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RESEARCH ARTICLE

Allelic divergence and heritable interrelationship studies for yield and submergence tolerance in rice (*Oryza sativa* L.)

Naveen-Kumar[1,2], Viswabharathy Sakthivel[1,2], Ameena Premnath[1,2], Manonmani Swaminathan[1,3], Senthil Alagarsamy[4], Sudha Manickam[2*] & Raveendran Muthurajan[2,5*]

[1]Department of Genetics and Plant Breeding, Centre for Plant Breeding and Genetics, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India

[2]Department of Plant Biotechnology, Centre for Plant Molecular Biology and Biotechnology, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India

[3]Department of Rice, Tamil Nadu Agricultural University, Coimbatore 641 003, India

[4]Department of Crop Physiology, Tamil Nadu Agricultural University, Coimbatore 641 003, India

[5]Directorate of Research, Tamil Nadu Agricultural University, Coimbatore 641 003, India

*Email: sudhatamil@gmail.com, raveendrantnau@gmail.com

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Abstract

Global low-lying rice cultivation faces a serious threat of flash floods, exacerbated by climate change. Significant progress has been made by plant breeders to introgress *Sub1* locus into elite rice background through marker-assisted breeding approaches. The F_2 population derived from ADT 36 × #91-27 (NIL of CO 43 Sub1) was used to identify high-yielding lines that are homozygous for the *Sub1* locus and *Pi54* gene. INDEL markers, ART 5 and Pi 54, were used for genotyping the *Sub1* locus and *Pi54* gene, respectively. Out of 83 F_2 plants, 21 plants were homozygotes and 45 plants were heterozygotes for the *Sub1* locus. Whereas 21 plants were homozygotes and 46 were heterozygotes for the *Pi54* gene. Four plants were identified to be homozygotes for the *Sub1* locus and *Pi54* gene. Genetic analysis of the F_2 plants identified that productive tillers (number/plant) and the filled grains (number/panicle) exerted the highest positive effect on single plant yield and also had the highest heritability. Also, these traits have a significant positive correlation *per se*. These traits, particularly productive tillers (number/plant), can potentially be used in subsequent generations to select high-yielding submergence tolerance and blast resistant lines of ADT 36 × #91-27 (NIL of CO 43 Sub1).

Keywords

rice; submergence tolerance; genetic analysis; yield

Introduction

In India, 195.4 million tonnes of rice are produced from 46.4 million hectares of land (1). Rice yield needs to be doubled in the next 25 years to ensure food supply to the growing population. Rice production reached a major leap due to the introduction of semi-dwarf varieties and hybrids (2). Any further increase in rice production is possible only when the challenges of yield plateau, degradation of natural resources and occurrence of abiotic and biotic stresses accelerated by climate change are addressed. Climate change has caused a rise in the frequency of floods in the recent past (3). Flash floods have a substantial impact on the agro-ecosystem and has been getting worse over the past few decades (4). Tailing heat and drought stress, a flash flood is the third most important stress that negatively impacts rice production in the rainfed ecosystem (5). Nearly 15 million hectares of area under rice cultivation in Asia are affected by flash floods (6). In India, ~0.5

million hectares of rice-growing areas are being affected by chronic flash floods (7). Flash floods in rice incur a yield loss between 10% and 100% based on the submergence tolerance status of the crop, followed by the severity and duration of the flash flood (8). Sustaining rice production under complete submergence conditions requires developing submergence-tolerant rice varieties adapted to the target regions (9).

Molecular breeding enables the improvement of an elite cultivar for a particular stress that is prevalent in the target environment (10). The selection of superior lines in early generations drives the success of breeding programs. Marker-assisted foreground selection coupled with genetic analysis of a bi-parental population facilitates the identification of superior lines. Selection of plants in a population based on traits that have high heritability coupled with high genetic advance is a reliable strategy (11) to accumulate the additive effect of the gene on the trait. On the other hand, when high heritability is combined with low genetic advance of a trait over the generations, it complicates the selection process due to the influence of non-additive gene action, such as epistasis and dominance. Consequently, the response to selection may be limited, which makes it challenging to achieve significant gains for those traits. Understanding these dynamics helps breeders to make decisions regarding the prioritization of traits during the selection process (12).

Yield is a polygenic trait controlled by several interrelated component traits influenced by the environment (13). Correlation analysis of yield and yield component traits offers a preliminary outlook in the selection of superior plants in a population (14). In addition, the selection of the best yielders in a population also requires consideration of the direct and indirect effects of yield components on the yield, which can be determined by path coefficient analysis (15). Here, we perform the preliminary genetic studies (correlation, heritability and genetic advancement) on yield and its component traits in a F_2 population (segregating for *Sub 1* locus and *Pi54* gene) derived from ADT 36 × #91-27 (NIL of CO 43 Sub1).

Materials and Methods

ADT 36 and #91-27 (NIL of CO 43 Sub1) were crossed. The true F_1 plants were selected using the *INDEL* markers, ART5 (Sub1 QTL) and forwarded to F_2 generation by selfing. The F_2 population consists of 83 plants which were used for genetic analysis of yield and yield components in rice. All the F_2progenies were individually tagged and genotyped with the *INDEL* markers ART 5 and Pi54 to check for the presence of the *Sub1* QTL and *Pi54* gene, respectively. The field experiment was undertaken at the Department of Rice, Tamil Nadu Agricultural University (TNAU), Coimbatore, with 83 F_2 segregants of the cross, ADT 36 × #91-27 (NIL of CO 43 Sub1). All eighty-three F_2 lines with two parents were sown during the *Summer* of 2024. Twenty-one days old seedlings were transplanted with a spacing of 20 × 20 cm, having one seedling per hill. Appropriate agronomic and crop protection practices were followed as per the recommendations given by the TNAU crop production guide (16). The plants were harvested at the physiological maturity. Twelve agro-morphological traits *viz.,* days to 50 % flowering (DFF; days), plant height (PH; cm), number of productive tillers (NPT; number/plant), flag leaf length (FLL; cm), panicle length (PL; cm), spikelet fertility (SF; percent), filled grains (FG; number/panicle), chaffy grains (CG; number/panicle), hundred seed weight (HSW; g), grain length (GL; mm), grain width (GW; mm) and single plant yield (SPY; g) were recorded. The agro-morphological traits measurements were subjected to statistical analysis. The genotypic variance (GV) and phenotypic variances (PV) were estimated based on the formula given by Johnson *et al.* (11). The computed GV and PV values were used to calculate the Phenotypic Coefficient of Variation (PCV) and Genotypic Coefficient of Variation (GCV) respectively based on the formula proposed by Mirza *et al.* (17). PCV, as well as GCV estimates, were graded to be low if the values are less than 10 %; moderate, if the values are 10-20 %; and high if the values are above 20 % (18). Broad-sense heritability (H^2) was categorized as low when the estimates fall below 30 %, medium when the estimates ranged between 30 and 60 % and high for estimates exceeding 60%. Genetic advance as percent of mean (GAM) was calculated based on the formula given by Johnson *et al.* (11). Skewness and kurtosis estimates were computed based on the formula given by Snedecor and Cochran (19). The distribution pattern of twelve agro-morphological traits in the F_2 population was comprehended using histograms generated from SPSS 16.0 software. PCV, GCV, heritability and GAM calculations were performed manually using MS Excel. Correlation coefficient analysis was performed in R software using “metan package” (20). Path coefficient analysis was done using TNAUSTAT (21).

Results

A total of 83 F_2 plants, along with their parental lines, were phenotyped for twelve agro-morphological traits and genotyped for *Sub1* locus and *Pi54* gene. Genotyping analysis of F_2 population displayed a clear segregation pattern for submergence tolerance, with 21 F_2 plants exhibiting homozygosity and 45 plants exhibiting heterozygosity for the *Sub1* locus (Fig. 1a). In case of blast resistance, 21 plants showed homozygosity and 46 plants showed heterozygosity for *Pi54* gene (Fig. 1b). A total of four plants were identified to be homozygous for *Sub1* locus and *Pi54* gene.

The extensive variation in the segregating population facilitates the selection of superior rice genotypes with favourable traits. The estimates of PCV, GCV, heritability, GAM, skewness and kurtosis are provided in Table 1. Among the twelve traits, chaffy grains per panicle were not discussed in this study, as it is not an important trait used in the selection. The PCV reflects both the genetic and environmental effects, while the GCV focuses on the genetic effect (22). The phenotypic coefficient of variation was higher than the genotypic coefficient of variation for all the twelve traits, which emphasize the influence of environment on these traits. High coefficient of variance for both phenotype and genotype were recorded for NPT (26.72 % and 26.08 %), followed by SPY (26.63 % and 26.61 %) and FG (22.17 % and 22.04 %). Similar results were reported by Bitew (23).

Heritability indicates the proportion of the observed phenotypic variation that can be attributed to its corresponding genetic differences, aiding in the reliable evaluation of trait-based selection (24). When the high GCV of a trait is complemented by its high heritability, the reliability of a trait to be used in the selection process is high, as the substantial genetic component can be reliably inherited by the next generation (25). High heritability was recorded for all the traits. Notably, FG, SF, NPT, SPY and GW recorded > 90% of broad-sense heritability. Since these traits showed high broad-sense heritability with reference to its female parent (ADT 36), these traits can be used in selecting a superior line in ADT 36 × # 91-27 (NIL of CO 43 Sub1) derived population. GAM is employed to determine the expected genetic gains of a particular trait during selection (26). GAM was least for DFF (8.48 %) whereas, it was highest for SPY (54.79 %). Similar results were stated by Babu *et al*. (27). High broad-sense heritability coupled with high GAM was observed for NPT, FLL, FG, SF and GL, suggesting that these traits are influenced by additive gene actions making them desirable for selection. High broad-sense heritability combined with low GAM was observed for DFF and PH, signifying the influence of the environment and making these traits undesirable for selection (Table 1).

Skewness and kurtosis were used to recognise the distribution characteristics of various traits (28). Positive skewness indicates the presence of average complementary interactions, while negative skewness suggests duplicate interactions (29). Kurtosis helps to identify gene interactions. The Kurtosis value (β_2)) indicates that $\beta_2 > 0$ means trait behaviour is leptokurtic, $\beta_2 < 0$ means trait behaviour is platykurtic and $\beta_2 = 0$ means trait behaviour is mesokurtic (30). Among all the agro-morphological traits, HSW exhibited positive skewness with leptokurtosis indicating a complementary gene action on this trait controlled by many genes (Fig. l). Further, DFF as well as SF were found to be controlled by duplicate gene interaction as shown by leptokurtic (2.12, 1.50) and negatively skewed (-1.30, -1.09) distribution in the F_2 population of ADT 36 × #91-27, respectively (Table 1; Fig. 2a, f). These results appeared to be in concordance with Patel *et al.* (31), Ardiarini *et al.* (32) and Pavithra *et al.* (33).

Correlation analysis of traits helps to determine the interrelationship between the traits (34). SPY exhibited a significant positive correlation ($p \leq 0.01$; Fig. 3) with NPT (0.61), PH (0.49), FG (0.35) and GW (0.32). A similar correlation between yield and yield component traits was reported by Reetisana *et al*. (35) in rice. Further, FG exhibited a positive correlation with four traits *viz.* SF, PL, PH and FLL. A significant negative correlation ($p \leq 0.01$) was observed between GL and HSW (Fig. 3).

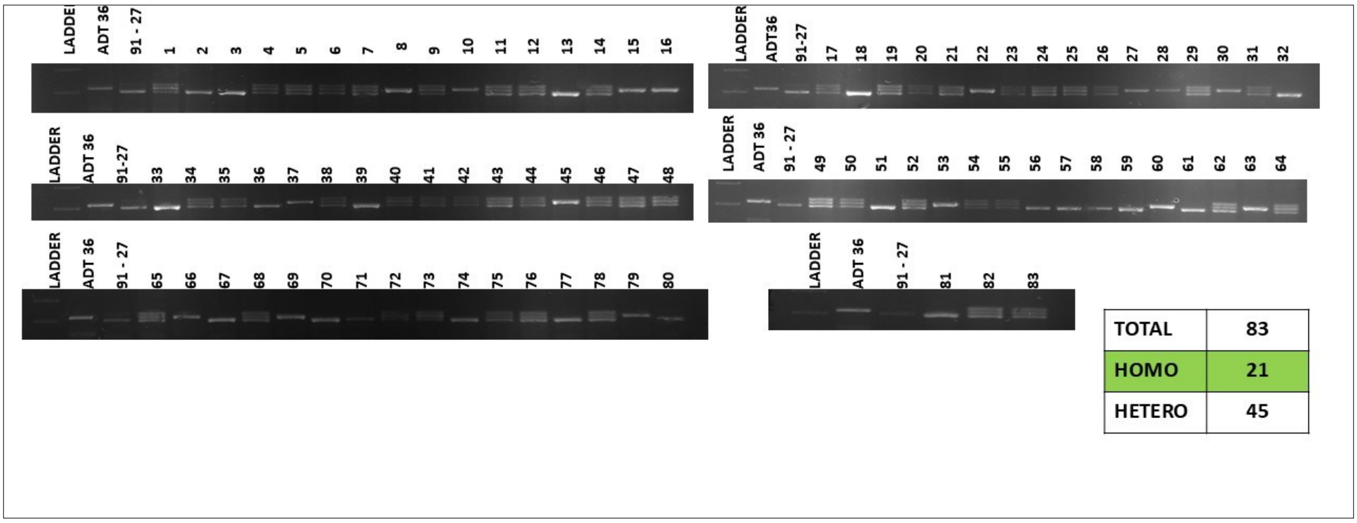
Correlation combined with path analysis offers a clear understanding of the interaction between different traits (36). This comprehensive approach enables the breeders to focus on traits that critically impact the yield (37). The path coefficient analysis of the F_2 population estimated the direct effect of the component traits on the single plant yield (SPY). A trait to be used for selection should have a high direct effect. NPT, PL, PH, SF, FG, GL and GW showed a positive direct effect on the SPY, with SF contributing more to SPY (Table 2, Fig. 4). This was like the results obtained by Thuy et al. (38). Three traits, namely FLL, HSW and DFF showed negative significant direct effect on SPY, similar to the results obtained by Sing et al. (39). The highest indirect positive effect for SPY was detected in NPT influenced by SPF, followed by CG through NPT, GL through NPT and PH through FG. SF had a significant negative indirect effect on SPY. This was followed by the NPT through SF, PH through FG, FLL through FG and FG through CG. The residual effect of path analysis (0.3900) was moderate, indicating the significant influence of the observed agro-morphological traits on the grain yield.

Out of all the traits, productive tillers had the highest direct effect on the single plant yield with a significant positive correlation along with a high H^2 and GCV. Hence, the selection of high-yielding plants based on this trait will be highly effective in ADT 36 × #91-27 (NIL of CO 43 Sub1) derived population.

Table 1. Range and genetic variability of agro-morphological traits of ADT36 × #91-27 (NIL of CO 43 Sub1) derived F_2 population

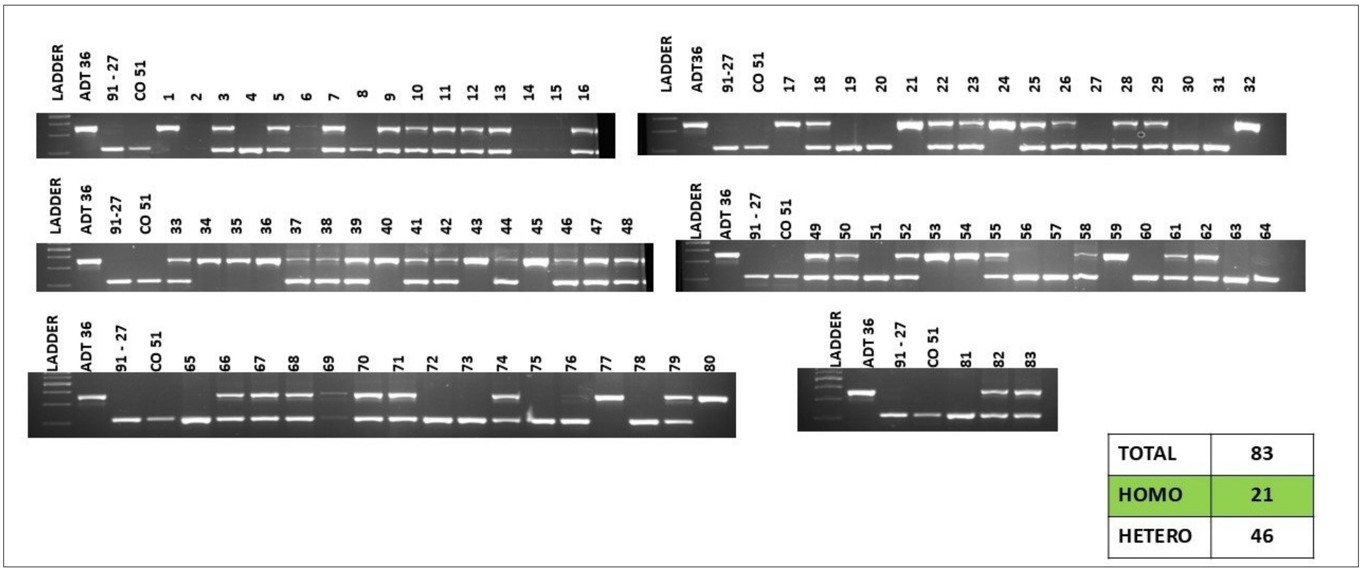
Traits	ADT 36	#91-27	Mean	Minimum	Maximum	PCV (%)	GCV (%)	Heritability (%)	GAM (%)	Skewness	Kurtosis
DFF (days)	101.00	98.00	101.00	86.00	109.00	4.80	4.44	85.72	8.48	-1.30**	2.12**
PH (cm)	85.00	109.00	95.81	82.00	110.00.	5.83	4.94	71.64	8.62	0.38^{ns}	0.12^{ns}
NPT (No./ plant)	17.00	22.00	17.09	5.00	28.00	26.72	26.08	95.33	52.47	-0.10^{ns}	0.56^{ns}
PL (cm)	25.40	21.60	23.79	20.00	28.00	7.35	6.64	81.69	12.37	-0.11^{ns}	-0.45^{ns}
FLL (cm)	23.84	30.20	26.85	19.30	36.00	15.02	13.44	80.17	24.80	-0.03^{ns}	-0.79^{ns}
FG (No./ panicle)	143.00	167.00	173.10	69.00	289.00	22.17	22.04	98.81	45.14	0.04^{ns}	0.63^{ns}
CG (No./ panicle)	50.00	50.00	43.97	10.00	90.00	50.17	49.93	57.03	102.36	0.55*	-0.56^{ns}
SF (%)	73.86	77.15	79.61	45.07	95.12	12.77	12.77	95.33	26.30	-1.09**	1.50**
SPY (g)	53.26	49.06	41.62	10.38	67.04	26.63	26.61	92.24	54.79	-0.064^{ns}	0.08^{ns}
GL (mm)	8.09	8.08	8.16	7.63	8.70	2.86	2.46	88.89	29.35	-0.10^{ns}	-0.14^{ns}
GW (mm)	2.57	2.53	2.57	2.23	2.83	4.81	4.50	90.23	15.05	-0.25^{ns}	-0.16^{ns}
HSW(g)	2.45	2.46	2.41	2.10	3.55	9.14	8.15	79.54	14.98	2.74**	10.08**

* $p \leq 0.05$; ** $p \leq 0.01$; *ns* denotes non-significance



TOTAL	83
HOMO	21
HETERO	45

Fig. 1a. Molecular screening for submergence tolerance in F$_2$ population of ADT 36 × #91-27 (NIL of CO 43 *Sub1*)using ART 5 primer.



TOTAL	83
HOMO	21
HETERO	46

Fig. 1b. Molecular screening for blast resistance in F$_2$ population of ADT 36 × #91-27 (NIL of CO 43 *Sub1*) using *Pi54* gene specific primer.

Table 2. Path coefficients of yield and its components in F$_2$ population of ADT36 × #91-27 (NIL of CO 43 *Sub1*)

Traits	DFF (days)	PH (cm)	NPT (No./plant)	PL (cm)	FLL (cm)	FG (No./panicle)	CG (No./panicle)	SF (%)	GL (mm)	GW (mm)	HSW (g)	SPY (g/plant)
DFF (days)	**-0.0190**	0.0238	-0.0105	-0.0057	-0.0019	-0.0330	-0.0168	-0.0245	-0.0051	0.0053	-0.0010	-0.04^{ns}
PH (cm)	-0.0015	**0.3091**	0.0667	0.0033	0.0011	0.1163	-0.0394	-0.0850	0.0124	0.0246	-0.0042	0.49^{**}
NPT (No./ plant)	0.0004	0.0380	**0.5421**	-0.0055	0.0038	-0.0063	0.1174	-0.1287	0.0140	0.0238	0.0008	0.61^{**}
PL (cm)	0.0014	0.0134	-0.0397	**0.0751**	-0.0191	-0.1551	-0.0733	0.0242	0.0046	0.0237	-0.0038	0.11^{ns}
FLL (cm)	-0.0007	-0.0067	-0.0390	0.0272	**-0.0526**	-0.1136	0.0679	0.0009	0.0143	0.0047	0.0085	0.01^{ns}
FG (No./ panicle)	0.0014	0.0777	0.0074	0.0252	-0.0129	**0.4626**	-0.1050	0.3575	0.0050	0.0208	-0.0049	0.35^{**}
CG (No./ panicle)	-0.0007	-0.0248	0.1299	0.0112	-0.0073	-0.0991	**-0.4900**	-0.5633	0.0030	0.0117	0.0013	0.09^{ns}
SF (%)	0.0007	0.0420	-0.1116	0.0029	0.0001	0.2646	-0.4416	**0.6251**	-0.0068	0.0020	-0.0022	0.03^{ns}
GL (mm)	-0.0014	0.0572	0.1125	-0.0051	0.0112	-0.0345	-0.0222	-0.0632	**0.0672**	0.0262	-0.0109	0.14^{ns}
GW (mm)	0.0007	0.0542	0.0917	0.0126	-0.0018	-0.0684	0.0409	-0.0089	0.0125	**0.1406**	-0.0081	0.32^{**}
HSW (g)	0.0004	-0.0277	0.0094	-0.0061	-0.0095	-0.0485	-0.0135	0.0293	-0.0156	0.0242	**-0.0471**	-0.03^{ns}

Residual effect = 0.3900

* $p \le 0.05$; ** $p \le 0.01$; *ns* denotes non-significance

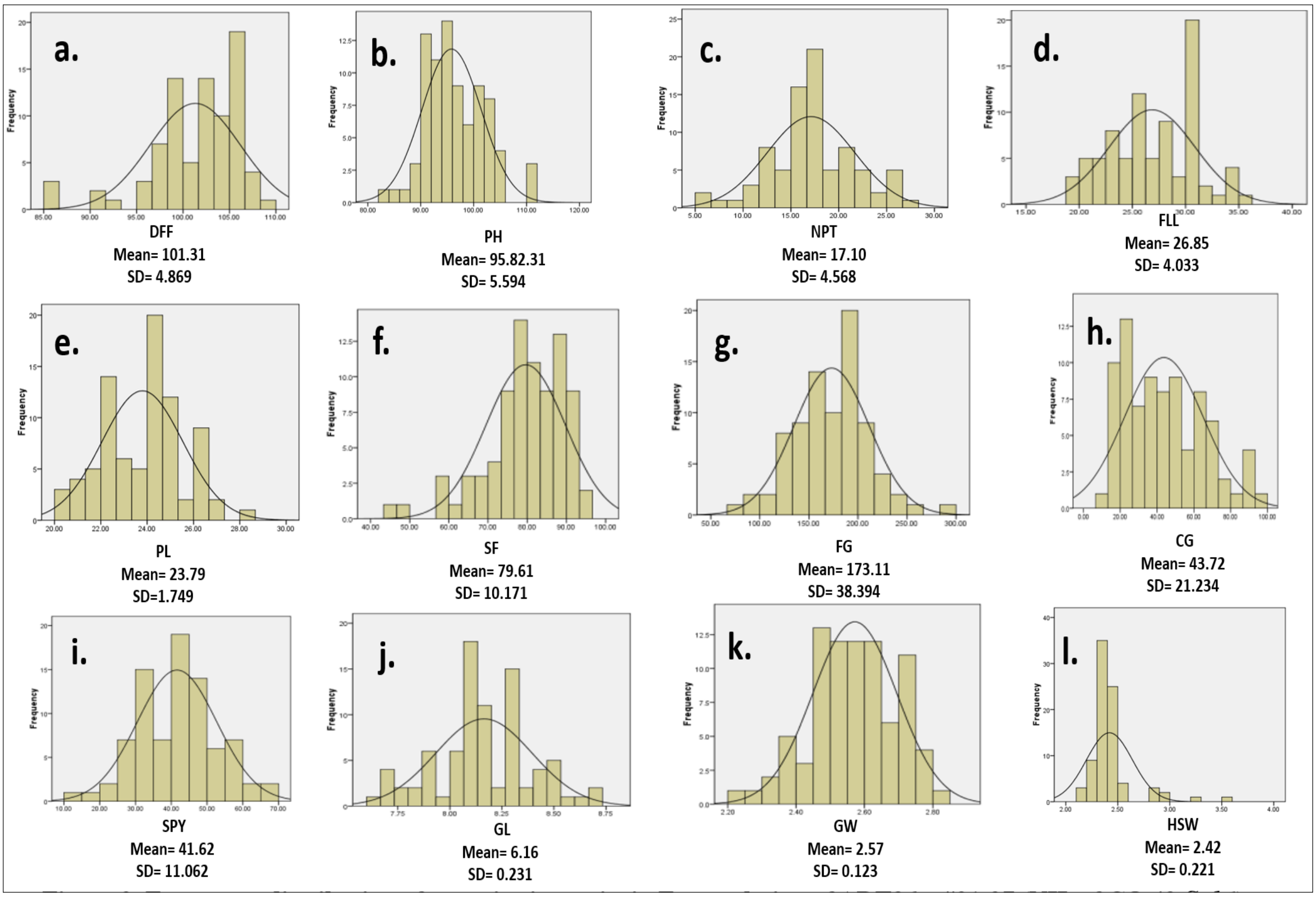


Fig. 2. Frequency distribution of agro-morphological traits in F_2 population of ADT36 × #91-27 (NIL of CO 43 *Sub1*).

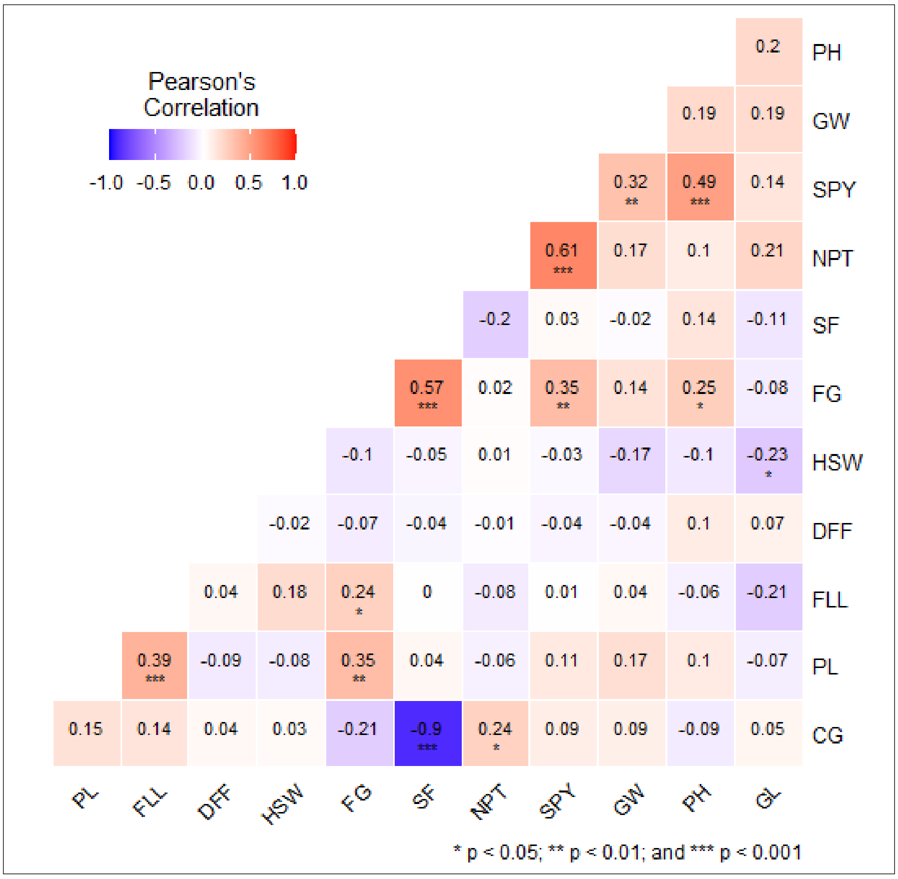
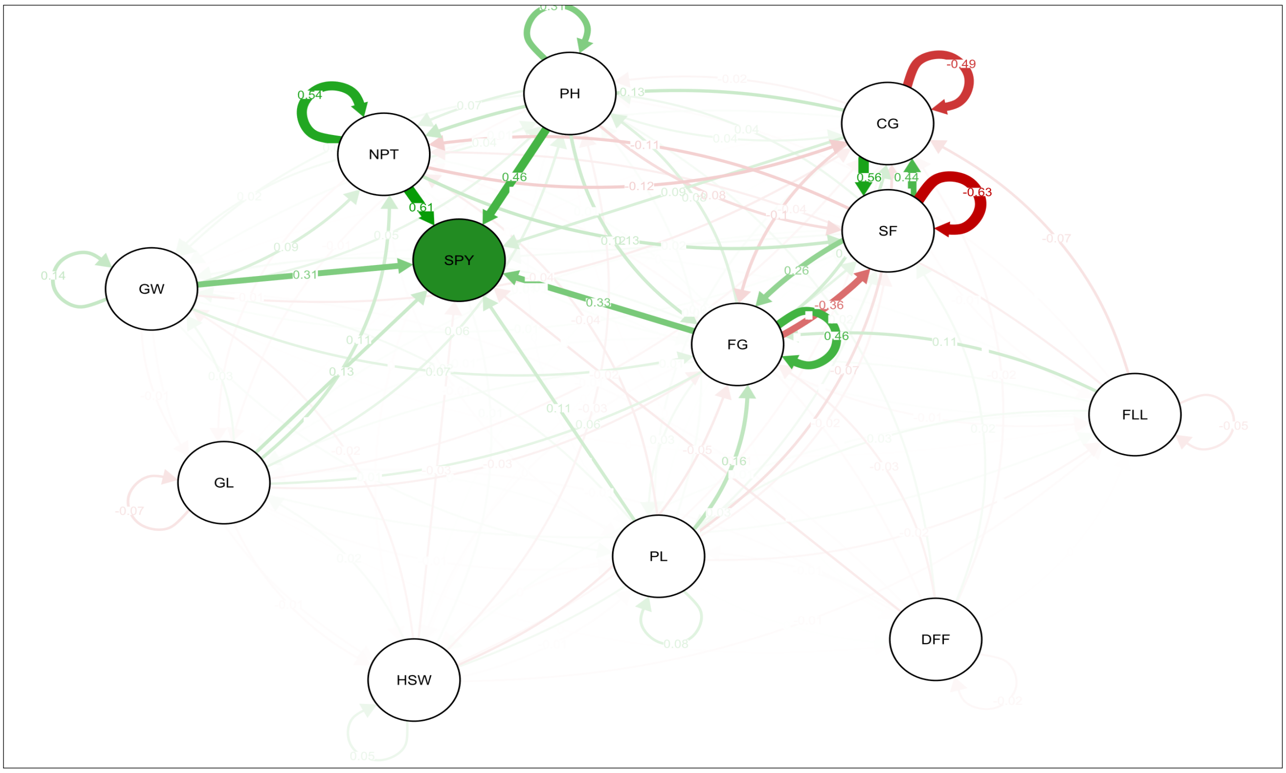


Fig. 3. Correlation analysis of agro-morphological traits in F_2 population of ADT36 × #91-27 (NIL of CO 43 Sub1).



Residual effect: 0.3900

Fig. 4. Path diagram for yield and its attributing traits in F2 population of ADT36 × #91-27 (NIL of CO 43 Sub1).

Conclusion

Succinctly, the genetic analysis of the F_2 population emphasises the effect of productive tillers on single plant yield. Furthermore, productive tillers can be potentially used to select the best yielders in the subsequent generations coupled with foreground selection of submergence tolerance and blast resistance in rice. The identified four double homozygotes for submergence and blast resistance can be subjected to marker assisted backcross breeding to be released as a variety in regions exposed to flash floods and blasts. Further, the identified double homozygote lines can be used as potential donors in the breeding pipeline for developing climate resilient rice cultivars by gene pyramiding.

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Authors' contributions

NK, RM and SM designed and carried out the genetic variability studies. NK conscripted the manuscript. NK and VS contributed to the design of the study and executed the statistical investigation. AP carried out the editing of the draft. MS and SA conceived the study and contributed to the planning and execution of the study. All the authors have read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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