	0.0325*
Flowering (100%)	<0.0001***	<0.0001***	0.0496*	0.2675	0.0113*	0.0361*	0.3980	0.1066	0.0278*
Maturity	0.0158*	<0.0001***	0.0029**	0.7139	0.0006***	0.0993	0.3181	0.2785	0.0396*
Leaf temperature	0.9996	<0.0001***	0.1000	0.5611	0.0931	0.0610	0.5476	0.1689	0.0547
Dry weight of fertile spikelets per plant	0.009**	<0.0001***	0.0877	0.3647	<0.0001***	0.0789	0.0134*	0.0593	0.0593
Spikelet fertility	0.3947	<0.0001***	0.0999	0.8484	<0.0001***	0.0670	0.1023	0.6800	0.0892
Harvest index	0.0105*	<0.0001***	0.0104*	0.3306	<0.0001***	0.0984	0.4038	0.0364*	0.0105*
Grain yield	<0.0001***	<0.0001***	0.0970	0.2366	<0.0001***	0.0881	0.0080**	0.0092**	0.0500
Leaf area at harvest	0.9751	0.0988	0.040*	0.6078	0.9244	0.0801	0.4223	0.6755	0.0341*
Leaf blast damage	0.6704	<0.0001***	0.0983	0.1224	0.0015**	0.0744	0.0160*	0.0643	0.0222*

* $P < 0.05$.** $P < 0.01$.*** $P < 0.001$.

5681 belongs to that group with 69% yield loss. Yield loss ranged between 20% and 31% for the second group and between 20% and 37% for the third group (Fig. 5).

Table 3 shows grain yield under the two irrigation regimes, grain yield loss (%) by drought and differences of values between fully irrigated and drought in grain yield, plant height, flowering (start, 50% and 100%), maturity, dry weight of fertile spikelets, spikelet fertility, and leaf area at harvest for the 15 top yielders under drought. IR 64 and TOG 5681 were additionally listed in Table 3 for comparison, although they were not included in the 15 top yielding genotypes. Under drought, yields of SEN-L13-2, MPL-15-3, SEN-L10-1, and SEN-L26-3 were significantly higher than those of NERICA-L 41 (variety with the highest yield among the NERICA-L varieties) and IR 64 (variety with the highest yield in the parents). These introgression lines were also the top four genotypes regarded as low grain yield reduction by drought. An average (not inclusive of the parents) of 45.3% of grain yield loss was observed for the 15 selected genotypes. The value was smaller than the parents. Only seven genotypes had grain yield loss smaller to that mean

value. A genotype with the most stable grain yield against drought was SEN-L13-2 (8.2% yield loss by drought), which also showed the highest yield under drought. Plant height reduction by drought ranged between 2.2 (SEN-L71-2) and 19.0 cm (SEN-L44-2), with a mean value of 11.1 cm for the 15 top yielding genotypes (Table 3). Genotypes with significantly smaller plant height reduction than the parents were SEN-L26-3, SEN-L71-2, SEN-L21-2 and SEN-L41-3. No significant difference was observed between the parents and the listed genotypes in phenologic data (start, 50% and 100% of flowering and maturity). For the top yielding genotypes, due to drought, the start of flowering was delayed from 2.3 (SEN-L10-1) to 8.0 (SEN-L33-3) days; 50% of plants per genotype flowered with a delay of 3.3 (SEN-L10-1) to 8.7 (SEN-L28-3) days. The least delay in 100% of flowering was observed for SEN-L26-3 and SEN-L33-3 (1.7 days) and the highest for NERICA-L 41 (20.0 days) with significant differences ($P \leq 0.05$) between the two means. Maturity was delayed from 5.33 (SEN-L13-2) to 12.50 (MPL-202-3) days. The reduction of dry the weight of fertile spikelets per plant due to drought ranged between 1.8 g (SEN-L13.2) and 11.9 g (NERICA-L 41) with a

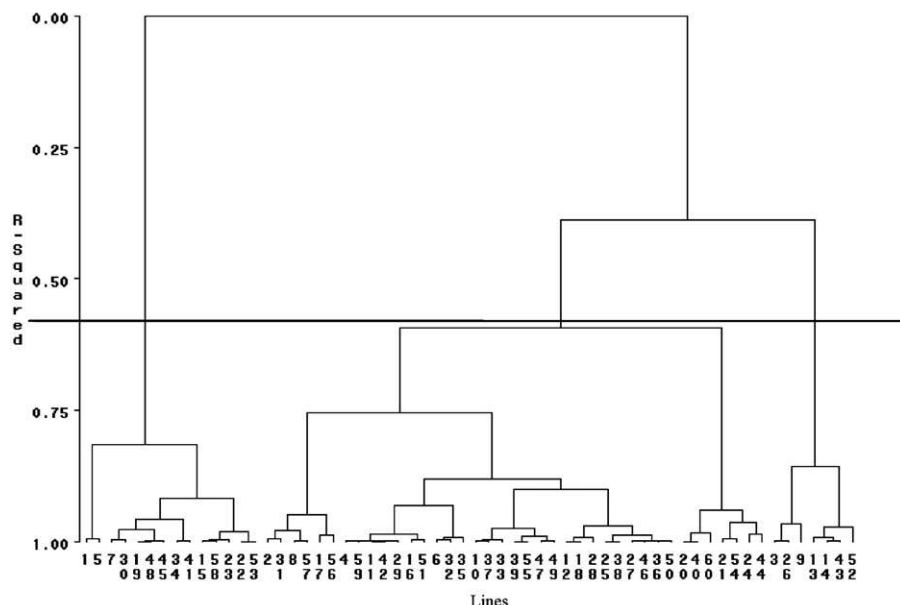


Fig. 5. The dendrogram of the 60 rice genotypes generated by similarity based on grain yield under drought and yield loss by drought.

Table 3
Grain yield in fully irrigated and drought conditions, grain yield loss by drought, and differences of grain yield and other eight traits between the two irrigation regimes in the top 15 yielders among the introgression lines and NERICA-L varieties under drought.

Trait Genotype	Grain yield in full irrigation (kg ha ⁻¹)	Grain yield in drought (kg ha ⁻¹)	Dif in grain yield (kg ha ⁻¹)	Grain yield loss by drought (%)	Dif in plant height (cm)	Dif in the start of flowering (days)	Dif in 50% flowering (days)	Dif in 100% flowering (days)	Dif in maturity (days)	Dif in dry weight of fertile spikelets (g)	Dif in spikelet fertility (%)	Dif in leaf area at harvesting (cm ²)
SEN-L13-2	3605b	3308a	297b	8.2	11.3ab	-4.3a	-5.7a	-4.8ab	-5.3a	1.8b	5.6cd	106c
MPL-15-3	4196a	2644b	1552ab	37.0	12.2ab	-4.8a	-6.3a	-8.5ab	-8.5a	5.8ab	10.9bcd	399bc
SEN-L10-1	3472b	2214b	1258ab	36.2	11.4ab	-2.3a	-3.3a	-4.0ab	-8.0a	6.0ab	12.4abcd	514b
SEN-L26-3	3366bc	2108b	1258ab	37.4	7.6b	-5.2a	-6.0a	-1.7b	-6.7a	3.5b	12.3abcd	823c
SEN-L71-2	3387bc	2099bc	1289ab	38.0	2.2b	-5.5a	-5.8a	-6.2ab	-5.8a	6.6ab	17.8abcd	402bc
SEN-L21-2	4213a	1926bc	2288a	54.3	6.8b	-5.2a	-6.0a	-6.2ab	-9.3a	8.2ab	18.73abcd	236bc
SEN-L24-2	3390bc	1904bc	1486ab	43.8	12.7ab	-4.8a	-5.5a	-10.7ab	-9.7a	6.7ab	24.4abcd	64c
MPL-64-3	3241bc	1703c	1538ab	47.5	14.6ab	-7.5a	-8.3a	-9.2ab	-10.3a	9.0ab	32.2abcd	555b
SEN-L11-2	3282bc	1681c	1601ab	48.8	10.0ab	-6.5a	-6.5a	-8.7ab	-8.9a	2.4b	2.9d	808ab
NERICA-L 41	4617a	1656c	2961a	64.1	13.5ab	-7.7a	-6.8a	-20.0a	-11.2a	11.8a	35.4abc	794ab
SEN-L44-2	3217c	1629cd	1588ab	49.4	19.0a	-5.0a	-5.3a	-4.3ab	-7.5a	7.0ab	43.5a	461b
SEN-L28-3	3949b	1617cd	2332a	59.0	12.2ab	-6.5a	-8.7a	-9.3ab	-11.2a	5.5ab	30.9abcd	341bc
MPL-202-3	4050a	1588d	2462a	60.8	12.3ab	-5.0a	-5.5a	-6.8ab	-12.0a	7.5ab	17.5abcd	82c
SEN-L33-3	2594d	1586d	1008ab	38.9	13.6ab	-8.0a	-8.3a	-1.7b	-8.3a	4.2ab	2.5d	955a
SEN-L41-3	3648b	1579d	2069a	56.7	7.7b	-5.5a	-6.2a	-6.5ab	-8.0a	6.5ab	15.6abcd	224bc
Mean	3615	1949	1666	45.3	11.1	-5.6	-6.3	-7.2	-8.8	6.2	18.8	402
IR 64	3035c	1443de	1592ab	52.5	14.4ab	-6.2a	-7.3a	-7.7ab	-8.2a	4.9ab	4.2cd	9c
TOG 5681	1415e	436e	979ab	69.2	19.0a	-2.8a	-2.3a	-3.3ab	-8.3a	2.8b	8.3cd	619ab

Values followed by different letters are significantly different ($P < 0.05$). Dif = difference of a given trait between the two irrigation regimes (value in the fully irrigated condition – value in the drought condition). The parents are included in the table as checks, although they were not listed as the top 15 high yielders under drought.

significant difference ($P \leq 0.05$). Spikelet fertility (%) was reduced by 2.5 (SEN-L33-3) to 43.5 points (SEN-L44-2) by drought. Difference in leaf area at harvest ranged between 9 cm (IR 64) and 955 cm (SEN-L33-3) (Table 3).

4. Discussion

This study was carried out to evaluate the drought tolerance ability of 60 rice genotypes including 54 introgression lines, four NERICA-L varieties all developed from the cross between the female parent IR 64 (*O. sativa*, Asiatic rice species) and the male parent TOG 5681 (*O. glaberrima*, African rice cultivated species). The two parents are invaluable genetic resources, with several traits that could be used in rice breeding programs in tropical areas. *O. glaberrima* is characterized by many traits including weed competitiveness, tolerance to drought, salinity, high temperatures, insects, viruses, nematodes and Striga. *O. sativa* is characterized by a high yielding potential. The transfer of beneficial traits from one species to another (interspecific crosses) is often difficult due to sterility barriers between these two species. As example, the success in using *O. glaberrima* in breeding with *O. sativa* has been hampered by a reproductive barrier between the two species. Lines recovered from crosses between these species are largely incompatible with *O. sativa* due to the systematical selection of the *O. glaberrima* allele at the S_1 sterility locus [28,29]. To overcome this situation, the concept of contig lines or introgression lines was introduced in 1997 [30] followed by the concept of interspecific bridges (iBridges) introduced in 2006 [31]. It facilitates the use of *O. glaberrima* in crossing programs leading to such materials that carry large introgressions of *O. glaberrima* genome, and that are compatible with *O. sativa* crosses. Chromosome segment substitution lines (CSSLs) and back-cross inbred lines (BILs) are also powerful tools for identifying and transferring agronomically desirable genes from one rice species into the genetic background of another, adapted species [32]. They help then improve elite cultivars and therefore productivity and are particularly valuable when complex, quantitatively inherited phenotypes are the breeding target. This study evaluated the drought tolerance potential of 54 introgression lines derived from *O. glaberrima* (TOG 5681) and *O. sativa* (IR 64). Some of the lines showed higher drought tolerance and yielding potential than their parents indicating the successful transfer of the beneficial genes controlling tolerance to drought and giving high productivity to the descendants from IR 64 and TOG 5681.

Although rice is an exception among cereal crops for its adaptability to a wide range of soil water conditions from upland to flooded lowland, Blum [33] observed a reduction in its vital functions under drought. Riou [34] reported the other essential roles of water in plant development than in photosynthesis, micronutrient transport and accumulation, cell division and temperature regulation. Debaeke et al. [35] observed some effects of drought on plant root development and also aerial parts: leaves, stems, reproductive organs. Blum [33] reported leaf area, root extension, plant phenology and leaf surface properties as constitutive traits that mainly exert the major control of plant water status in crop plants subjected to drought. This is in concordance with observations of Efiuse [36] who reported the complexity of rice drought tolerance that should be defined relative to several plant traits. The results of our study confirmed this and corroborated those of Debaeke et al. [35], Hounkpatin [37], Bocco [38] and Ndjiondjop et al. [39] who additionally reported some significant relationships among the traits.

The rainfall recorded during the drought period of the 2 years of the study was much lower (mean of 1.2 and 3.3 mm day⁻¹, respectively, in the first experiment and in the repeat experiment) than the rainfall needed for rice development: 5.0–6.0 mm day⁻¹

[40]. Therefore, an expected drought treatment was successfully imposed to the plants and the differences in traits' values between fully irrigated and drought-subjected plots could be attributed to the differences of water availability.

Drought negatively affected plant height and leaf area. This can be caused by a result of reduced leaf water potential by drought but there might also be an effect of reduced root growth under drought, leading to a reduction in transport of nutrients to the aerial parts of the plants. Blum et al. [41] made similar observation when drought occurred at the vegetative stage and Ndjiondjop et al. [39] found negative coefficients of correlations between these traits and grain yield under drought. Blum [33] reported that the small size of leaves presents sometimes some advantage for the plant development as plants of small leaf area index (LAI) use relatively less water and are expected to enter a state of water deficit later than plants of larger LAI. Thus, varieties possessing small LAI may possibly have a larger ratio of yield in drought to that in well-watered conditions than those with large LAI. Furthermore, smaller LAI will be a convenient character for survival under severe drought compared to larger LAI. But a larger plant size may be associated with higher yield. If the target of drought breeding is to improve an absolute value of yield under drought, however, the designing of a rice plant ideotype for drought-prone environments should consider benefits and losses to increase/decrease a plant size including leaf area with taking target population environments into account.

Leaf temperature is a sensitive indicator of a plant water status and is associated with leaf stomatal conductance [42]. Lower stomatal conductance (reduced stomatal aperture) by drought brings a lower transpiration rate, i.e. lower latent heat flux released from leaves, and causes higher leaf temperature. Leaf temperature is thus correlated with a plant stress level. Garrity and O'Toole [43] found mean leaf temperature increased from 28 to 37 °C during a drought period and significant relationship of both grain yield and spikelet fertility to midday leaf temperature on the day of flowering. They also found highly significant differences in leaf temperature among rice cultivars, reporting that cultivars with high drought-avoidance potential consistently remained coolest under drought. Although higher leaf temperatures were not always observed in all genotype groups, there was a significant correlation between leaf temperature and yield under drought in our study. Under drought, stomatal regulation (closure) in response to soil drying is triggered by root-shoot chemical and hydraulic signaling prior to the reduction of leaf water potential [44] and is a key adaptation strategy to avoid tissue dehydration. However, this adaptation strategy will not be convenient for the growth maintenance under mild drought stress since stomatal closure causes a lower leaf photosynthetic rate too. In our study, leaf temperature depicted a significant positive correlation with yield under drought, suggesting that lines better possessing this avoidance strategy showed higher yield under the drought imposed in the study.

Leaf greenness plays an important role in leaf photosynthesis which is inhibited by water deficits [33]. If a genotype is found to sustain relatively better photosystem activity, e.g. maintained leaf greenness, under drought, it would be assumed to possess some form of tolerance in photosystem function under drought such as maintenance of turgor potential by osmotic adjustment or to possess a capacity to sustain high water potential. This study revealed higher value of leaf greenness under drought as compared to full irrigation, which is in concordance with observations of Ndjiondjop et al. [39] but in contradiction with those of Zinolabedin et al. [45] 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 the yellowing of the leaves. High leaf greenness in drought compared to in full irrigation was clearly observed in the introgression lines and NERICA-L varieties in the first experiment in 2006, whereas that

was not seen in the repeated experiment (Table 3). The reduction of grain yield by drought was severer in the first experiment than the repeated one for both genotype groups (Table 3). A relationship between leaf greenness and drought tolerance in these genotypes seems to be changed according to a drought level. However, this is a further research topic since no physiological characteristics directly associated with water relations such as leaf water potential were measured in this study.

The first responses to drought in rice are leaf rolling [46] and leaf tip drying, which are a consequence of turgor loss of the plants [45]. Rice plants roll their leaves to maintain a favorable internal water status under drought. So, genotypes with high leaf rolling ability, i.e. with high leaf water maintenance potential during drought will be able to yield better than genotypes with lower ability [47]. The relationship observed between leaf rolling and grain yield under drought confirmed this statement. Leaf rolling and leaf tip burning are also good indicators of a drought level [48]; they are often regarded as drought avoidance mechanisms [49]. During this study some plants were observed with tightly rolled leaves explaining the severity of drought in the stressed plots or the presence of highly susceptible genotypes in the genetic materials used. As indicated in (Fig. 4), a significant negative correlation between leaf drying and yield under drought in our study will simply indicate that more damaged plants showed lower yield; however, leaf rolling had a significant positive correlation with yield under drought—although its correlation coefficient with yield was lowest among the 16 traits—so that leaf rolling could contribute to drought avoidance under the situation of our experiment.

Leaf blast damage was evaluated only in the first experiment in 2006. Leaf blast symptoms were identified in both irrigation regimes (Table 3). However, there was a tendency that more severe damages were seen under fully irrigated than under drought conditions (Table 3), suggesting that water deficits accentuated damage by the disease. Although leaf blast development is favored under humid air and dew rather than dried environments [50], drought might provide damages on the plants and increase the susceptibility against the disease attack in the study. It was speculated that leaf blast damage was not too severe to affect grain yield and a negative correlation between leaf blast damage and grain yield under drought (Fig. 4) may happen by chance through the indirect influence of some other factors.

The data of the panicle initiation were not recorded in this study and therefore the panicle initiation dates estimated. According to Yin and Kropff [51] who used 12 varieties with various photoperiod sensitivities for their study, growth duration from the panicle initiation to 50% flowering stages was between 25 and 30 days under short day conditions for almost all varieties, and 25 days for IR 64. If this duration of 25 days from the panicle initiation to 50% flowering stages is used to estimate the time of the panicle initiation for the materials (not including the checks), an average and standard deviation values of estimated durations from the seeding to panicle initiation were 50.6 and 4.7 days, respectively, for the first experiment (direct seeding), and 60.0 and 3.8 days, respectively, for the repeated experiment (transplanting) under the full irrigated conditions (data not shown). On the other hand, the drought treatment was imposed in the period from 45 to 66 days after sowing for both experiments, suggesting that most of the materials tested had the panicle initiation during the drought treatment. In our study, the drought treatment started on the same day for all genotypes tested. However, the drought was imposed at similar growth stages for the genotypes. In this study, flowering (start, 50% and 100% of flowering) and maturity were delayed as a result of water shortage. Arraudeau [50] made similar observations and additionally reported the effect of prolonged extreme temperature regimes on flowering and maturity. The length of flowering delay varies with the intensity and period of occurrence of drought and

longer flowering delay was observed when drought occurred during early tillering than mid-tillering [52]. The largest delay, which was 20 days, was observed in 100% flowering of NERICA-L 41 in this study. Pantuwan et al. [53] have reported a negative correlation between growth duration and grain yield under drought in both the cases of vegetative and reproductive stages. Our results corroborated those of Pantuwan et al. [53]. Spikelet fertility can sensitively be influenced by drought; the production of viable pollen, panicle exertion, pollen shed and germination, and embryo development, which are involved in fertilization and initiation of grain filling, are all negatively affected by drought. This induces reduced spikelet fertility and dry weight of fertile spikelets and consequently indices grain yield loss as observed in this study.

In the study, significant relationship between all the traits evaluated and grain yield was observed under drought, suggesting that the traits are good secondary indicators that could be used to evaluate the drought tolerance potential of rice plants. The study also showed that this relationship varied with the genotype group expressed by the probability values indicated in Table 5 for genotypes and $G \times E$ interactions.

In the 15 top yielding genotypes under drought, only one NERICA-L variety (NERICA-L 41) was included and no parent was. This justifies the superior yielding ability of the descendants over the parents under drought and the possibility of developing new NERICA varieties from these 15 genotypes after further studies including multi-location trials. Attention could be paid on the genotypes of MPL-15-3, SEN-L10-1, SEN-L13-2 and SEN-L26-3 since their yields were significantly higher than those of the best NERICA-L variety (NERICA-L 41) and parent (IR 64), particularly SEN-L13-2 for low yield reduction by drought (drought tolerance) and MPL-15-3 for high yield potential under full irrigation with relatively low yield reduction by drought.

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