

Transgressive segregation and generation mean analysis reveal the gene action underlying the inheritance of drought tolerance in rice

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ABSTRACT

Climate change, an effective driver of unprecedented seasonal droughts, is greatly affecting rice production in Africa by threatening food security and safety. Rice, one of the major staple crops on the continent, can save the situation through the development of drought-tolerant cultivars, presenting a major challenge for future rice improvement programs as drought is regarded as a critical limitation in rain-fed ecosystems. This study sought to understand the genetic basis and inheritance behind the expression of tolerance of rice breeding lines to drought-stress through generation mean analysis. To achieve these objectives, two drought-sensitive genotypes (Jasmine 85 and CRI-Agrarice) were crossed with a drought-tolerant genotype (APO) to develop six populations (F₁, F₂, BC₁, BC₂, P₁ and P₂) under greenhouse drought-stress and non-stress evaluation. Data were collected on grain yield and yield-related traits among which the generation mean analysis was conducted. At least one transgressive phenotype was produced in the F₂ population for each trait whether there is a significant difference or not among the parental lines under drought-stress. Under non-stress conditions, there was a significance for all six types of gene action for days to flowering in both crosses. Among both crosses and water-regimes, additive x additive gene interaction was significant for most of the traits even though the scaling tests were not significant indicating the effectiveness of selection in early generations. Therefore, either forward breeding or backcross breeding can be adopted as breeding strategies for rapid improvement for these lines to drought tolerance.

1. Introduction

At the global level, agricultural drought frequency and area are predicted to increase by 50 to 200 % in a relative sense during this 21st century (Zhao and Dai, 2017) causing rice yield loss by 25.4 % (Zhang et al., 2018), because of the unpredictable occurrence of drought due to the ongoing climate changes (Serraj et al., 2009). As projected by global climate models, recurrent drought events under future climate change may result in increased losses when droughts overlap with sensitive stages of crop growth (Kumar et al., 2014). Most of the severe droughts in the last ten years have been in Africa, the continent which already has the lowest level of crop production and drought adaptive capacity.

Drought has adversely affected agriculture and livelihoods (Bates et al., 2008; Serraj et al., 2009) in different parts of the continent, with rice production declining in many parts of West Africa due to increasing water deficit. There is the need to develop improved crops tolerant to drought to ensure food adequacy for the increasing population in Africa, especially in West Africa. Rice, which is one of important staple foods in West Africa, is an ideal crop to address the problem.

The responses of rice to drought-stress depend on the genotype, severity of the environmental stress, and the interaction between both factors. The combination of these three factors may either result in biomass reduction under moderate effects, or complete crop failure under severe circumstances. Because drought severity varies among rice

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genotypes, this factor is exploited during breeding for improving varieties under drought-stress. The responses of rice vary according to the growth stage of the plant, namely seedling, vegetative and reproductive stages. The reproductive stage is the most sensitive to drought and can result in 100 % grain yield loss due to low rate of spikelet fertility/number of filled grains (Shahryari et al., 2008; Centritto et al., 2009). There are broadly four resistance mechanisms under drought-stress: drought escape, (Kooyers, 2015; Shavruk et al., 2017), drought avoidance (Fang and Xiong, 2015; Shavruk et al., 2017), drought tolerance (Mitra, 2001), and the last mechanism being recovery from drought-stress, which functions by maximizing available water rather than the maximization of water use efficiency (Lafitte et al., 2003). It functions if the wilting point of the soil is not reached.

The gathering of necessary information about the genetic effects on agronomic and morphological traits is important in formulating effective breeding strategies for the development of drought-tolerant rice varieties (Boubacar Gaoh et al., 2020). Insights into the nature and different types of gene action is also crucial for achieving the genetic improvement in rice for drought tolerance. Notwithstanding, despite several years of studies on the types of gene action controlling rice agromorphological traits, no consensus has yet been reached on the type of gene action that controls these characteristics because the results of the reported studies depend largely on the trial environments and the source of genetic materials used in those trials. A genetic study has been conducted to determine the inheritance and gene action that control drought tolerance in five segregating generations using interspecific crosses involving two parents and their F_1 , F_2 and F_3 populations through generation mean analysis (Lamo, 2010). The results revealed that additive effects were more predominant than non-additive effects for pollen viability and seed set in the crosses (Lamo, 2010). The results also showed that additive effects for filled grains were predominant under both drought-stress and non-stress conditions than the non-additive effects (Lamo, 2010). On the other hand, high heritability estimates were recorded for leaf rolling under drought-stress, implying that additive effects were more important (Lamo, 2010). A study on genetic effects of morphological and physiological traits under drought-stress tolerance revealed that both additive and non-additive genetic effects were predominant in controlling these traits (Efisue et al., 2009).

Thus, to throw more light on the inheritance of rice yield and yield-related traits, this study aimed to contribute to the understanding of the genetic basis and inheritance behind the expression of tolerance of the rice breeding lines to drought-stress. Additionally, it sought to identify whether extreme phenotypes (transgressive phenotypes) can be produced when both parents involved in a cross have similar phenotypes for a given trait under non-stress and drought-stress conditions.

2. Material and methods

2.1. Plant materials

The plant materials used in this study consisted of F_1 and F_2 hybrid plants obtained from two crosses, their respective three parents involved in the crosses and the Backcrosses 1 and 2 (BC_1 and BC_2). The selected parental lines contrast with respect to tolerance to drought-stress. The first parent – APO, is drought-tolerant, while the other two parents, CRI-Agrarice and Jasmine 85, are drought-sensitive varieties. These genotypes also contrasted in terms of performance for some agronomic traits such as flowering date, tiller number, hundred-grain weight and presence of aroma.

2.2. Development of F_2 and backcross generations

Two F_1 hybrid generations were developed using selected parents with contrasting drought tolerance characteristics. The crossing was done from January 2021 to March 2022 to develop segregating populations namely F_2 and backcross generations. The F_2 populations for

each cross were developed through the selfing of F_1 individuals. To develop the backcross populations (BC_1 and BC_2) for each cross combination, F_1 individuals were crossed with their respective parent P_1 (female parent) and parent P_2 (male parent). To develop the BC_1 and BC_2 populations, only true F_1 plants with the base of the rice plants coloured in pink were used as the two female parents do not have pink basal while the male parent has.

2.3. Crossing scheme

During the development of BC_1 and BC_2 populations, both parents (P_1 and P_2) plants were used as donors (pollen sources), and F_1 plants as receivers (female plants/recurrent parents), (Fig. 1). The crossed panicles were harvested at maturity, sun-dried for 2 weeks, and threshed to collect crossed seeds. The seeds at only the mid-centre of the crossed panicles were collected to ensure high quality of crossed seeds and to reduce the probability of collecting selfed seeds (Pujar et al., 2022).

2.4. Evaluation of the six populations under drought-stress

The six populations (P_1 , P_2 , F_1 , BC_1 , BC_2 , and F_2) for each cross were evaluated in a completely randomized block design (RCBD), with three replications at CSIR-CRI, Fumesua, Ghana, in a greenhouse between June and December 2022. The rainout shelter was used to keep the plants off rainfall. A block of RCBD consisted of three rows with 10 P_1 and 10 P_2 plants per row, and one F_1 plant per row; two rows with 20 BC_1 and 20 BC_2 plants per row; and six rows with 20 F_2 plants per row, thereby using all the F_1 and backcross progenies. Direct sowing was done for the F_2 and Parents, while F_1 and backcross progenies were pre-germinated before transplanting. The direct sowing was done on 11/06/2022, while transplanting of the F_1 , BC_1 and BC_2 progenies was done on 16/06/2022. The plants were grown using 1.5-l pots filled with topsoil, with one plant per pot. All recommended agronomic practices were followed for good crop growth. Observations made were recorded on all three replications and respective plants. The drought-stress condition was imposed on 09/08/2022 at vegetative stage by withholding the water from the experimental pots for 5 days during which close to 80 % of the rice plants showed severe leaf rolling. The stressed plants were scored just before the pots were flooded with water. Twenty-four (24) hours after, the water was drained out of the pots and the drought-stress condition resumed for another 5 days. The stress cycle continued by following this process throughout the vegetative and reproductive stages of the rice plant growth. At each stress cycle at vegetative stage, the leaf rolling score and leaf drying score were recorded. Well-watered plants were used as controls.

2.5. Morphological and physiological traits performance

Data were collected on 30 P_1 plants, 30 P_2 plants, 3 F_1 plants, 120 F_2 plants, 40 BC_1 plants and 40 BC_2 plants on all 3 repetitions for each cross combination. Grain yield in grams, plant height (PH) in cm, number of effective tillers (TN), panicle length (PL) in cm, spikelet fertility score (SPFS), leaf rolling score, leaf drying score and recovery from drought were recorded on each plant per replicate at physiological maturity of the rice crop and days to flowering (DTF).

2.6. Transgressive segregation analysis

For the F_2 populations, descriptive statistics such as the coefficient of variation (C.V., %), range, maximum and minimum values, variance and standard error for each variable were determined as a measure of the variability.

The transgressive segregants in the F_2 populations (extreme values of progenies compared to their parental lines) were identified by counting the number of plants whose values were below that of the inferior parent or above that of the superior parent by a difference of 5 % (Cazzola et al.,

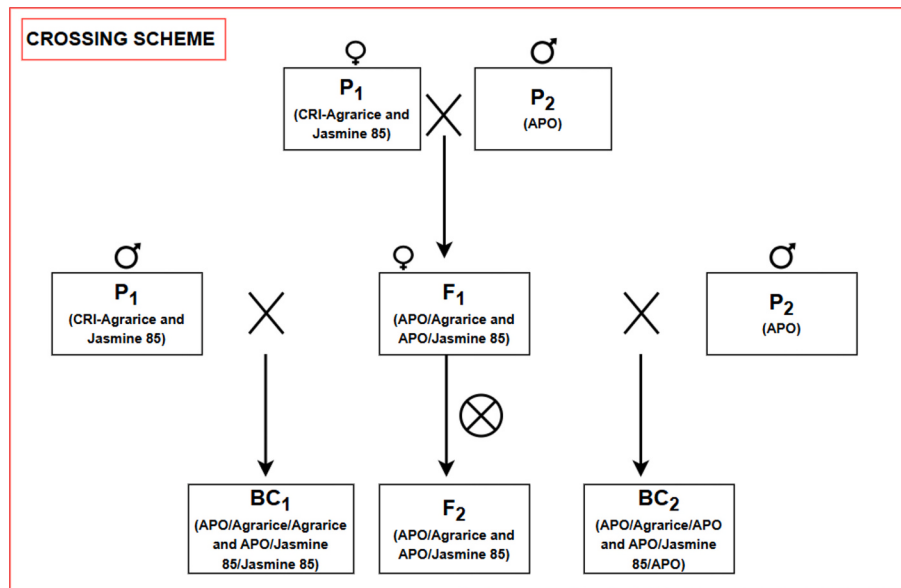


Fig. 1. Crossing scheme between drought-tolerant APO (P_2) and drought-sensitive genotypes CRI-Agrarice (P_{1-1}) and Jasmine 85 (P_{1-2}). APO is the male donor and CRI-Agrarice and Jasmine 85 are the female receivers in the development of the F_1 population. To develop the backcross populations 1 and 2 (BC_1 and BC_2), the F_1 population was used as female, while P_1 and P_2 were donors. The F_1 generation was selfed to develop F_2 seeds.

2020). For traits like plant height and days to flowering, the segregants with values lower than those of the parents were recorded as transgressive. The limit was 70 cm for plant height and 75 days for the flowering date for all the crossing populations. The transgression index (TI) was calculated to assess the presence of transgressive segregants in the crossing generations according to Koide et al. (2019).

$$\text{Transgression Index (TI)} = \frac{R}{D}$$

Where, R is the range of variation between F_2 progenies for any trait; D is the difference between the average values of the parents for the same trait. For the sake of conformity, we took the absolute value of $D = |P_1 - P_2|$.

2.7. Generation mean analysis

Analysis of variance was performed following a completely randomized block design.

- Test for epistasis

The four scaling tests (A, B, C, and D) according to Mather (1949) were used for the testing of epistasis, and were as computed below:

$$A = 2BP_1 - P_1 - F_1$$

$$B = 2BP_2 - P_2 - F_1$$

$$C = 4F_2 - 2F_1 - P_1 - P_2$$

$$D = 2F_2 - BC_1 - BC_2$$

Where, P_1 , P_2 , F_1 , F_2 , BC_1 , and BC_2 are means of different populations.

Variances for the quantities A, B, C, and D were estimated from the variances of different populations as below:

$$VA = 4V(BC_1) + V(P_1) + V(F_1)$$

$$VB = 4V(BC_2) + V(P_2) + V(F_1)$$

$$VC = 16V(F_2) + 4V(F_1) + V(P_1) + V(P_2)$$

$$VD = 4V(F_2) + V(BC_1) + V(BC_2)$$

Where,

VA , VB , VC , and VD are variances of the A, B, C, and D scales, respectively. $V(P_1)$, $V(P_2)$, $V(F_1)$, $V(F_2)$, $V(BC_1)$ and $V(BC_2)$ are the variances of P_1 , P_2 , F_1 , F_2 , BC_1 , and BC_2 generations, respectively.

Standard errors for the scales A, B, C, and D were estimated by taking the square root of the four variances. The t -test was used to test for the presence of epistasis at the significance level of 0.05 and 0.01, with their corresponding degrees of freedom. For a given test, the degrees of freedom were calculated as the sum of the degrees of freedom of various generations involved in that scaling test, whereas the degrees of freedom for any population were calculated as the total number of observations minus the number of replications (Pujar et al., 2022). The t values were calculated as follows:

$$t \text{ value of scale A} = \frac{A}{\sqrt{VA}}$$

$$t \text{ value of scale B} = \frac{B}{\sqrt{VB}}$$

$$t \text{ value of scale C} = \frac{C}{\sqrt{VC}}$$

$$t \text{ value of scale D} = \frac{D}{\sqrt{VD}}$$

- Six parameters model

If any of the scaling tests were significant, then the genetic effects were estimated by fitting the data into six-parameter models of the generation mean analysis according to Hayman (1958, 1960). The genetic parameters estimated are mean effect (m), additive gene effects (d), dominance gene effects (h), and three types of non-allelic gene interactions namely additive $\times$ additive (i), additive $\times$ dominance (j), and dominance $\times$ dominance (l). These genetic parameters were calculated according to the following parameters:

Mean effect (m) = $\underline{F_2}$

Additive effects (d) = $\underline{BC_1} - \underline{BC_2}$

Dominance effects (h) = $\underline{F_1} - 4\underline{F_2} - 0.5\underline{P_1} - 0.5\underline{P_2} + 2\underline{BC_1} + 2\underline{BC_2}$

Additive $\times$ Additive gene interaction (i) = $2\underline{BC_1} - 2\underline{BC_2} - 4\underline{F_2}$

Additive $\times$ Dominance gene interaction (j) = $\underline{BC_1} - \underline{BC_2} - 0.5\underline{P_1} + 0.5\underline{P_2}$

Dominance $\times$ Dominance gene interaction (l)

$$= \underline{P_1} + \underline{P_2} + 2\underline{F_1} + 4\underline{F_2} - 4\underline{BC_1} - 4\underline{BC_2}$$

Where, $\underline{P_1}$, $\underline{P_2}$, $\underline{F_1}$, $\underline{F_2}$, $\underline{BC_1}$, and $\underline{BC_2}$ are means of different populations.

The variances of the above gene interactions were estimated according to the expressions below:

$$Vm = V(\underline{F_2})$$

$$Vd = V(\underline{BC_1}) + V(\underline{BC_2})$$

$$Vh = V(\underline{F_1}) + 16V(\underline{F_2}) + 0.25V(\underline{P_1}) + 0.25V(\underline{P_2}) + 4V(\underline{BC_1}) + 4V(\underline{BC_2})$$

$$Vi = 4V(\underline{BC_1}) + 0.25V(\underline{BC_2}) + 16V(\underline{F_2})$$

$$Vj = V(\underline{BC_1}) + V(\underline{BC_2}) + 0.25V(\underline{P_1}) + 0.25V(\underline{P_2})$$

$$Vl = V(\underline{P_1}) + V(\underline{P_2}) + 4V(\underline{F_1}) + 16V(\underline{F_2}) + 16V(\underline{BC_1}) + 16V(\underline{BC_2})$$

Where,

$V(\underline{P_1})$, $V(\underline{P_2})$, $V(\underline{F_1})$, $V(\underline{F_2})$, $V(\underline{BC_1})$ and $V(\underline{BC_2})$ are the variances of P_1 , P_2 , F_1 , F_2 , BC_1 , and BC_2 populations, respectively.

The significance of the gene effects m , d , h , i , j , and l were tested using the t -test. Standard errors were calculated by taking the square root of the variance of each component. The significance of the gene effects was determined using the t -test as in the case of the scaling test above. Statistical analyses were done using the R scripts according to Nadarajan et al. (2016).

- Heterosis

Heterosis over mid-parent (HMP) was estimated as the increase or reduction in percentage observed in the F_1 population over that of the mid-parent according to Fonseca and Patterson (1968). The mid-parent residual heterosis (MRH) was also estimated in the F_2 progeny following the formula of Rao (1980).

$$HMP (\%) = \left(\frac{(F_1 - MP)}{MP} \right) \times 100$$

$$MRH (\%) = \left(\frac{(F_2 - MP)}{MP} \right) \times 100$$

- Heritability and genetic advance

Broad-sense heritability (h_{bs}^2), narrow-sense heritability (h_{ns}^2), and genetic advance (GA) were estimated according to Warner (1952). The genetic advance as a percentage of the mean (GAM) was calculated according to Johnson et al. (1955). The calculations were done using the following formulas:

$$h_{bs}^2 (\%) = \left(\frac{V(F_2) - \frac{V(P_1) + V(P_2) + V(F_1)}{3}}{V(F_2)} \right) \times 100$$

$$h_{ns}^2 (\%) = \left(\frac{2V(F_2) - (V(\underline{BC_1}) + V(\underline{BC_2}))}{V(F_2)} \right) \times 100$$

$$GA = \frac{V(F_2) - V(F_1)}{\sqrt{V(F_2)}} \times K$$

$$GAM (\%) = \frac{GA}{\underline{F_2}} \times 100$$

$V(P_1)$, $V(P_2)$, $V(F_1)$, $V(F_2)$, $V(\underline{BC_1})$ and $V(\underline{BC_2})$ are the variances of P_1 , P_2 , F_1 , F_2 , BC_1 , and BC_2 populations, respectively. K is the selection differential, and K is 2.06 at a 5 % selection intensity.

Broad-sense heritability (h_{bs}^2) and narrow-sense heritability (h_{ns}^2) estimates were classified as: Low (0–30 %), moderate (30–60 %) and High (above 60 %), while the genetic advance as percent of mean (GAM) was classified as: Low (less than 10 %), moderate (10–20 %), high (more than 20 %) according to Johnson et al. (1955).

- Degree of dominance

The degree of dominance (DD), which is calculated as the square root of the ratio of dominance variance (Vh) to additive variance (Vd), was estimated following Robinson et al. (1949). The calculation was done using the following formula:

$$\text{Degree of dominance (DD)} = \sqrt{\frac{Vh}{Vd}}$$

2.8. Statistical analysis

Analysis of variance (ANOVA) for each trait was done by using the GLM procedure of the Statistical Analysis System (SAS) version 9.4. A trait with a skewness from -2 to $+2$, and kurtosis from -7 to $+7$ is normally distributed. Descriptive statistics and paired samples t -test between traits performance under drought and non-stress conditions were performed with the SPSS software package, version 25. Graphics were made using Microsoft Excel. R software codes were used to run the generation mean analyses (Additional file 1_S1). Pearson correlation (SAS software) was used to understand variations and relationships among various traits and treatments.

3. Results

The phenotype performance of the various populations screened under drought and drought is presented in on Fig. 2.

3.1. Mean comparison of rice parents used to develop the six generations under non-stress and drought-stress conditions

Under non-stress conditions, there was no significant difference between the two parental varieties, namely CRI-Agrarice (Agra) and Apo, for tiller number, panicle number, panicle length (cm), DTF and grain yield per plant (g) based on t -test_{0.05}, whereas plant height (cm) showed a significant difference in the mean performance of Agra and Apo (Table 1). There was also no significant difference between the two parental varieties, namely Jasmine 85 (J.85) and Apo, for tiller number, panicle length (cm) and grain yield per plant (g) based on t -test_{0.05}, whereas panicle number, plant height (cm) and DTF, showed a significant difference in the mean performance of J.85 and Apo under non-stress conditions (Table 1).

Under drought-stress, there was no significant difference between the two parental varieties, namely Agra and Apo, for tiller number, panicle number, panicle length (cm), SPFS, LRS, LDS and grain yield per plant (g) based on t -test_{0.05}, but significant differences were observed in these two parents for DRR, plant height (cm) and DTF (Table 1). There

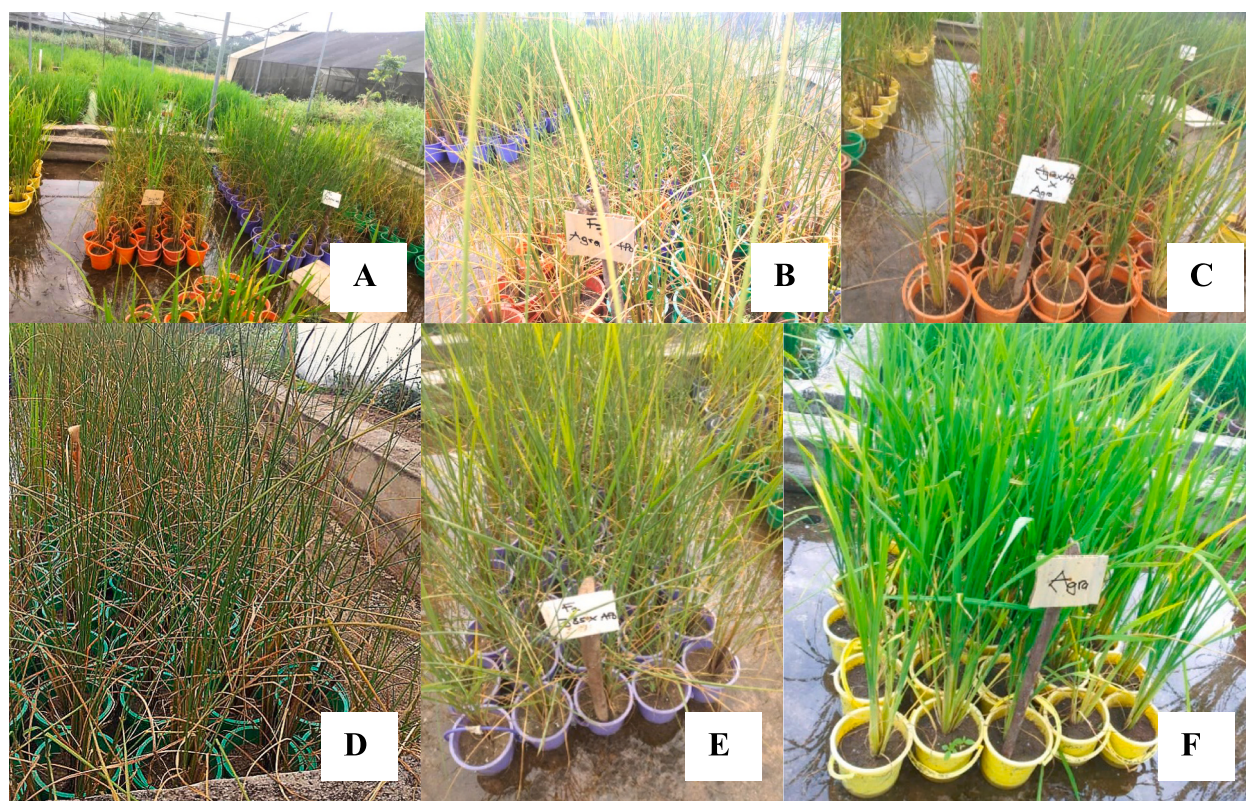


Fig. 2. Phenotypic performances of some of the progenies F_1 , F_2 , BC_1 , BC_2 , and the parents (P_1 and P_2) developed from the crosses between Agra/Apo and J.85/Apo under drought-stress and non-stress conditions under the screenhouse screening in 2022 at Fumesua-Kumasi, CSIR-Crops Research Institute. Overview of the stressed plants one hour after rewatering (A); Cross Agra/APO (F_2) one hour after rewatering (B); Cross Agra/Apo/Agra (BC_2) one hour after rewatering (C); Cross J.85/APO (F_2) five days of continuous drought-stress (D); Cross J.85/APO (F_2) one hour after rewatering (E); Parent Agra (P_{1-1}) under non-stress condition (F). These pictures were taken during active vegetative tillering stage of the rice growing cycle and were showing the differences in the leaves rolling before and after rewatering, as well as the recovering ability of the lines.

Table 1

Differences in the mean performance of parents involved in Agra/Apo and J.85/Apo crosses evaluated under non-stress and drought-stress conditions at both vegetative and reproductive stages at CSIR-Crops Research Institute, Fumesua, Ghana in 2022.

Experimental Conditions	Drought-stress conditions						Non-stress conditions					
	AGRA/APO			J.85/APO			AGRA/APO			J.85/APO		
Cross	CRI-Agrarice	APO	<i>p</i> -value	Jasmine 85	APO	<i>p</i> -value	CRI-Agrarice	APO	<i>p</i> -value	Jasmine 85	APO	<i>p</i> -value
Parents												
TN	4.17	4.70	0.19	4.43	4.70	0.52	8.21	8.93	0.25	7.73	8.93	0.08
PN	2.69	3.17	0.31	2.93	3.17	0.62	6.93	8.07	0.07	6.40	8.07	0.01*
PH	75.48	85.67	0.00**	86.10	85.67	0.88	92.21	100.64	0.00**	95.13	100.64	0.01**
PL	18.21	20.10	0.14	20.30	20.10	0.88	22.31	23.18	0.75	23.60	23.18	0.43
DTF	94.77	90.43	0.00**	93.93	90.43	0.00**	92.60	91.46	0.07	93.13	91.46	0.01**
GYP	9.00	8.44	0.70	9.32	8.44	0.44	14.29	15.71	0.30	14.66	15.71	0.48
LRS	4.73	4.86	0.89	0.83	4.86	0.00**	—	—	—	—	—	—
LDS	2.90	2.97	0.77	3.47	2.97	0.09	—	—	—	—	—	—
DRR	4.00	4.93	0.01*	3.37	4.93	0.00**	—	—	—	—	—	—
SPFS	7.07	6.00	0.06	2.87	6.00	0.00**	—	—	—	—	—	—

** Significant at 1 % based on two-tails *t*-test.

* Significant at 5 % based on two-tails *t*-test; LRS-Leaf rolling score; LDS-Leaf drying score; DRR-Recovery from drought; SPFS-Spikelet fertility score; TN-Tiller number; PN-Panicle number; PH-Plant height; PL-Panicle length; DTF-Days to flowering; GYP- Grain yield per plant.

was no significant difference between the two parental varieties, namely J.85 and Apo, for tiller number, panicle number, plant height (cm), panicle length (cm), LDS and grain yield per plant (g) based on *t*-test_{0.05}, whereas significant differences were observed in the mean performance of Agra and Apo under drought-stress for SPFS, LRS, DRR, and DTF (Table 1).

3.2. Mean performance of the parents and their progenies under drought-stress

Under non-stress conditions, ANOVA across the six populations (recipient parent (P_1), donor parent (P_2) and their respective progenies (F_1 , F_2 , BC_1 and BC_2) revealed significant differences for tiller number, panicle number, plant height and DTF at 1 % in Agra/Apo cross, whereas in J.85/Apo cross in addition to these traits, grain yield per plant showed significance at 5 %. Only panicle length did not show significant differences among the six populations of both crosses under non-stress

conditions (Additional file 1_S2). Under drought-stress, ANOVA showed significant differences in all the traits (LRS, LDS, DRR, SPFS, tiller number, plant height, DTF and grain yield per plant) except panicle number and panicle length in Agra/Apo cross, whereas in J.85/Apo cross, ANOVA showed significant differences in all the traits (LRS, LDS, DRR, SPFS, tiller number, plant height and DTF), except panicle number, panicle length and grain yield per plant (Additional file 1_S3).

Overall, the mean performance of the six populations has decreased significantly under drought-stress compared to the non-stress conditions for both crosses Agra/Apo and J.85/Apo for all the studied traits. The paired *t*-test conducted in Agra/Apo cross revealed significant differences in the mean performance among the lines of the six populations between non-stress and drought-stress conditions for tiller number (*p*-value = 0.004), panicle number (*p*-value = 0.012), plant height (*p*-value = 0.001), panicle length (*p*-value = 0.043) and grain yield (*p*-value = 0.035), whereas days to flowering showed no significance (*p*-value = 0.954). In J.85/Apo cross, the paired *t*-test revealed significant differences in tiller number (*p*-value = 0.013), plant height (*p*-value = 0.035), whereas no significant differences were shown for panicle number (*p*-value = 0.098), panicle length (*p*-value = 0.297), days to flowering (*p*-value = 0.798) and grain yield (*p*-value = 0.159) (Tables 2 and 3). The highest reduction in tiller number (57.14 %) was observed on the F₁ populations of the Agra/Apo cross (F₁-Agra/Apo), and 53.13 % in the BC₁ of the J.85/Apo cross (BC₁-J.85/Apo/J.85), while the lowest reduction of 30.76 % for Agra/Apo cross was observed in the BC₂ (BC₂-Agra/Apo/Apo) cross and 27.27 % in the F₁ of the J.85/Apo (F₁-J.85/Apo) cross. The highest reduction in panicle number of 61.19 % was observed on the P₁ of the cross Agra/Apo (P₁-Agra), and 60.77 % in the P₂ of the cross J.85/Apo (P₂-Apo), while the lowest reduction of 11.43 % for Agra/Apo cross was observed in the BC₁ cross (BC₁-Agra/Apo/Agra) and 0.00 % in the F₁ from the J.85/Apo cross (F₁-J.85/Apo). The backcross 1, BC₁-J.85/Apo/J.85 recorded a 52.00 % increase for panicle number. The highest reduction in plant height of 25.97 % was observed in the F₂ of the Agra/Apo cross (F₂-Agra/Apo), and 26.42 % in the BC₂ of the J.85/Apo cross (BC₂-J.85/Apo/Apo), while the lowest reduction of 10.45 % for the Agra/Apo cross was observed in the F₁ cross (F₁-Agra) and 2.71 % in the BC₁ of the cross J.85/Apo (BC₁-J.85/Apo/J.85). The highest reduction in panicle length of 24.71 % was observed on the BC₂ of the Agra/Apo cross (BC₂-Agra/Apo/Apo), and 20.36 % in the BC₂ of the J.85/Apo cross (BC₂-J.85/Apo/Apo), while the lowest reduction of 11.32 % for Agra/Apo cross was observed in the P₂ (P₂-Apo) and 2.82 % in the F₁ of the cross J.85/Apo (F₁-J.85/Apo). The F₁ progenies, F₁-Agra/Apo recorded an increase of 14.67 % for panicle length, whereas the backcross 1, BC₁-J.85/Apo/J.85 recorded an increase of 17.54 %. The reductions of 1.13 % and 4.64 % were observed on the donor parent Apo and BC₁ of the Agra/Apo cross (BC₁-Agra/Apo/Agra), respectively for days to flowering (DTF), while the increase of 2.29 %, 1.77 %, 2.09 % and 0.69 % were observed in P₁ and for Agra/Apo cross; F₁-Agra/Apo, F₂-Agra/Apo and BC₂-Agra/Apo/Apo, respectively. A reduction of 6.94 % was observed on the BC₁ of the cross Agra/Apo (BC₁-Agra/Apo/Agra)

for DTF, while the increase of 0.85 %, 3.47 %, 0.54 % and 0.57 % for Agra/Apo cross were observed in the Agra, F₁-Agra/Apo, F₂-Agra/Apo and BC₂-Agra/Apo/Apo, respectively. The highest reduction of 46.29 % in grain yield in gram per plant was observed in Apo and its crosses with P₁ parents (Agra/Apo) and J.85/Apo (P₂-Apo), while the lowest reduction of 10.74 % for Agra/Apo cross was observed in the F₂ (F₂-Agra/Apo) and 29.07 % in the F₂ of the cross J.85/Apo (F₂-J.85/Apo). The BC₁ progenies, BC₁-Agra/Apo/Agra recorded an increase of 5.74 %, whereas the backcross 1, BC₁-J.85/Apo/J.85 recorded an increase of 42.71 % for grain yield in grams per plant.

3.3. Transgressive segregation analysis

All the agro-morphological traits studied in the F₂ populations generated from the Agra/Apo and J.85/Apo crosses showed normal distributions based on the skewness and kurtosis data, which respectively ranged from -2 to +2 and -7 to +7 under both non-stress and drought-stress conditions. Descriptive statistics showing the variations among the F₂ lines derived from the Agra/Apo and J.85/Apo crosses for all the traits under non-stress and drought-stress conditions are presented in Additional file 1_S4 and S5, respectively. Under non-stress conditions, the F₂ plants from the Agra/Apo cross ranged from 2 to 14 for tiller number, 1 to 12 for panicle number, 69 to 145 cm for plant height, 0 to 51 cm for panicle length, 87 to 96 days for DTF and 1 to 30 g for grain yield per plant. The transgressive index (TI) of the Agra/Apo population was high for tiller number (11.28), panicle number (9.86), plant height (67.91), panicle length (50.64) and grain yield per plant (20.30), while moderate for DTF (7.86), indicating that tiller number, panicle number, plant height, panicle length and grain yield per plant of many lines of the Agra/Apo F₂ progenies exceeded those of the range between their parents showing the presence of transgressive phenotypes. Days to flowering (DTF) recorded zero extreme phenotypes, while the lowest plant height was equivalent to that of an extremely short line (Fig. 3). Under non-stress conditions, the F₂ lines from the J.85/Apo cross ranged from 2 to 14 for tiller number, 1 to 14 for panicle number, 73 to 134 cm for plant height, 11 to 40 cm for panicle length, 87 to 94 days for DTF and 5 to 30 g for grain yield per plant. The transgressive index (TI) of the J.85/Apo population was high for tiller number (10.04), plant height (11.81), panicle length (31.07) and grain yield per plant (23.60), while moderate for panicle number (7.78) and DTF (4.19), indicating that tiller number, panicle number, plant height, panicle length and grain yield per plant of several lines of the J.85/Apo F₂ population exceeded those of the range between their parents, showing then the presence of transgressive phenotypes. Days to flowering (DTF) recorded zero transgressive phenotypes, while the lowest plant height was equivalent to that of an extremely short line (Fig. 4). Descriptive statistics showing the variation among the F₂ lines derived from the Agra/Apo and J.85/Apo crosses for all the traits under drought-stress is presented in Additional file 1_S4 and S5, respectively. Under drought-stress, the F₂ plants from the Agra/Apo cross ranged from 0 to 9

Table 2

Mean performance of the lines of six populations of Agra/Apo cross-evaluated under non-stress and drought-stress at both vegetative and reproductive stages at CSIR-Crops Research Institute, Fumesua, Ghana in 2022.

Generation ID	TN		PN		PH		PL		DTF		GYP	
	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
P1-Agra	8.21	4.17	6.93	2.69	92.21	75.48	22.31	18.21	92.60	94.77	14.29	9.00
P2-Apo	8.93	4.70	8.07	3.17	100.30	85.67	22.67	20.10	91.46	90.43	15.71	8.44
F1-Agra/Apo	7.00	3.00	6.00	2.67	89.33	80.00	21.33	25.00	92.67	94.33	10.00	6.67
F2-Agra/Apo	7.73	4.28	6.35	2.86	110.08	81.49	23.01	19.22	91.68	93.64	12.20	10.89
BC1-Agra/Apo/Agra	5.16	3.21	2.84	2.52	99.61	77.86	24.22	18.86	102.16	97.42	8.73	9.26
BC2-Agra/Apo/Apo	4.90	3.39	4.10	2.39	103.15	77.21	23.10	17.39	93.90	94.56	10.63	8.40
<i>t</i> -test	0.004		0.012		0.001		0.043		0.954		0.035	

LRS-Leaf rolling score; LDS-Leaf drying score; DRR-Recovery from drought; SPFS-Spikelet fertility score; TN-Tiller number; PN-Panicle number; PH-Plant height; PL-Panicle length; DTF-Days to flowering; GYP- Grain yield per plant; NS-Non-stress; DS-Drought-stress. The two-tails *t*-test was conducted for each trait across the six population to check if there is significance in mean performance for each trait between non-stress and drought-stress.

Table 3

Mean performance of the lines of six populations of J.85/Apo cross-evaluated under non-stress and drought-stress at both vegetative and reproductive stages at CSIR-Crops Research Institute, Fumesua, Ghana in 2022.

Generation ID	TN		PN		PH		PL		DTF		GYP	
	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
P1-J.85	7.73	4.43	6.40	2.93	95.13	86.10	23.60	20.30	93.13	93.93	14.66	9.32
P2-Apo	8.93	4.70	8.07	3.17	100.30	85.67	22.67	20.10	91.46	90.43	15.71	8.44
F1-J.85/Apo	3.67	2.67	2.33	2.33	88.33	82.33	23.67	23.00	92.67	96.00	10.00	6.67
F2-J.85/Apo	7.89	4.04	7.03	2.87	106.73	82.22	23.94	20.56	91.39	91.88	15.44	10.95
BC1-J.85/Apo/J.85	5.33	2.50	1.00	2.08	73.83	71.83	14.50	17.58	102.00	94.92	6.25	10.91
BC2-J.85/Apo/Apo	6.04	3.84	4.46	2.00	101.04	74.34	22.19	17.67	92.15	92.68		8.65
t-test	0.013		0.098		0.035		0.297		0.798		0.159	

LRS-Leaf rolling score; LDS-Leaf drying score; DRR-Recovery from drought; SPFS-Spikelet fertility score; TN-Tiller number; PN-Panicle number; PH-Plant height; PL-Panicle length; DTF-Days to flowering; GYP- Grain yield per plant; NS-Non-stress; DS-Drought-stress. The two-tails *t*-test was conducted for each trait across the six population to check if there is significance in mean performance for each trait between non-stress and drought-stress.

for LRS, 0 to 7 for LDS, 1 to 7 for DRR, 1 to 9 for SPFS, 2 to 8 for tiller number, 0 to 7 for panicle number, 54 to 110 cm for plant height, 4 to 34 cm for panicle length, 86 to 101 days for DTF and 1 to 25 g for grain yield per plant.

The transgressive index (TI) of the Agra/Apo progenies was high for LRS (69.91), LDS (105.00), tiller number (11.37), panicle number (14.67), panicle length (15.85) and grain yield per plant (42.86), while moderate for DRR (6.43), SPFS (7.50), plant height (5.50) and DTF (3.46), indicating that LRS, LDS, DRR, SPFS, tiller number, panicle number, plant height, panicle length and grain yield per plant of many lines of the Agra/Apo F₂ progenies exceeded those of the range between their parents, showing the presence of transgressive phenotypes. Days to flowering (DTF) recorded zero favorable extreme phenotypes, and 5 unfavorable, while the lowest plant height was equivalent to that of an extremely short line (Figs. 5 and 6). Under drought-stress, the F₂ lines from the J.85/Apo cross ranged from 0 to 9 for LRS, 0 to 9 for LDS, 0 to 7 for DRR, 1 to 9 for SPFS, 2 to 7 for tiller number, 0 to 7 for panicle number, 54 to 104 cm for plant height, 8 to 33 cm for panicle length, 84 to 97 days for DTF and 1 to 50 g for grain yield per plant. The transgressive index (TI) of the Agra/Apo progenies was high for LDS (18.00), tiller number (18.75), panicle number (30.00), plant height (124.62), panicle length (125.00) and grain yield per plant (55.59), while low to moderate for LRS (2.23), DRR (4.47), SPFS (2.55) and DTF (3.71), indicating that LRS, LDS, DRR, SPFS, tiller number, panicle number, plant height, panicle length and grain yield per plant for several lines of the J.85/Apo F₂ progenies exceeded those of the range between their parents by exhibiting the presence of transgressive phenotypes. Days to flowering (DTF) recorded one favorable extreme phenotype which was equivalent to that of an extreme early-flowering line in F₂ population of J.85/Apo, while five transgressive late-flowering phenotypes were observed in F₂ progenies of Agra/Apo (Figs. 7 and 8). Under non-stress conditions, despite the absence of significant differences in the two parental varieties, namely Agra and Apo, for tiller number, panicle number, panicle length and grain yield per plant, and in respect of J.85 and Apo, for tiller number, panicle length and grain yield per plant, it was observed that transgressive phenotypes were however generated for these traits. On the other hand, no transgressive segregants were observed for DTF both in the F₂ progenies for Agra/Apo and J.85/Apo crosses, despite the significant differences observed between J.85 and Apo, but no differences between Agra and Apo under non-stress conditions. Under drought-stress, at least one transgressive phenotype was produced for each trait whether there were significant differences among the parental lines involved in the development of the F₂ populations or not.

3.4. Generation means analysis

3.4.1. Test for epistasis

Under non-stress conditions, the scaling tests A and D out of the four (A, B, C, and D) for DTF trait were significant for both crosses – Agra/

Apo (Scale A: $t\text{-cal} = 7.52 > t\text{-tab}_{0.05} = 2.01$; Scale D: $t\text{-cal} = 13.131 > t\text{-tab}_{0.05} = 1.96$) and J.85/Apo (Scale A: $t\text{-cal} = 5.06 > t\text{-tab}_{0.05} = 2.01$; Scale D: $t\text{-cal} = 13.691 > t\text{-tab}_{0.05} = 1.96$), indicating the presence of epistasis or gene interactions, in particular additive $\times$ additive type of gene effects as per the significance of scale D for the days to flowering trait. The remaining traits, namely tiller number, panicle number, plant height, panicle length and grain yield per plant showed no significance for all four scaling tests (A, B, C and D) for both crosses Agra/Apo and J.85/Apo, indicating that variations observed for these traits can be explained by simple additive and dominant model (Tables 4 and 5). Under drought-stress, all four scaling tests were non-significant for all the traits (LRS, LDS, DRR, SPFS, tiller number, panicle number, plant height, panicle length, DTF and grain yield per plant) in both Apo/Agra and J.85/Apo crosses, indicating that the appropriate model to explain the variations observed for these traits are the simple additive and dominant model (Tables 4 and 5).

3.4.2. Genetic effects

The partitioning of the generation means into six different genetic components, namely direct genetic effects, mean effect (m), additive (d) and dominant (h), and the interaction effects – additive $\times$ additive (i), additive $\times$ dominant (j), and dominant $\times$ dominant (l), showed that the mean effect was significant at 1 % for the studied traits (LRS, LDS, DRR, SPFS, tiller number, panicle number, plant height, panicle length, DTF and grain yield per plant) in both Apo/Agra and J.85/Apo crosses under both non-stress and drought-stress conditions, except for the mean effect of LRS and grain yield per plant in J.85/Apo cross under drought-stress. In Agra/Apo cross under non-stress conditions, despite the absence of significance for all the four scaling tests indicating the absence of epistasis, among gene interaction effects, additive $\times$ additive effects showed significance at 1 % for tiller number, panicle number, plant height, panicle length and grain yield per plant. In DTF where the scaling tests A and D were significant for Agra/Apo cross, all the six genetic effects were significant at 1 %. However, the magnitude of the dominance effect was 68.27 % greater than that of the additive effect, while the magnitude of the additive $\times$ additive was 86.26 % greater than that of the dominant $\times$ dominant gene interaction.

In J.85/Apo cross under non-stress conditions, despite the absence of significance of all four scaling tests, indicating the absence of epistasis, among gene interaction effects, additive $\times$ additive effects showed significance at 1 % for tiller number, plant height and panicle length. In the view of panicle number where all the scaling tests were non-significant too for J.85/Apo cross, the dominance effect and additive $\times$ additive gene interaction effect were significant. However, the magnitude of the additive $\times$ additive effect was 36.95 % greater than that of the dominant genetic effect. In DTF where the scaling tests A and D were significant for J.85/Apo cross, all the six genetic effects were significant at 1 %. However, the magnitude of the dominant genetic effect was 57.38 % greater than that for the additive effect, while the magnitude of the additive $\times$ additive was 88.11 % greater than that for the dominant $\times$

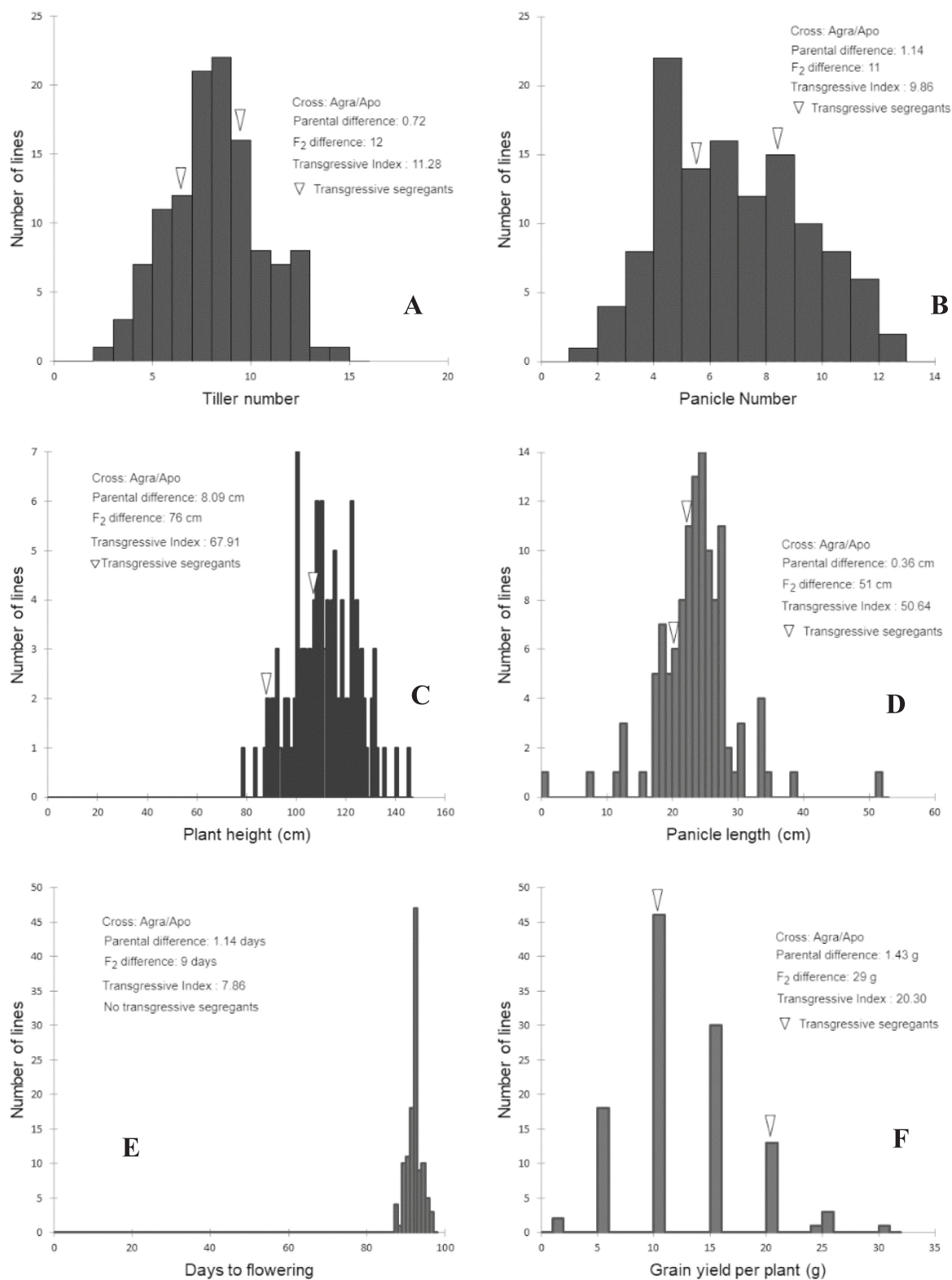


Fig. 3. Histogram showing the transgressive analysis in the F_2 population of Agra/Apo cross evaluated under non-stress conditions in 2022 for tiller number (A), panicle number (B), plant height (C), panicle length (D), days to flowering (E) and grain yield per plant (F) at CSIR-Crops Research Institute, Fumesua-Kumasi, Ghana. Histograms were conducted using 120 F_2 individual plants.

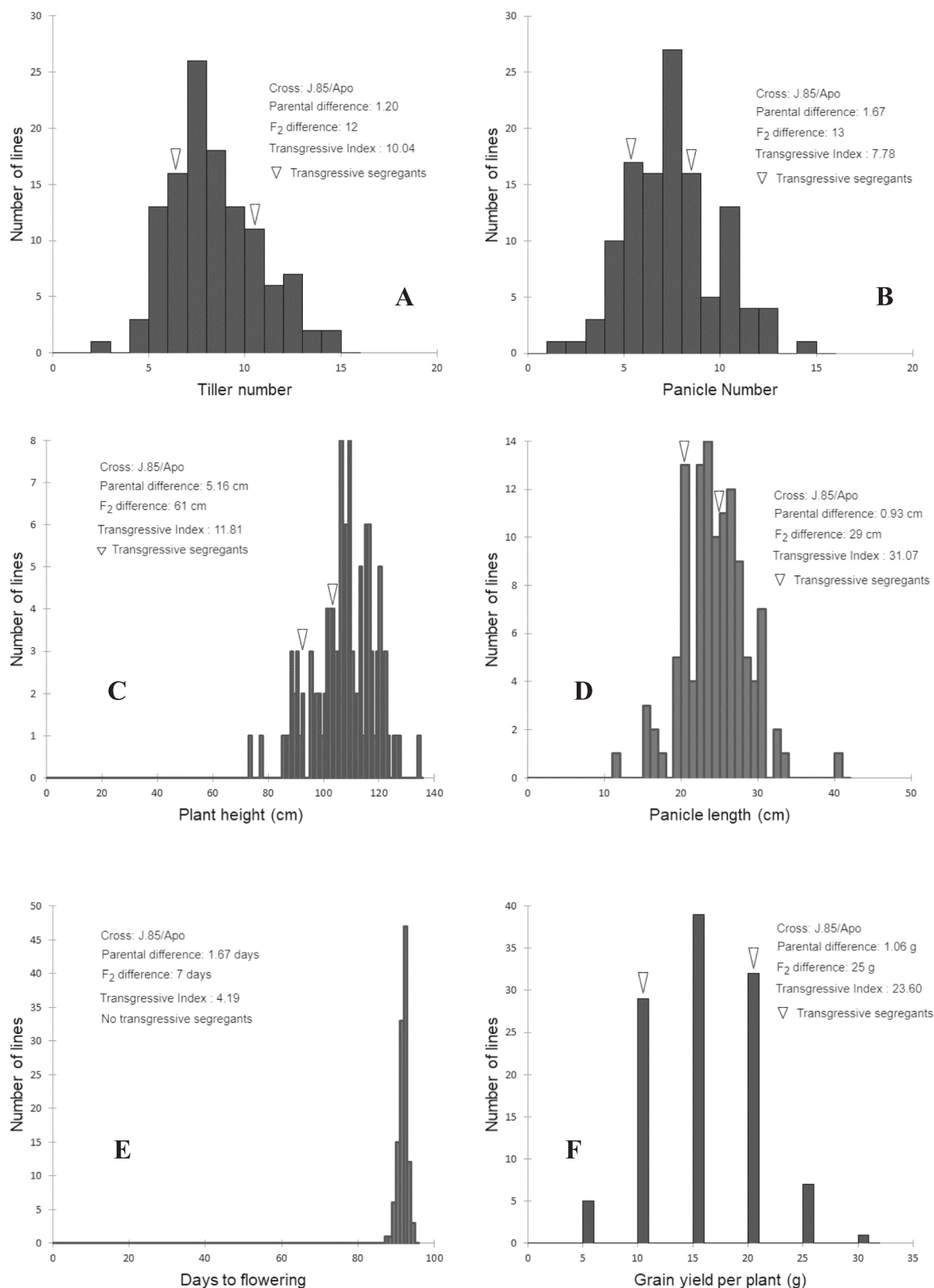


Fig. 4. Histogram for transgressive analysis in the F₂ population of J.85/Apo cross-evaluated under non-stress conditions in 2022 for tiller number (A), panicle number (B), plant height (C), panicle length (D), days to flowering (E) and grain yield per plant (F) at CSIR-Crops Research Institute, Fumesua-Kumasi, Ghana. Histograms were conducted using 120 F₂ individual plants.

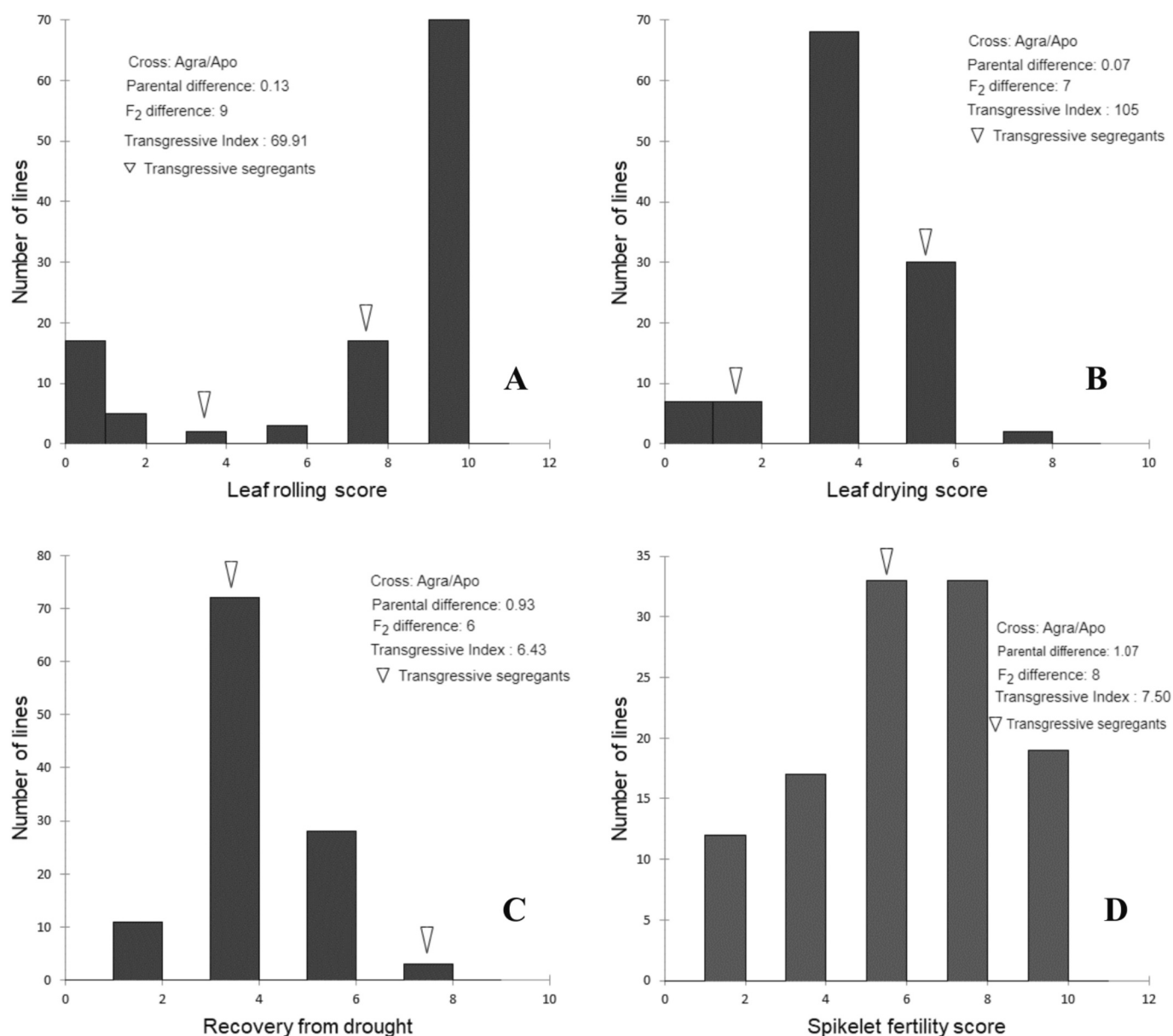


Fig. 5. Histogram for transgressive analysis in the F₂ population of Agra/Apo cross-evaluated under drought-stress in 2022 for leaf rolling score (A), leaf drying score (B), recovery from drought (C) and spikelet fertility score (E) at CSIR-Crops Research Institute, Fumesua-Kumasi, Ghana. Histograms were conducted using 120 F₂ individual plants.

dominant gene interaction. In Agra/Apo cross under drought-stress, despite the absence of significance of all four scaling tests, indicating the absence of epistasis, the additive $\times$ additive gene interaction showed significance at 5 % for all the studied traits (LDS, DRR, SFPS, tiller number, panicle number, plant height, panicle length, DTF and grain yield), except for LRS (Table 6). In J.85/Apo cross under drought-stress, even though all four scaling tests showed non-significance which indicates that epistasis is absent, the additive $\times$ additive gene interaction was found to be significant for all the studied traits (DRR, SFPS, tiller number, panicle number, plant height, panicle length and DTF), except for LRS, LDS and grain yield per plant. Nonetheless, the magnitude of the additive $\times$ additive gene interaction was preponderant for these traits, namely LRD, LDS and grain yield per plant as compared to the other genetic effects (Table 7). From the analysis of the direct genetic effects and inter-allelic interaction effects above, it was revealed that the additive $\times$ additive type of gene interaction was predominant in the two crosses Agra/Apo and J.85/Apo across both non-stress and drought-stress conditions of this study.

3.4.3. Heterosis and degree of dominance

Under non-stress conditions, in Agra/Apo cross, negative heterosis over mid-parent (HMP) was recorded for all the traits except for DTF which recorded a positive HMP with a relatively low magnitude compared to the other traits. The highest magnitude of HMP was recorded in grain yield per plant (-33.33), and the lowest in DTF (0.69). Negative mid-parent residual heterosis (MRH) was recorded for all the traits except for plant height (14.37) and panicle length (2.31) which recorded a positive MRH with a high magnitude for plant height and low for panicle length compared to most of the other traits. The highest magnitude of MRH was recorded in grain yield per plant (-18.65), and the lowest was in DTF (-0.38). The highest degree of dominance among the traits was observed in DTF (4.84), while the lowest value of 3.88 was in plant height (Table 8). In J.85/Apo cross under non-stress conditions, negative heterosis over mid-parent (HMP) was recorded for all the traits except for the panicle length and DTF which recorded a positive HMP with a relatively low magnitude compared to the other traits. The highest magnitude of HMP was recorded in panicle number (-67.75),

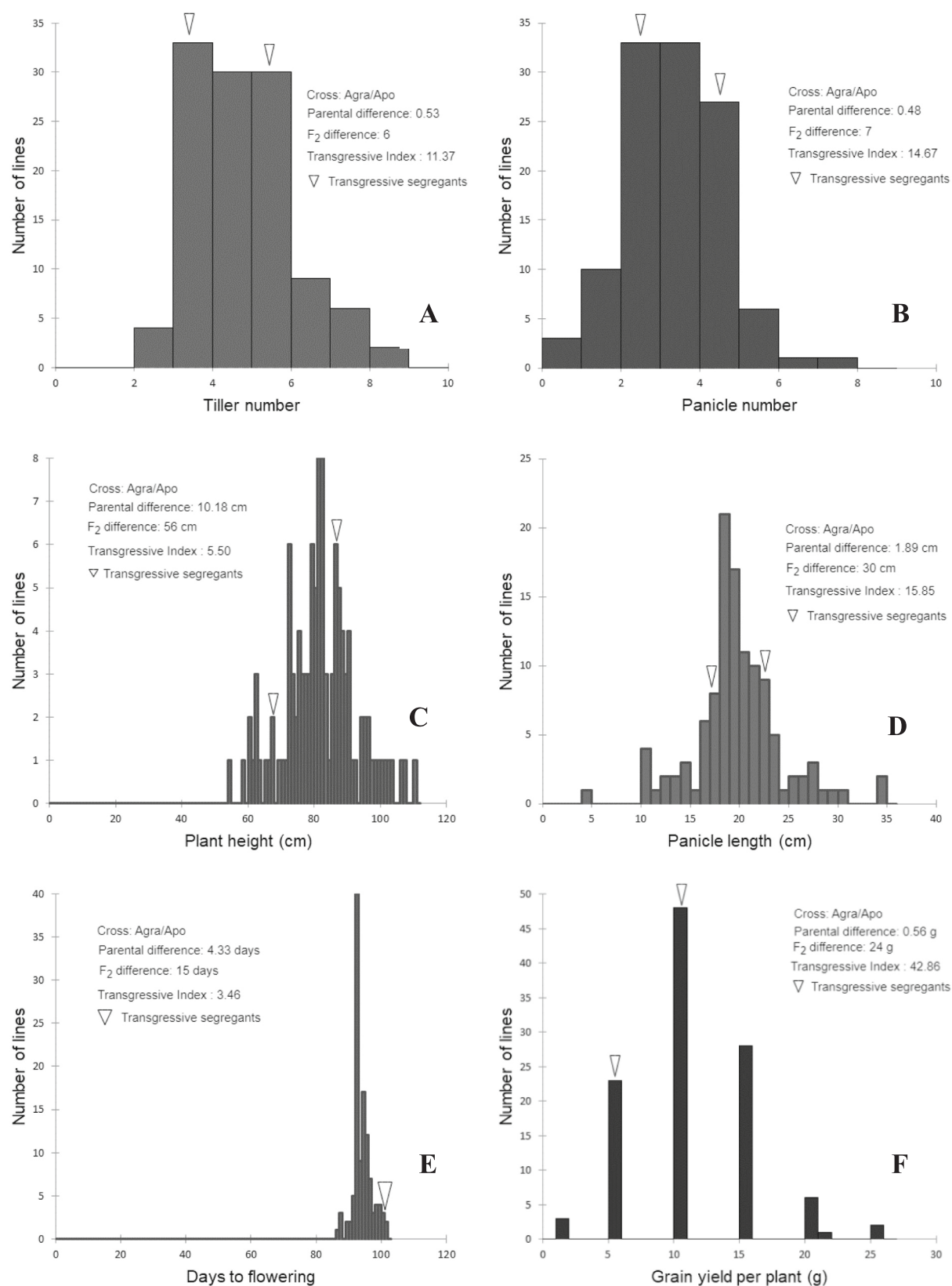


Fig. 6. Histogram for transgressive analysis in the F₂ population of Agra/Apo cross-evaluated under drought-stress conditions in 2022 for tiller number (A), panicle number (B), plant height (C), panicle length (D), days to flowering (E) and grain yield per plant (F) at CSIR-Crops Research Institute, Fumesua-Kumasi, Ghana. Histograms were conducted using 120 F₂ individual plants.

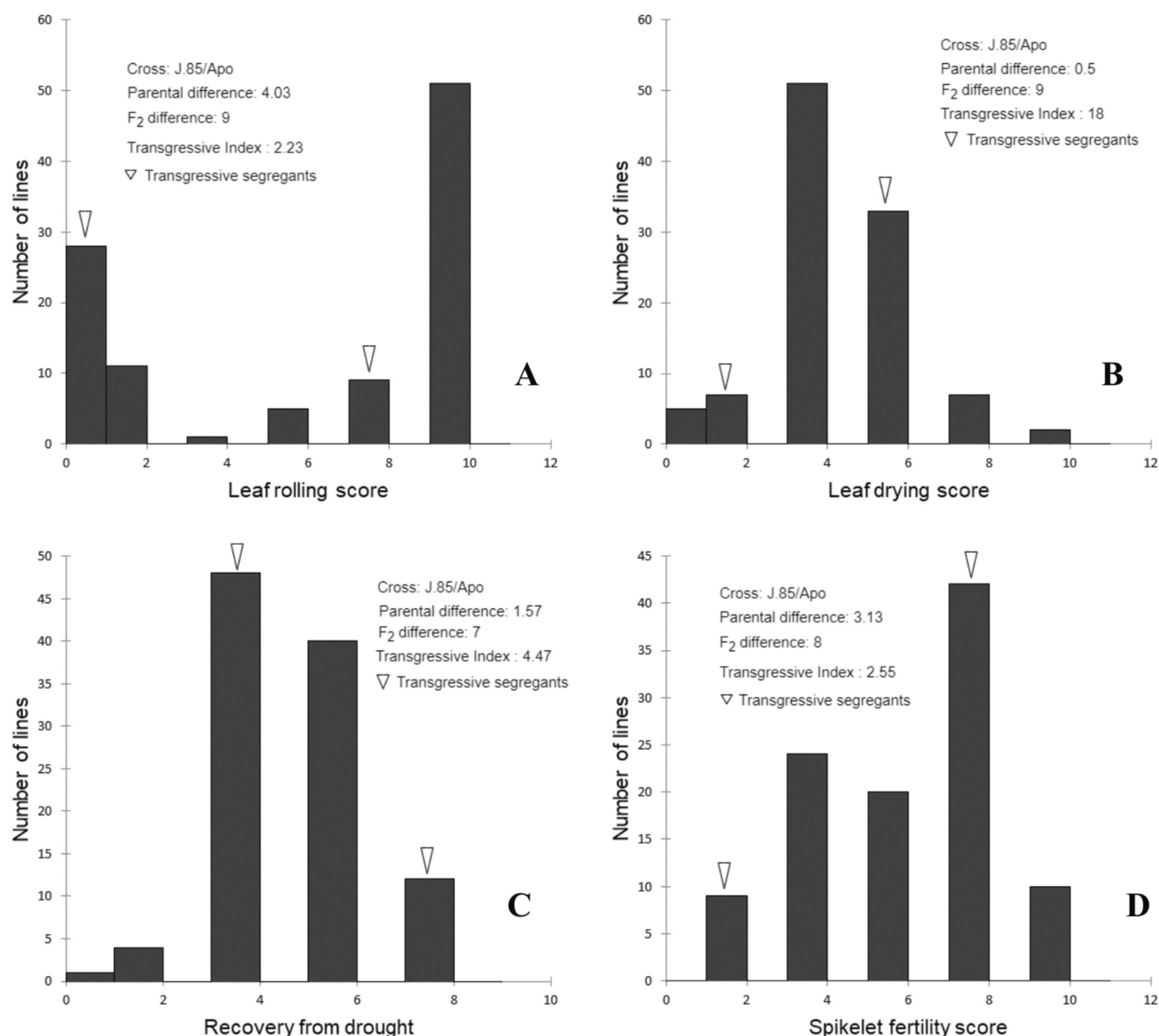


Fig. 7. Histogram for transgressive analysis in the F₂ population of J.85/Apo cross evaluated under drought-stress in 2022 for leaf rolling score (A), leaf drying score (B), recovery from drought (C) and spikelet fertility score (D) at CSIR-Crops Research Institute, Fumesua-Kumasi, Ghana. Histograms were conducted using 120 F₂ individual plants.

whereas the lowest was in DTF (0.40). Negative mid-parent residual heterosis (MRH) was recorded for tiller number, panicle number and DTF, while positive MRH was recorded for plant height, panicle length and grain yield. The highest magnitude of MRH was recorded in plant height (9.22), and the lowest was in DTF (−0.98). The highest degree of dominance among the traits was observed in tiller number (4.68) while the lowest value of 2.93 was in plant length (Table 9). Under drought-stress, in Agra/Apo cross, negative heterosis over mid-parent (HMP) was recorded for all the traits, except for panicle length (30.52) and DTF (1.87). The highest magnitude of HMP was recorded in SPFS (−84.69), and the lowest in plant height (−0.71). Negative mid-parent residual heterosis (MRH) was recorded for DRR, SPFS, tiller number and panicle number, while positive MRH was observed for LRS, LDS, plant height, panicle length, DTF and grain yield per plant. The highest magnitude of MRH was recorded in LRS (42.22), and the lowest was in panicle length (0.37). The highest degree of dominance among the traits was observed in tiller number (5.29), while the lowest value of 3.15 was in LRS

(Table 8). In J.85/Apo cross under drought-stress, negative heterosis over mid-parent (HMP) was recorded for all the traits except for panicle length (13.86) and DTF (4.14). The highest magnitude of HMP was recorded in LRS (−100), and the lowest in plant height (−4.13). Negative mid-parent residual heterosis (MRH) was recorded for DRR, SPFS, tiller number, panicle number, plant height and DTF, while positive MRH was observed for LRS, LDS, panicle length and grain yield per plant. The highest magnitude of MRH was recorded on LRS (90.21), whereas the lowest was in DTF (−0.33). The highest degree of dominance among the traits was observed on panicle number (5.17), while the lowest value of 3.00 was on panicle length (Table 9).

3.4.4. Heritability and genetic advance

Under non-stress conditions, in Agra/Apo cross, a high broad-sense heritability was observed for plant height (73.58 %) and panicle length (65.03 %), while the other traits recorded low broad-sense heritability. Moreover, high narrow-sense heritability was observed among

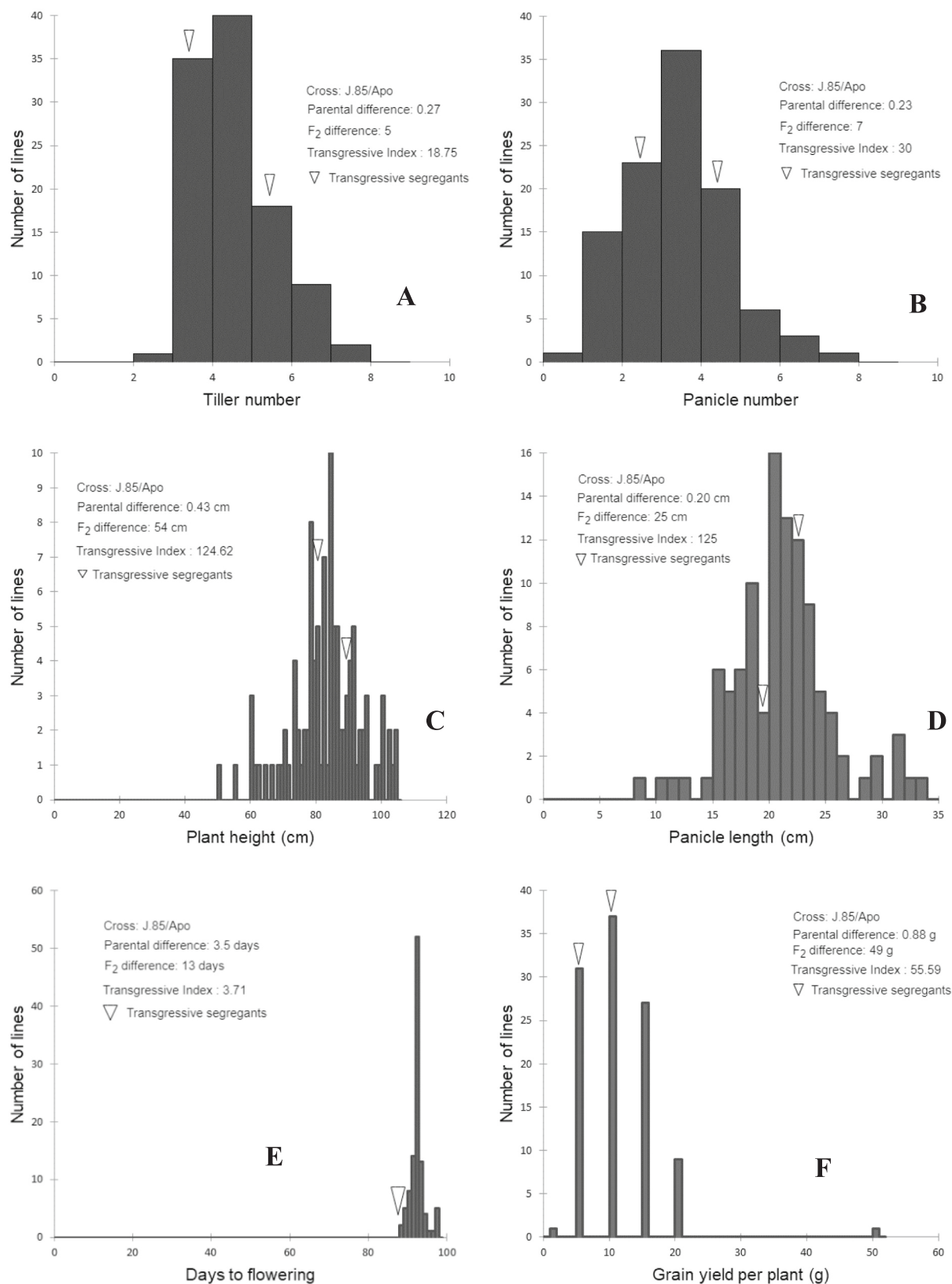


Fig. 8. Histogram for transgressive analysis in the F_2 population of J.85/Apo cross-evaluated under drought-stress conditions in 2022 for tiller number (A), panicle number (B), plant height (C), panicle length (D), days to flowering (E) and grain yield per plant (F) at CSIR-Crops Research Institute, Fumesua-Kumasi, Ghana. Histograms were conducted using 120 F_2 individual plants.

Table 4
Scaling tests for grain yield and yield-related traits for Agra/Apo cross under non-stress and drought-stress conditions evaluated under both vegetative and reproductive stages in 2022 at CSIR-Crops Research Institute, Fumesua, Ghana.

Variable	LRS		LDS		DRR		SPFS		TN		PN		PH		PL		DTF		GYP			
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS		
A	Scale A	-1.42	0.07	1.70	-0.35	-4.89	-0.76	-7.25	-0.32	17.68	0.24	4.80	5.88	914.54	581.89	133.77	85.52	6.41	19.05	5.73	-6.82	2.86
	Var	80.89	10.57	28.69	5.04	30.83	5.04	26.96	5.88	914.54	581.89	133.77	85.52	6.41	19.05	5.73	85.52	6.41	19.05	5.73	130.68	68.61
	S-D	8.99	3.25	5.36	2.25	5.55	2.25	5.19	2.42	30.24	24.12	11.57	9.25	2.53	7.52**	0.65	0.65	0.65	0.65	0.65	0.65	0.35
	t-cal	-0.16	0.02	0.54	-0.07	-0.88	-0.34	-1.40	-0.13	0.58	0.01	0.42	-0.59	0.01	-10.31	3.67	4.34	-10.31	3.67	4.34	-10.31	1.69
B	Scale B	0.40	1.90	0.13	5.80	-0.91	-5.87	-1.05	-0.32	16.67	-11.24	0.20	18.85	7.93	435.75	83.64	83.08	19.11	29.06	11.32	10.55	79.76
	Var	92.01	13.84	11.53	39.27	17.82	6.61	18.85	7.93	339.23	435.75	83.64	83.08	19.11	29.06	11.32	83.08	19.11	29.06	11.32	10.55	8.93
	S-D	9.59	3.72	3.40	6.27	4.22	2.57	4.34	2.82	18.42	20.87	9.15	9.12	9.12	9.12	9.12	9.12	9.12	9.12	9.12	9.12	9.12
	t-cal	0.04	0.04	0.93	-0.36	-1.45	-0.36	-1.35	-0.37	0.91	-0.54	0.24	-1.13	0.84	0.81	-0.42	0.81	0.81	-0.42	0.81	-0.42	0.19
C	Scale C	13.70	3.28	1.48	7.52	-0.24	2.24	-1.60	0.25	69.17	4.82	4.39	32.17	3142.30	2328.46	589.60	390.05	70.20	151.69	631.28	25.13	12.79
	Var	237.59	47.51	35.19	105.60	114.99	35.87	129.05	32.17	56.06	48.25	24.28	56.06	3142.30	2328.46	589.60	390.05	70.20	151.69	631.28	25.13	464.54
	S-D	15.41	6.89	5.93	10.28	10.72	5.99	11.36	5.67	17.41	7.91	1.31	1.23	0.10	-0.58	0.18	19.75	8.38	12.32	25.13	21.55	21.55
	t-cal	0.89	0.48	0.25	0.73	-0.02	0.37	-0.14	0.04	1.23	0.10	0.18	0.10	0.10	-0.58	0.18	19.75	8.38	12.32	25.13	21.55	21.55
D	Scale D	7.36	0.65	-0.18	1.04	5.39	1.96	5.76	0.81	17.41	7.91	1.31	1.23	0.10	-0.58	0.18	19.75	8.38	12.32	25.13	21.55	21.55
	Var	79.62	12.69	10.39	38.80	30.89	7.99	32.37	7.77	960.44	640.27	182.40	960.44	640.27	182.40	13.51	10.68	7.38	12.43	10.68	7.38	10.68
	S-D	8.92	3.56	3.22	6.23	5.56	2.83	5.69	2.79	30.99	25.30	13.51	30.99	25.30	13.51	10.68	7.38	12.43	10.68	7.38	12.43	10.68
	t-cal	0.82	0.18	-0.06	0.17	0.97	0.69	1.01	0.29	0.56	0.31	-0.10	0.56	0.31	-0.10	0.21	0.21	-0.64	-3.13**	0.41	0.41	0.39

Scaling tests (A, B, C and D); Var-Variance, S.D-Standard deviation; t-cal- calculated t-value; LRS-Leaf rolling score; LDS-Leaf drying score; DRR-Recovery from drought; SPFS-Spikelet fertility score; TN-Tiller number; PN-Panicle number; PH-Plant height; PL-Panicle length; DTF-Days to flowering; GYP- Grain yield per plant in gram; NS-Non-stress; DS-Drought-stress.

the traits with a magnitude ranging from 62.51 % for tiller number to 94.04 % for panicle number, whereas plant height recorded a moderate narrow-sense heritability of 50.35 %. High genetic advance over a mean (GAM) in % was noted for tiller number (30.56 %), panicle number (30.75 %) and panicle length (50.44 %), whereas the magnitude ranged from 2.49 % for DTF to 50.44 % for panicle length (Table 8). In J.85/Apo cross under non-stress conditions, a moderate broad-sense heritability was observed for plant height (41.45 %) and panicle number (30.71 %), while the other traits recorded low broad-sense heritability. High genetic advance over a mean (GAM) in % was noted for tiller number (56.84 %), panicle number (64.57 %) and panicle length (33.38 %), whereas the magnitude ranged from 0.64 % for plant height to 64.57 % for panicle number (Table 9).

Under drought-stress, in Agra/Apo cross, a moderate broad-sense heritability was observed for SPFS (49.30 %) and DTF (33.95 %), while the other traits recorded low broad-sense heritability. Moreover, high narrow-sense heritability was observed for panicle number (90.27 %), plant height (63.91 %) and panicle length (59.91 %), whereas LDS recorded a low narrow-sense heritability of 1.57 % (Table 8). High GAM (%) was noted for LRS (40.32 %), SPFS (89.56 %), tiller number (25.67 %), panicle number (69.46 %), panicle length (46.90 %) and grain yield per plant (59.55 %), whereas low to moderate magnitudes were observed for DTF (4.43 %) and 14.27 % for DRR (Table 8). Under drought-stress, in J.85/Apo cross, a high broad-sense heritability was observed for LRS (67.50 %) and grain yield per plant (62.62 %), while the other traits recorded low to moderate broad-sense heritability with the lowest broad-sense heritability of 5.50 % on panicle length. Moreover, high narrow-sense heritability was observed for tiller number (94.74 %), DTF (69.87 %) and grain yield per plant (87.35 %), whereas the other traits recorded a moderate narrow-sense heritability, with the lowest value of 18.16 % for SPFS. High GAM (%) was noted for all the traits except for plant height which recorded a moderate value of 16.31 % and a DTF low value of 3.24 % (Table 9).

3.4.5. Correlations among grain yield and yield-related traits across segregating populations

Pearson's correlation analysis was done to assess the relatedness of grain yield with yield-related traits across the three segregating populations in each cross – F₂, BC₁ and BC₂, and water regime. Pearson's correlation analysis revealed significant positive correlations for grain yield per plant with most of the other traits studied in this evaluation among all crosses under non-stress and drought-stress. Under non-stress conditions in Agra/Apo cross, grain yield per plant recorded a significant positive association with tiller number, panicle number, plant height, and non-significant positive correlation with panicle length, but non-significant negative relation with DTF. Under non-stress conditions in J.85/Apo cross, grain yield per plant recorded a significant positive association with panicle number and plant height, while non-significant positive correlation with tiller number and panicle length, but significant negative relation with DTF (Additional file 1_S6). Under drought-stress in Agra/Apo cross, grain yield per plant recorded a significant positive association with tiller number, panicle number, while non-significant positive correlation with panicle length and plant height, but a non-significant negative relation with DTF and SPFS. The relationship of grain yield per plant with the other traits were non-significant but positive (Additional file 1_S7). Under drought-stress in J.85/Apo cross, grain yield per plant recorded a significant positive association with panicle number, while non-significant positive correlation with panicle length, plant height and LRS, but non-significant negative relation with DTF, tiller number and SPFS. The relationship of grain yield per plant with the other traits were non-significant but negative values (Additional file 1_S7).

4. Discussions

This study appraised the genetic basis and inheritance behind the

Table 5

Scaling tests for grain yield and yield-related traits for J.85/Apo cross under non-stress and drought-stress conditions evaluated under both vegetative and reproductive stages in 2022 at CSIR-Crops Research Institute, Fumesua, Ghana.

Variable		LRS	LDS	DRR	SPFS	TN		PN		PH		PL		DTF		GYP
		DS	DS	DS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	DS
A	Scale A	3.83	1.37	1.30	1.13	-0.73	-2.10	-6.73	-1.10	-35.80	-24.77	-18.27	-8.13	18.20	-0.10	5.83
	Var	60.18	15.29	11.12	23.47	14.28	5.09	17.02	5.49	1436.98	595.52	183.03	95.57	12.92	11.55	94.63
	S.D.	7.76	3.91	3.33	4.84	3.78	2.26	4.13	2.34	37.91	24.40	13.53	9.78	3.59	3.40	9.73
	t-cal	0.49	0.35	0.39	0.23	-0.19	-0.93	-1.63	-0.47	-0.94	-1.01	-1.35	-0.83	5.06**	-0.03	0.60
B	Scale B	8.94	2.45	-1.71	7.68	-0.52	0.31	-1.48	-1.50	13.45	-19.32	-1.95	-7.75	0.18	-1.07	2.19
	Var	66.41	13.30	9.53	25.43	19.41	4.95	21.39	6.83	423.24	786.63	114.19	218.73	20.49	13.66	124.58
	S.D.	8.15	3.65	3.09	5.04	4.41	2.23	4.63	2.61	20.57	28.05	10.69	14.79	4.53	3.70	11.16
	t-cal	1.10	0.67	-0.55	1.52	-0.12	0.14	-0.32	-0.57	0.65	-0.69	-0.18	-0.52	0.04	-0.29	0.20
C	Scale C	15.97	4.57	-0.63	11.39	7.57	1.68	9.00	0.72	54.82	-7.55	2.16	-4.18	-4.36	-8.83	12.72
	Var	278.33	60.31	45.37	95.74	100.43	22.92	100.56	35.17	2436.96	2436.85	325.59	365.92	49.48	61.95	666.60
	S.D.	16.68	7.77	6.74	9.78	10.02	4.79	10.03	5.93	49.37	49.36	18.04	19.13	7.03	7.87	25.82
	t-cal	0.96	0.59	-0.09	1.16	0.76	0.35	0.90	0.12	1.11	-0.15	0.12	-0.22	-0.62	-1.12	0.49
D	Scale D	1.60	0.38	-0.11	1.29	4.41	1.73	8.61	1.66	38.59	18.27	11.19	5.85	-11.37	-3.83	2.35
	Var	93.24	17.98	13.43	31.24	26.57	5.33	28.69	8.19	856.39	746.56	134.47	140.97	9.48	17.39	192.11
	S.D.	9.66	4.24	3.67	5.59	5.15	2.31	5.36	2.86	29.26	27.32	11.60	11.87	3.08	4.17	13.86
	t-cal	0.17	0.09	-0.03	0.23	0.86	0.75	1.61	0.58	1.32	0.67	0.96	0.49	-3.69**	-0.92	0.17

Scaling tests (A, B, C and D); Var-Variance, S.D-Standard deviation; t-cal- calculated t-value; LRS-Leaf rolling score; LDS-Leaf drying score; DRR-Recovery from drought; SPFS-Spikelet fertility score; TN-Tiller number; PN-Panicle number; PH-Plant height; PL-Panicle length; DTF-Days to flowering; GYP- Grain yield per plant in gram; NS-non-stress; DS-Drought-stress.

expression of tolerance of the rice breeding lines to drought-stress and demonstrated that transgressive phenotypes can be produced when both parents in a cross have similar phenotypes, and determined the right breeding strategies to adopt in developing drought-tolerant varieties using this current breeding populations.

Most of the traits in this study combined moderate to high heritability and genetic advance as percentage of the mean, indicative of possible effective selection in early generation for these traits (Asante et al., 2019). Grain yield per plant has combined high broad-sense and narrow-sense heritability with high genetic advance as percentage of mean in J.85/Apo cross under drought-stress, indicating that direct selection for grain yield in this population will be rewarding. Such high heritability (>60 %) for grain yield and its related traits were also reported by several authors (Vikram et al., 2011; Swamy et al., 2017; Solis et al., 2018; Venkateshwarlu et al., 2022). The relatively identical narrow-sense heritability estimates for panicle number, plant height and panicle length and their positive association with grain yield under drought-stress and non-stress conditions imply that selection for these traits as indirect contributors for grain yield under drought-stress in rice lines might be rewarding with the same precision as that under non-stress conditions (Kumar et al., 2008), provided that the appraisals are well conducted. Overall, the mean performance of the six populations decreased significantly under drought-stress compared to the non-stress conditions for both Agra/Apo and J.85/Apo crosses for all the studied traits, indicating the effectiveness of the imposed stress conditions. Severe decrease in grain yield of rice under drought-stress has been reported by Maisura et al. (2014) and Torres and Henry (2018), while Singh et al. (2010) observed a reduction in many phenological traits including grain yield under drought-stress in six generations of six crosses of rice under non-stress and drought-stress conditions.

Unlike heterosis, transgressive segregation is the formation of transgressive phenotypes (extreme phenotypes) in a segregating population (F₂, BC, RILs) towards a negative or positive direction outside the range of the two parental lines, and the heritability of these extreme phenotypes are stable (Nirubana et al., 2021). It provides an opportunity for the development of new hybrid species, that are more fit when compared to their ancestors. It is helpful to create varieties that are more adaptable and resilient in stress environments than their counterpart parents, therefore useful in robust hybrids production (Nirubana et al., 2021). In the view to check whether extreme phenotypes can be produced when both parents in a cross have similar phenotypes, it is observed in this current study that under non-stress conditions, despite

the absence of significant differences in the two parental varieties, namely Agra and Apo for tiller number, panicle number, panicle length, DTF and grain yield per plant, whereas J.85 and Apo for tiller number, panicle length and grain yield per plant, transgressive phenotypes were, however, formed for these traits. Under drought-stress, at least one transgressive phenotype was produced for each trait whether there is a significant difference or not among the parental lines involved in the development of the F₂ populations. While the progenies from parents with the proximal phenotypes are expected to exhibit a very narrow phenotypic variation (Kim and Rieseberg, 1999; Mansur et al., 1993), the presence of transgressive phenotypes in the F₂ progenies in this current study despite the similarity of the two parents for most traits, can be explained by various reasons among which a high mutation rate in hybrids, low developmental stability, epistasis, overdominance, the expression of unexpressed rare recessive heterozygous alleles in the parents genome, variation in chromosome number or complementary action of dispersed additive alleles between the parental lines. Based on a genome-wide SNP analysis, Koide et al. (2019) deciphered that the transgressive phenotypes for DTF were formed through the exchange of complementary alleles of a few minor QTL in a cross of two identical parental phenotypes. No transgressive phenotypes were observed for DTF in both F₂ progenies for Agra/Apo with a transgressive index (TI) of 7.86 and no significance between Agra and Apo, whereas J.85/Apo with a TI of 4.19 and a significant difference observed between J.85 and Apo under non-stress conditions. On the other hand, under drought-stress, lower TI of 3.46 and 3.71 for Agra/Apo and J.85/Apo, respectively, resulted in the production of transgressive phenotypes. Such a relatively low transgressive segregation was not noted in the F₂ progenies of six crosses between the genotype A58 and the other varieties where the TIs ranged from 0.91 to 2.12 (Ota et al., 2014), while a strong transgressive segregation of 25.7 was observed in the A58/Kitaake cross, indicating that DTF of several progenies of F₂ population surpassed the range between their parents (Koide et al., 2019). Across both water regimes, the tiller number recorded an identical phenotype performance between the recipient's parents (Agra and J.85) with the donor parent (Apo), but both Agra/Apo and J.85/Apo crosses resulted in strong transgressive segregation with TI ranging from 10.04 under non-stress to 18.75 under drought-stress. Such a high transgressive segregation was not seen in any of the evaluations of 378 and 425 progenies of the F₂ population (Fukuta et al., 2003), while it was observed in the study of Reddyamini et al. (2019). These high frequencies of desirable transgressive segregants associated with polygenic inheritance for grain yield and its

Table 6
Generation mean analysis for grain yield and yield-related traits for Agra/Apo cross under non-stress and drought-stress evaluated under both vegetative and reproductive stages in 2022 at CSIR-Crops Research Institute, Fumesua, Ghana.

Variable		LRS	LDS	DRR	SFPS	TN		PN		PH		PL		DTF		GY	
		DS	DS	DS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
m	m	6.82	3.29	3.44	5.65	7.73	4.28	6.35	2.86	110.1	81.49	23	19.22	91.68	93.64	12.2	10.89
	var	11.54	2.12	1.64	6.03	5.75	1.69	6.4	1.52	174.7	119.4	34.4	21.11	3.37	8.05	29.91	23.64
	S.D.	3.4	1.46	1.28	2.45	2.4	1.3	2.53	1.23	13.22	10.93	5.86	4.59	1.84	2.84	5.47	4.86
	t-cal.	2.01**	2.26**	2.69**	2.30**	3.22**	3.29**	2.51**	2.32**	8.33**	7.46**	3.93**	4.18**	49.93**	33.01**	2.23**	2.24**
d	d	-0.98	-0.95	0.32	-2.54	0.26	-0.19	-1.26	0.12	-3.54	0.65	1.12	1.47	8.26	2.86	-1.89	0.86
	var	33.47	4.21	3.83	14.7	7.9	1.22	6.78	1.67	261.5	162.5	45	29.57	2.98	22.25	34.84	19.69
	S.D.	5.79	2.05	1.96	3.83	2.81	1.1	2.6	1.29	16.17	12.75	6.71	5.44	1.73	4.72	5.9	4.44
	t-cal.	-0.17	-0.46	0.16	-0.66	0.09	-0.17	-0.48	0.1	-0.22	0.05	0.17	0.27	4.78**	0.61	-0.32	0.19
h	h	-17.51	-2.24	-2.44	-7.61	-12.4	-5.35	-13.02	-1.88	-41.73	-16.39	1.46	1.46	26.03	11.12	-15.1	-10.3
	var	331.72	54.17	43.79	158	129.3	34.17	136.2	33.02	3928	2665	740	469.1	69.95	223.5	656.2	478.6
	S.D.	18.21	7.36	6.62	12.6	11.37	5.85	11.67	5.75	62.68	51.63	27.2	21.66	8.36	14.95	25.62	21.88
	t-cal.	-0.96	-0.3	-0.37	-0.61	-1.09	-0.92	-1.12	-0.33	-0.67	-0.32	0.05	0.07	3.11**	0.74	-0.59	-0.47
i	i	-29.25	-15.04	-13.1	-27.7	-30.4	-17.48	-27.92	-11.19	-447.4	-324.7	-89.8	-73.96	-350.2	-369	-52.6	-41.8
	var	318.47	50.77	41.54	155	123.6	31.98	129.5	31.08	3842	2561	730	456	65.88	217.7	618	457.1
	S.D.	17.85	7.13	6.45	12.5	11.12	5.65	11.38	5.57	61.98	50.61	27	21.35	8.12	14.76	24.86	21.38
	t-cal.	-1.64	-2.11**	-2.03**	-2.22**	-2.73**	-3.09**	-2.45**	-2.01**	-7.22**	-6.42**	-3.32**	-3.46**	-43.15**	-25.00**	-2.12**	-1.96*
j	j	-0.91	-0.91	0.79	-3.08	0.62	0.08	-0.69	0.36	0.51	5.74	1.3	2.42	7.69	0.69	-1.18	0.58
	var	39.73	4.6	4.75	17	10.66	2.41	9.45	3.28	278.8	241.9	53.7	41.65	5.71	25.65	48	32.92
	S.D.	6.3	2.15	2.18	4.12	3.27	1.55	3.07	1.81	16.7	15.55	7.33	6.45	2.39	5.06	6.93	5.74
	t-cal.	-0.14	-0.43	0.36	-0.75	0.19	0.05	-0.22	0.2	0.03	0.37	0.18	0.37	3.22**	0.14	-0.17	0.1
l	l	15.73	-0.67	-2.19	-3.37	21.8	5.59	24.63	2.99	0.46	26.82	-9.61	20.18	-48.11	-19.5	21.37	3.68
	var	773.15	114.85	96.52	341	241.4	55.37	237.5	58.93	7326	4929	1310	863.2	117.94	507.7	1189	779.6
	S.D.	27.81	10.72	9.82	18.5	15.54	7.44	15.41	7.68	85.59	70.21	36.2	29.38	10.86	22.53	34.48	27.92
	t-cal.	0.57	-0.06	-0.22	-0.18	1.4	0.75	1.6	0.39	0.01	0.38	-0.27	0.69	-4.43**	-0.86	0.62	0.13

** Significant at 0.01; NS-Non-stress; DS-Drought-stress; Var-Variance; S.D-Standard deviation; t-cal- calculated t-value; LRS-Leaf rolling score; LDS-Leaf drying score; DRR-Recovery from drought; SFPS-Spikelet fertility score; TN-Tiller number; PN-Panicle number; PH-Plant height; PL-Panicle length; DTF-Days to flowering; GYP- Grain yield per plant; d-additive gene effect; d-dominant gene effect; i- additive × additive gene interaction; j-additive × dominant gene interaction; l-dominant × dominant gene interaction.

Table 7

Generation mean analysis for grain yield and yield-related traits for J.85/Apo cross under non-stress and drought-stress evaluated under both vegetative and reproductive stages in 2022 at CSIR-Crops Research Institute, Fumesua, Ghana.

Variable		LRS	LDS	DRR	SFPS	TN		PN		PH		PL		DTF		GYP
		DS	DS	DS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	DS
m	m	5.42	3.75	4.08	5.56	7.89	4.04	7.03	2.87	106.7	82.22	23.94	20.56	91.39	91.88	10.95
	var	16.4	3.11	2.4	5.37	5.39	1.05	5.51	1.72	117.9	123.1	17.61	19.11	1.42	3.28	37.47
	S.D.	4.05	1.76	1.55	2.32	2.32	1.03	2.35	1.31	10.86	11.1	4.2	4.37	1.19	1.81	6.12
	t-cal.	1.34	2.13**	2.64**	2.40**	3.40**	3.93**	3.00**	2.19**	9.83**	7.41**	5.70**	4.70**	76.78**	50.73**	1.79
d	d	-4.57	-0.29	0.72	-4.8	-0.71	-1.34	-3.46	0.08	-27.21	-2.51	-7.69	-0.09	9.85	2.23	2.26
	var	27.65	5.52	3.85	9.76	5.03	1.11	6.66	1.3	384.7	254.2	64.02	64.53	3.82	4.27	42.21
	S.D.	5.26	2.35	1.96	3.12	2.24	1.05	2.58	1.14	19.61	15.94	8	8.03	1.95	2.07	6.5
	t-cal.	-0.87	-0.12	0.37	-1.6	-0.31	-1.27	-1.34	0.07	-1.39	-0.16	-0.96	-0.01	5.04**	1.08	0.35
h	h	-6.04	-1.97	0.41	-6	-13.48	-5.37	-22.11	-4.04	-86.55	-40.08	-21.8	-8.91	23.11	11.48	-6.91
	var	376.9	74.5	55.5	127	109.84	22.82	117.9	34.66	3563	3103	548.8	578.91	44.63	71.93	785.19
	S.D.	19.42	8.63	7.45	11.3	10.48	4.78	10.86	5.89	59.69	55.71	23.43	24.06	6.68	8.48	28.02
	t-cal.	-0.31	-0.23	0.06	-0.5	-1.29	-1.12	-2.04**	-0.69	-1.45	-0.72	-0.93	-0.37	3.46**	1.35	-0.25
i	i	-30.8	-15.6	-14.9	-32	-32.97	-18.83	-35.06	-11.32	-481.3	-333.9	-111	-82.4	-345.87	-363.1	-39.29
	var	373	71.9	53.7	125	106.28	21.31	114.8	32.77	3426	2986	537.9	563.87	37.93	69.56	768.44
	S.D.	19.31	8.48	7.33	11.2	10.31	4.62	10.71	5.72	58.53	54.65	23.19	23.75	6.16	8.34	27.72
	t-cal.	-1.6	-1.84	-2.03**	-2.86**	-3.20**	-4.08**	-3.27**	-1.98**	-8.22**	-6.11**	-4.79**	-3.47**	-56.16**	-43.53**	-1.42
j	j	-2.55	-0.54	1.5	-3.3	-0.11	-1.21	-2.63	0.2	-24.62	-2.72	-8.16	-0.19	9.01	0.48	1.82
	var	31.65	6.15	4.72	12.2	8.25	2.4	9.44	2.97	407.9	320.1	73.64	77.57	6.19	5.97	50.64
	S.D.	5.63	2.48	2.17	3.5	2.87	1.55	3.07	1.72	20.2	17.89	8.58	8.81	2.49	2.44	7.12
	t-cal.	-0.45	-0.22	0.69	-0.9	-0.04	-0.78	-0.85	0.12	-1.22	-0.15	-0.95	-0.02	3.62**	0.2	0.26
l	l	-9.58	-3.06	0.18	-6.2	10.07	5.25	25.43	5.92	99.52	80.62	42.59	27.6	-41.12	-6.5	-3.32
	var	720.7	149	107	252	180.83	40.67	207.1	55.89	8592	6504	1350	1398.4	110.53	130.26	1342
	S.D.	26.85	12.2	10.3	15.9	13.45	6.38	14.39	7.48	92.69	80.64	36.74	37.4	10.51	11.41	36.63
	t-cal.	-0.36	-0.25	0.02	-0.4	0.75	0.82	1.77	0.79	1.07	1	1.16	0.74	-3.91**	-0.57	-0.09

** Significant at 0.01; NS-Non-stress; DS-Drought-stress; Var-Variance; S.D-Standard deviation; t-cal- calculated t-value; LRS-Leaf rolling score; LDS-Leaf drying score; DRR-Recovery from drought; SFPS-Spikelet fertility score; TN-Tiller number; PN-Panicle number; PH-Plant height; PL-Panicle length; DTF-Days to flowering; GYP- Grain yield per plant; d-additive gene effect; d-dominant gene effect; i- additive $\times$ additive gene interaction; j-additive $\times$ dominant gene interaction; l-dominant $\times$ dominant gene interaction.

Table 8
Heritability/repeatability, genetic advance, heterosis and degree of dominance for grain yield and yield-related traits for Agra/Apo cross under non-stress and drought-stress conditions evaluated under both vegetative and reproductive stages in 2022 at CSIR-Crops Research Institute, Fumesua, Ghana.

Variable	LRS		LDS		DRR		SPFS		TN		PN		PH		PL		DTF		GYP	
	DS		DS		DS		DS		NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
HMP	-58.31	-31.82	-62.69	-84.69	-18.30	-32.37	-20.01	-8.93	-7.19	-0.71	-5.14	30.52	0.69	1.87	-33.33	-23.55				
MRH	42.22	12.01	-23.05	-13.57	-9.84	-3.56	-15.35	-2.30	14.37	1.14	2.31	0.37	-0.38	1.12	-18.65	24.91				
Vg	4.54	-0.88	0.30	6.03	2.75	0.69	2.40	1.19	105.41	94.43	33.01	20.11	2.04	5.71	4.91	15.31				
h ² _{ns}	7.50	28.11	-	49.30	18.58	-	23.46	-	73.58	4.41	63.03	22.12	-	33.95	13.48	13.64				
h ² _{ns}	-	1.57	-	-	62.51	-	94.04	90.27	50.35	63.91	68.96	59.91	-	-	83.53	-				
GA	2.75	-	0.49	5.06	2.36	1.10	1.95	1.99	16.43	17.80	11.60	9.02	2.29	4.15	1.85	6.49				
GAM	40.32	-	14.27	89.56	30.56	25.67	30.75	69.46	14.92	21.84	50.44	46.90	2.49	4.43	15.17	59.55				
DD	3.15	3.59	3.38	3.27	4.05	5.29	4.48	4.44	3.88	4.05	4.05	3.98	4.84	3.17	4.34	4.93				

HMP- Heterosis over mid-parent; MRH- Mid-parent residual heterosis; Vg- Genetic variance; h²_{ns} - Broad-sense heritability; h²_{ns} - Narrow-sense heritability; GA- Genetic advance; GAM- Genetic advance as percentage of mean; DD- Degree of dominance; LRS-Leaf rolling score; LDS-Leaf drying score; DRR-Recovery from drought; SPFS-Spikelet fertility score; TN-Tiller number; PN-Panicle number; PH-Plant height; PL-Panicle length; DTF-Days to flowering; GYP- Grain yield per plant; NS-Non-stress; DS-Drought-stress.

Table 9
Heritability/repeatability, genetic advance, heterosis and degree of dominance for grain yield and yield-related traits for J.85/Apo cross under non-stress and drought-stress conditions evaluated under both vegetative and reproductive stages in 2022 at CSIR-Crops Research Institute, Fumesua, Ghana.

Variable	LRS		LDS		DRR		SPFS		TN		PN		PH		PL		DTF		GYP	
	DS		DS		DS		DS		NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
HMP	-100.00	-37.82	4.42	-77.44	-55.99	-41.61	-67.75	-23.50	-9.60	-4.13	2.31	13.86	0.40	4.14	-34.14	-24.93				
MRH	90.21	16.58	-1.61	25.51	-5.28	-11.61	-2.79	-5.85	9.22	-4.27	3.49	1.76	-0.98	-0.33	1.70	23.33				
Vg	16.40	1.11	1.51	5.37	5.05	0.83	5.17	1.50	3.59	72.21	16.28	17.11	-	2.61	-	29.14				
h ² _{ns}	67.50	51.85	39.27	38.88	-	-	-	-	-	14.81	-	5.50	-	24.12	-	62.62				
h ² _{ns}	31.36	22.61	39.41	18.16	18.00	94.74	30.71	-	41.45	-	24.67	-	-	69.87	-	87.35				
GA	8.34	1.30	2.01	4.77	4.49	1.67	4.54	2.36	0.68	13.41	7.99	8.06	-	2.97	-	9.81				
GAM	154.00	34.66	49.13	85.78	56.84	41.35	64.57	82.05	16.31	16.31	33.38	39.22	-	3.24	-	89.53				
DD	3.69	3.67	3.80	3.61	4.68	4.53	4.21	5.17	3.04	3.49	2.93	3.00	3.42	4.10	-	4.31				

HMP- Heterosis over mid-parent; MRH- Mid-parent residual heterosis; Vg- Genetic variance; h²_{ns} - Broad-sense heritability; h²_{ns} - Narrow-sense heritability; GA- Genetic advance; GAM- Genetic advance as percentage of mean; DD- Degree of dominance; LRS-Leaf rolling score; LDS-Leaf drying score; DRR-Recovery from drought; SPFS-Spikelet fertility score; TN-Tiller number; PN-Panicle number; PH-Plant height; PL-Panicle length; DTF-Days to flowering; GYP- Grain yield per plant; NS-Non-stress; DS-Drought-stress.

related traits indicate the presence of a large scope for transferring favorable alleles into a single line through adequate selection in later generations (Reddyamini et al., 2019).

Epistasis is defined as any form of non-allelic interaction (Boubacar Gaoh et al., 2020), making the expression of gene interaction more complex. This complexity can be overcome when intensity of the epistasis is relatively low, but when epistasis is the primary source of genetic variation, no measure of additive or dominance variation is possible (Hayman, 1960). The non-significance of the four scaling tests for most of the grain yield and yield-related traits in both Agra/Apo and J.85/Apo crosses under both non-stress and drought-stress conditions indicates that epistatic interaction effects is not the primary source of genetic variation in the inheritance genes governing grain yield and yield-related traits in these rice lines; therefore, additive or dominance effects are more likely to express themselves.

In this current study, among the direct gene effect, the magnitude of the dominance effect was preponderant compared to the additive in both crosses under non-stress and drought-stress conditions, providing the evidence that the dominance gene effect is predominant in the inheritance of these traits. Dominance gene effect was in the negative direction for most of the traits, except days to flowering which showed consistent positive direction across all crosses and water regimes. The predominance of dominant effect is further emphasized by the high values of the degree of dominance calculated for all the traits in this study under both crosses and water regimes. Such level of dominance was also observed by Yogameenakshi et al. (2019) and Gobu et al. (2021) for agronomic traits, including grain yield, hundred grains weight, panicle number, filled grains per panicle, harvest index, flag leaf width and spikelet fertility.

In this current study, among the interaction effects, additive $\times$ additive gene interaction was significant for most of the traits, even though the scaling tests were not significant. Other authors reported similar significance for additive $\times$ additive gene interaction in panicle length and number of filled grains per panicle (Yogameenakshi et al., 2019). Moreover, the magnitude of additive $\times$ additive gene interaction was higher than the dominance $\times$ dominance gene interaction which was also higher than additive $\times$ dominance type of gene interaction for most of the studied traits in both crosses and in both non-stress and drought-stress conditions, independent of the $-$ or $+$ signs. The predominance of significant additive $\times$ additive gene action for most traits in this study across both water regimes indicates that selection could be effective in early generations since additive gene effect and additive $\times$ additive gene interaction effects constitute the fixable genetic variance (Pujar et al., 2022).

Apart from the significance of all the six types of gene actions (mean effect, additive effect, dominance effect, additive $\times$ additive effect, additive $\times$ dominance effect and dominance $\times$ dominance effect) for days to flowering under non-stress conditions in both crosses and the dominance gene effects and dominance $\times$ dominance gene effect were having opposite sign for days to flowering which indicate the presence of duplicate epistasis, clearly explaining the complex nature of this trait, thereby making early generation selection a difficult task since super lines development could only be achieved through population improvement using pedigree selection in the later generation. Similar duplicate epistasis is reported by Gobu et al. (2021) and Pujar et al. (2022), while Yogameenakshi et al. (2019) reported additive $\times$ dominance and dominance $\times$ dominance gene interaction effects in days to flowering.

Under both non-stress and drought-stress conditions, all the F_1 hybrid lines obtained in the present study did not exceed the mean of the better parent for all the traits except for panicle length and days to flowering which showed consistency across the crosses and water regimes. This indicates that there was no heterosis over the better parent. Moreover, the predominance of additive $\times$ additive type of gene interaction for these traits' inheritance would render it difficult to obtain better parent heterosis. Most of the heterosis over mid-parent (HMP) and

residual heterosis over mid-parent (HRM) were in a negative direction implying that most of the HMP obtained in the F_1 generation are retained in F_2 generation.

In general, the correlation between grain yield per plant and its related traits were positive and significant except for DTF and SPFS which recorded consistent negative correlation across both crosses in these segregating populations in the present study, signifying that these traits are co-segregating. Thus, these results tend to indicate that indirect selection of grain yield in rice could be effective in improving grain yield under drought using secondary traits such as tiller number, panicle number, plant height, panicle length and SPFS.

5. Conclusion

One major challenge in rice production is to increase production under increasing drought as a result of climate change, but the use of drought-tolerant cultivars can be one of the solutions as they can secure high yields under drought. This study sought to understand the genetic basis and inheritance behind the expression of tolerance of the rice breeding lines to drought-stress. Under the greenhouse evaluation, overall mean performance of the six populations (P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2) has decreased significantly under drought-stress compared to non-stress conditions for Agra/Apo cross as well as J.85/Apo cross for all the studied traits, indicating the effectiveness of stress imposition. To check whether extreme phenotypes can be produced when both parents in a cross have similar phenotypes, it is observed that under drought-stress, at least one transgressive phenotype was produced for each trait whether there is a significant difference or not among the parental lines involved in the development of the F_2 populations. In this current study, among the interaction effects, additive $\times$ additive gene interaction was significant for most of the traits even though the scaling tests were not significant. The predominance of significant additive $\times$ additive gene action for most traits in this study across both water regimes indicates that selection could be effective in early generations. With the predominance of the additive $\times$ additive type of gene interaction among these segregating populations, selection for grain yield using secondary traits can be done in early generations using either forward breeding or backcross breeding.

CRedit authorship contribution statement

Kossi Lorimpo Adjah: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Maxwell Darko Asante:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Aboubacar Toure:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Mawuli Aziadekey:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Shailesh Yadav:** Writing – review & editing, Validation. **Felix Frimpong:** Writing – review & editing, Validation. **Francis Osei Amoako-Andoh:** Writing – review & editing, Validation. **Daniel Dzorkpe Gamenyah:** Writing – review & editing, Validation, Data curation.

Declaration of competing interest

The authors declare that they have no competing interests.

Data availability

All data generated or analysed during this study are included in this published article and its supplementary information files.

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Appendix A. Supplementary data

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References

- Asante, M.D., Adjah, K.L., Annan-Afful, E., 2019. Assessment of genetic diversity for grain yield and yield component traits in some genotypes of rice (*Oryza Sativa* L.). *J. Crop. Sci. Biotechnol.* 22 (2), 123–130. <https://doi.org/10.1007/S12892-019-0008-0/METRICS>.
- Bates, B.C., Kundzewicz, Z.W., Wu, S., Palutikof, J.P., 2008. June. Climate Change and Water – IPCC. Technical Paper of the Intergovernmental Panel on Climate Change. IPCC Secretariat, Geneva. <https://www.ipcc.ch/publication/climate-change-and-water-2/>.
- Boubacar Gaoh, B.S., Gangashetty, P.I., Mohammed, R., Dzidzienyo, D.K., Tongoono, P., 2020. Generation mean analysis of pearl millet [*Pennisetum glaucum* (L.) R. Br.] grain iron and zinc contents and agronomic traits in West Africa. *J. Cereal Sci.* 96, 103066. <https://doi.org/10.1016/J.JCS.2020.103066>.
- Cazzola, F., Bermejo, C.J., Cointin, E., 2020. Transgressive segregations in two pea F2 populations and their respective F2:3 families. *Pesq. Agrop. Brasileira* 55. <https://doi.org/10.1590/S1678-3921.PAB2020.V55.01623>.
- Centritto, M., Lauteri, M., Monteverti, M.C., Serraj, R., 2009. Leaf gas exchange, carbon isotope discrimination, and grain yield in contrasting rice genotypes subjected to water deficits during the reproductive stage. *J. Exp. Bot.* 60 (8), 2325–2339. <https://doi.org/10.1093/JXB/ERP123>.
- Efise, A.A., Tongoono, P., Derera, J., Ubi, B.E., Oselebe, H.O., 2009. Genetics of morpho-physiological traits in segregating populations of interspecific hybrid rice under stress and non-stress conditions. *J. Crop Improv.* 23 (4), 383–401. <https://doi.org/10.1080/15427520902976471>.
- Fang, Y., Xiong, L., 2015. General mechanisms of drought response and their application in drought resistance improvement in plants. *Cell. Mol. Life Sci.* 72 (4), 673–689. <https://doi.org/10.1007/S00018-014-1767-0>.
- Fonseca, S., Patterson, F.L., 1968. Hybrid vigor in a seven-parent diallel cross in common winter wheat (*Triticum aestivum* L.). *Crop Sci.* 8 (1), 85–88. <https://doi.org/10.2135/CROPSCI1968.0011183X000800010025X>.
- Fukuta, Y., Araki, E., Ebron, L.A., Cuevas, P.R., Mercado-Escueta, D., Khush, G.S., Sheehy, J.E., Tsunematsu, H., Kato, H., 2003. Identification of the low-tillering gene in rice (*Oryza sativa* L.). In: *JIRCAS Research Highlights*.
- Gobu, R., Lal, J.P., Anandan, A., 2021. Generation mean analysis for yield and drought tolerant traits under rainfed and irrigated conditions in rice (*Oryza sativa* L.). *Int. J. Environ. Clim. Chang.* 11 (11), 170–178. <https://doi.org/10.9734/IJECC/2021/V11I1130530>.
- Hayman, B.I., 1958. The separation of epistatic from additive and dominance variation in generation means. *Heredity* 12, 371–390.
- Hayman, B.I., 1960. The separation of epistatic from additive and dominance variation in generation means. II. *Genetica* 31 (1), 133–146. <https://doi.org/10.1007/BF01984430>.
- Johnson, H.W., Robinson, H.F., Comstock, R.E., 1955. Estimates of genetic and environmental variability in soybeans. *Agron. J.* 47 (7), 314–318. <https://doi.org/10.2134/AGRONJ1955.0002196200470009X>.
- Kim, S.C., Rieseberg, L.H., 1999. Genetic architecture of species differences in annual sunflowers: implications for adaptive trait introgression. *Genetics* 153 (2), 965. <https://doi.org/10.1093/GENETICS/153.2.965>.
- Koide, Y., Sakaguchi, S., Uchiyama, T., Ota, Y., Tezuka, A., Nagano, A.J., Ishiguro, S., Takamura, I., Kishima, Y., 2019. Genetic properties responsible for the transgressive segregation of days to heading in rice. *G3 Genes/Genomes/Genetics* 9 (5), 1655–1662. <https://doi.org/10.1534/G3.119.201011>.
- Kooyers, N.J., 2015. The evolution of drought escape and avoidance in natural herbaceous populations. *Plant Sci.* 234, 155–162. <https://doi.org/10.1016/J.PLANTSCI.2015.02.012>.
- Kumar, A., Bernier, J., Verulkar, S., Lafitte, H.R., Atlin, G.N., 2008. Breeding for drought tolerance: direct selection for yield, response to selection and use of drought-tolerant donors in upland and lowland-adapted populations. *Field Crop Res.* 107 (3), 221–231. <https://doi.org/10.1016/J.FCR.2008.02.007>.
- Kumar, A., Dixit, S., Ram, T., Yadav, R.B., Mishra, K.K., Mandal, N.P., 2014. Breeding high-yielding drought-tolerant rice: genetic variations and conventional and molecular approaches. *J. Exp. Bot.* 65 (21), 6265. <https://doi.org/10.1093/JXB/ERU363>.
- Lafitte, H.R., Blum, A., Atlin, G., 2003. Using secondary traits to help identify drought-tolerant genotypes. In: Fischer, K.S., Lafitte, R.H., Fukai, S., Atlin, G., Hardy, B. (Eds.), *Breeding Rice for Drought-Prone Environments*. International Rice Research Institute, pp. 37–48.
- Lamo, J., 2010. Genetic Studies on Drought Tolerance and Grain Shattering in Rice. PhD. University of KwaZulu-Natal. <https://researchspace.ukzn.ac.za/handle/10413/7357/show=full>.
- Maisura, Chozin, M., Lubis, I., Junaedi, A., Ehara, H., 2014. Some Physiological Character Responses of Rice under Drought Conditions in a Paddy System. Undefined.
- Mansur, L.M., Lark, K.G., Kross, H., Oliveira, A., 1993. Interval mapping of quantitative trait loci for reproductive, morphological, and seed traits of soybean (*Glycine max* L.). *Theor. Appl. Genet.* 86 (8), 907–913. <https://doi.org/10.1007/BF00211040/METRICS>.
- Mather, K., 1949. *Biometrical Genetics: The Study of Continuous Variation* (1st Edition). Metuen and Co.Ltd. <https://www.abebooks.com/first-edition/Biometrical-Genetics-Study-Continuous-Variation-Mather/30685509296/bd>.
- Mitra, J., 2001. Genetics and genetic improvement of drought tolerance in crop plants. *Curr. Sci.* 80, 758–762.
- Nadarajan, N., Manivannan, N., Gunasekaran, M., 2016. *Quantitative Genetics and Biometrical Techniques in Plant Breeding*, 1st ed. Kalyani Publishers <http://kalyanipublishers.co.in/index.php/welcome/searchbook>.
- Nirubana, V., Palaniyappan, S., Ramamoorthy, P., Karthikeyan, M., Deepika, C., 2021. Transgressive segregation and its importance in crop improvement. <https://ssrn.com/abstract=3800538>.
- Ota, Y., Ishiguro, S., Aoyama, E., Aiba, R., Iwashiro, R., Tanabata, T., Takamura, I., Fujino, K., Kishima, Y., 2014. Isolation of a major genetic interaction associated with an extreme phenotype using assorted F2 populations in rice. *Mol. Breed.* 33 (4), 997–1003. <https://doi.org/10.1007/s11032-013-9998-6>.
- Pujar, M., Govindaraj, M., Gangaprasad, S., Kanatti, A., Gowda, T.H., Dushyantha Kumar, B.M., Satish, K.M., 2022. Generation mean analysis reveals the predominant gene effects for grain iron and zinc contents in pearl millet. *Front. Plant Sci.* 12, 3269. <https://doi.org/10.3389/FPLS.2021.693680/BIBTEX>.
- Rao, N.G., 1980. *Statistics for Agricultural Sciences Second Edition, Second edition*. Oxford and IBH Publishing Co. Pvt. Ltd, New Delhi.
- Reddyvamin, B., Hariprasad Reddy, K., Narayana Reddy, V.L., Ramesh Babu, P., Sudhakar, P., 2019. Transgressive segregation for yield and its component traits in rice (*Oryza sativa* L.). *Int. J. Curr. Microbiol. App. Sci.* 8 (06), 2450–2455. <https://doi.org/10.20546/ijcmas.2019.806.292>.
- Robinson, H.F., Comstock, R.E., Harvey, P.H., 1949. Estimates of heritability and the degree of dominance in corn. *Agron. J.* 41 (8), 353–359. <https://doi.org/10.2134/AGRONJ1949.00021962004100080005X>.
- Serraj, R., Kumar, A., McNally, K.L., Slamet-Loedin, I., Bruskiewich, R., Mauleon, R., Cairns, J., Hijmans, R.J., 2009. Chapter 2 Improvement of drought resistance in rice. In: *Advances in Agronomy*, vol. 103. Academic Press Inc., pp. 41–99. [https://doi.org/10.1016/S0065-2113\(09\)03002-8](https://doi.org/10.1016/S0065-2113(09)03002-8).
- Shahryari, R., Gurbanov, E., Gadimov, A., Hassanpanah, D., 2008. Tolerance of 42 bread wheat genotypes to drought stress after anthesis. *Pak. J. Biol. Sci.* 11 (10), 1330–1335. <https://doi.org/10.3923/pjbs.2008.1330.1335>.
- Shavrukov, Y., Kurishbayev, A., Jatayev, S., Shvidchenko, V., Zotova, L., Koekemoer, F., De Groot, S., Soole, K., Langridge, P., 2017. Early flowering as a drought escape mechanism in plants: how can it aid wheat production? *Front. Plant Sci.* 8. <https://doi.org/10.3389/FPLS.2017.01950>.
- Singh, A.K., Mall, A.K., Singh, P.K., Verma, O.P., 2010. Interrelationship of genetics parameters for quantitative and physiological traits in rice under irrigated and drought conditions. In: *Oryza*, vol. 47, Issue 2. Short Communication. www.pdfactory.com.
- Solis, J., Gutierrez, A., Mangu, V., Sánchez Timm, E., Bedre, R., Linscombe, S., Baisakh, N., 2018. Genetic mapping of quantitative trait loci for grain yield under drought in rice under controlled greenhouse conditions. *Front. Chem.* 5, 129. <https://doi.org/10.3389/fchem.2017.00129>.
- Swamy, B.P.M., Shamsudin, N.A.A., Rahman, S.N.A., Mauleon, R., Ratnam, W., Sta Cruz, M.T., Kumar, A., 2017. Association mapping of yield and yield-related traits under reproductive stage drought stress in rice (*Oryza sativa* L.). *Rice* 10 (1), 1–13. <https://doi.org/10.1186/s12284-017-0161-6>.
- Torres, R.O., Henry, A., 2018. Yield stability of selected rice breeding lines and donors across conditions of mild to moderately severe drought stress. *Field Crop Res.* 220, 37–45. <https://doi.org/10.1016/J.FCR.2016.09.011>.
- Venkateshwarlu, C., Kole, P.C., Paul, P.J., Singh, A.K., Singh, V.K., Kumar, A., 2022. Capturing genetic variability and identification of promising drought-tolerant lines in exotic landrace derived population under reproductive drought stress in rice. *Front. Plant Sci.* 13, 115. <https://doi.org/10.3389/FPLS.2022.814774/BIBTEX>.
- Vikram, P., Swamy, B.P.M., Dixit, S., Ahmed, H.U., Teresa Sta Cruz, M., Singh, A.K., Kumar, A., 2011. QDTY1.1, a major QTL for rice grain yield under reproductive-stage drought stress with a consistent effect in multiple elite genetic backgrounds. *BMC Genet.* 12. <https://doi.org/10.1186/1471-2156-12-89>.
- Warner, J.N., 1952. A method for estimating heritability. *Agron. J.* 44 (8), 427–430. <https://doi.org/10.2134/AGRONJ1952.00021962004400080007X>.
- Yogameenakshi, P., Vivekanandan, P., Nadarajan, N., 2019. Genetic effects of yield and root parameters in rice (*Oryza sativa* L.) at reproductive stage drought stress as ascertained by generation mean analysis. *Oryza* 175–184. <https://doi.org/10.35709/ory.2019.56.2.1>.
- Zhang, J., Zhang, S., Cheng, M., Jiang, H., Zhang, X., Peng, C., Lu, X., Zhang, M., Jin, J., 2018. Effect of drought on agronomic traits of rice and wheat: A meta-analysis. *Int. J. Environ. Res. Public Health* 15 (5). <https://doi.org/10.3390/ijerph15050839>.
- Zhao, T., Dai, A., 2017. Uncertainties in historical changes and future projections of drought. Part II: model-simulated historical and future drought changes. *Clim. Chang.* 144 (3), 535–548. <https://doi.org/10.1007/S10584-016-1742-X/FIGURES/6>.