



## Research Article

### Evaluation of altered biomass mutant contributing increased grain yield in rice (*Oryza sativa* L.)

**S. Vinothini Bakya<sup>1\*</sup>, S. Geetha<sup>1</sup>, P. Jeyaprakash<sup>2</sup>, S. Rajeswari<sup>1</sup>, M. Raveendran<sup>3</sup>, P. Jeyakumar<sup>4</sup>, S. Athira<sup>1</sup> and S. Robin<sup>1</sup>**

<sup>1</sup>Centre for Plant Breeding and Genetics, Tamil Nadu Agricultural University, Coimbatore, Pin code - 641 003, Tamil Nadu, India.

<sup>2</sup>Department of Plant Breeding and Genetics, Anbil Dharmalingam Agricultural College and Research Institute, Trichy, Pin code- 620 009, Tamil Nadu, India.

<sup>3</sup>Dept. of Plant Biotechnology, CPMB&B, Tamil Nadu Agricultural University, Coimbatore, Pin code - 641 003, Tamil Nadu, India.

<sup>4</sup>Dept. of Plant Physiology, Tamil Nadu Agricultural University, Coimbatore, Pin code - 641 003, Tamil Nadu, India.  
**E-Mail:**vinothinisankaran@gmail.com

#### Abstract

Yield improvement through crop breeding is a constant process to meet increasing yield demand in context of decreasing cultivable land and erratic climatic conditions. Breeding for yield improvement can be achieved through altering plant type. Improving plant biomass can pave way for improving grain yield as grain yield is product of biomass and harvest index. EMS induced mutants serve as a source for creating novel variations for altering plant type. In this view, EMS mutant of Nagina 22 was identified with altered biomass and grain yield. A mapping population of N22 x N22-CC-M4-HT-1333 was studied in  $F_2$  and  $F_3$  for traits contributing for altered biomass and grain yield. The correlation analysis in  $F_2$  and  $F_3$  showed that dry matter produced was significantly correlated with grain yield showing the increase in grain yield of the mutant was contributed by dry biomass. This mutant is potential for unraveling the novel ways to improve grain yield and further functional genomics studies.

#### Keywords

mutant, altered biomass, grain yield, variability, correlation, rice

#### INTRODUCTION

Rice is staple food crop for 3.5 billion people across the globe covering major countries of Asia, Africa (GRiSP, 2013). By 2050, the estimated increase of total global population will be 9.7 billion from 7.6 billion populations. This demands an increase of 100 % crop yield increase in major food crops (FAO, 2015). This necessitates an increase in rice production - through breeding of high yielding varieties, improved agronomic practices in spite of erratic climate and shrinking cultivable land. First phase leap of yield increase was through green revolution by introducing semi dwarf rice varieties and improved fertilizer usage. This gave yield increase from 6 to 10 t/ha. Later, the second leap in yield was due to hybrids with increased grain yield and heterosis. Again the yield increase has attained plateau and further developments should have novel breeding methods. Grain yield is process of dry

matter accumulation and distribution. Grain yield is product of biomass and harvest index (Wu *et al.*, 2008). Hence, future thrust of breeding for yield improvement can be planned based on increasing biomass or harvest index.

The varieties released from IRRI prior to 1980 were reported to have high harvest index leading to yield increase. The yield increase in varieties released after 1980 were due to increased aboveground biomass and concluded that future breeding to increase yield can be fruitful by improving biomass (Peng *et al.*, 2000). New plant type concept introduced in IRRI for improving the yield through modifying the plant architecture (Khush, 1995). This can be used to improve lodging resistance, improving sink capacity and less unproductive tillers. This

led to breeding of cultivars having large panicles with few unproductive tillers but the grain yield was poor. This was reported due to poor aboveground biomass and poor grain filling. In breeding for second generation NPT, increased tillering capacity, pest and disease resistance were identified to improve grain yield. This resulted in high yield than *Indica* check and increased yield was associated with increased aboveground biomass and grain weight (Peng *et al.*, 2008). Super hybrid rice Liangyoupeijiu reported to have 12% hike in above ground total biomass than Shanyou63. The high biomass was associated with high leaf area index, leaf area duration, thick leaf, high chlorophyll content and photosynthetic rate. The increased yield of Liangyoupeijiu was due to high leaf area duration before heading, biomass accumulation before heading, number of grains and more translocation of carbohydrates from source to sink during grain filling period (Katsura *et al.*, 2007). In this view, an attempt was made to characterize the altered biomass mutant of Nagina 22. EMS treated N22 mutant screened for altered plant architecture resulted in identifying a mutant and named as N22-CC-M4-HT-1333. This was characterized for seedling vigour, crop growth rate to identify the biomass of N22-CC-M4-HT-1333 in comparison with N22. It was also studied in  $F_2$  and  $F_3$  generation of mapping population of N22 x N22-HT-1333.

#### MATERIALS AND METHOD

The research was focused to exploit the altered biomass mutant N22-CC-M4-HT-1333 in terms of biomass accumulation. The traits contributing for increased biomass accumulation and grain yield pertinent to mutant was studied using  $F_2$  and  $F_3$  of N22 x N22-CC-M4-HT-1333 mapping population. The study was carried at Department of Rice, Centre for plant breeding and Genetics, Tamil Nadu Agricultural University, Coimbatore during 2018-2019. One hundred and forty plants were raised in  $F_2$  in 20 cm x 20 cm spacing and evaluated for biometrical traits. The 140  $F_3$  families were raised from  $F_2$  as ear to row method. Each family was raised in two rows in 2.4 m row with a spacing of 20 cm x 20 cm. Three

plants per family were tagged and a total of 420 plants in  $F_3$  were evaluated for biometrical traits. The plants were observed for plant height, number of tillers and productive tillers, days to fifty per cent flowering, flag leaf length, flag leaf width, panicle length, third leaf length, third leaf breadth, third leaf weight, leaf area, specific leaf weight, wet biomass, dry matter produced, harvest index and single plant yield. The data were collected and analyzed for the estimation of phenotypic and genotypic coefficients of variation as suggested by Burton (1952). Heritability was estimated according to Lush (1940) and genetic advance as percentage of mean was calculated according to Johnson *et al.* (1955). The correlation was performed using R package (Pearson's coefficient using Corrplot, v.0.84) and significant correlation coefficient was observed at 5 and 1 % level of significance.

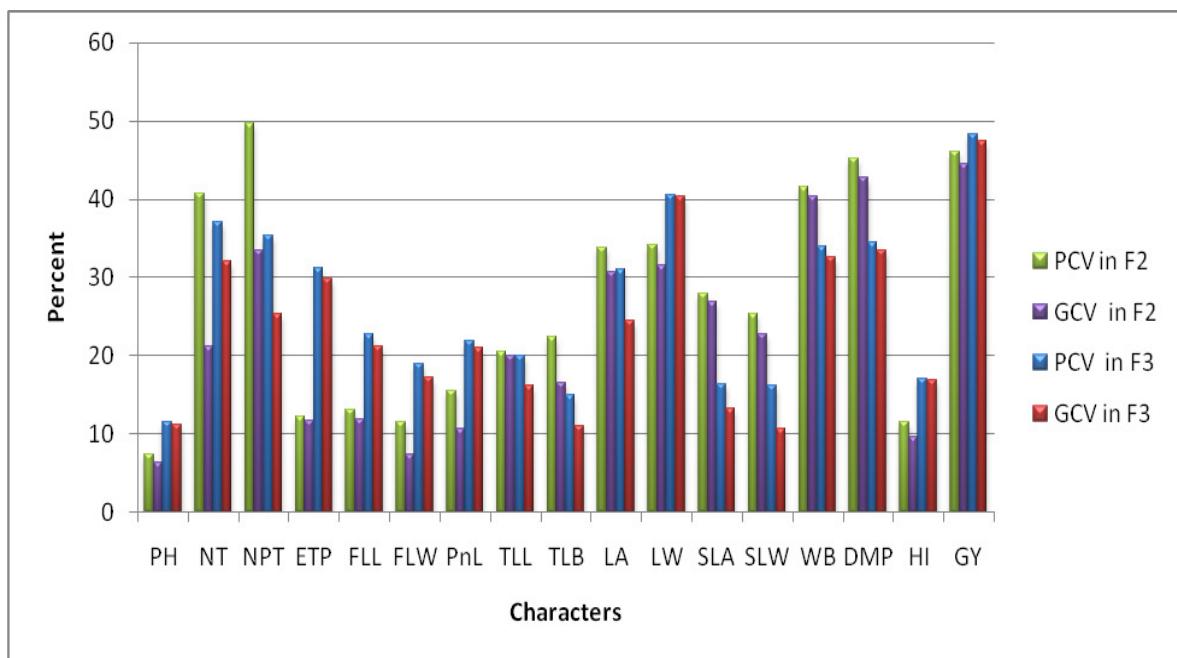
#### RESULTS AND DISCUSSION

The phenotypic characterization for plant height, number of tillers, number of productive tillers, days to fifty per cent flowering, flag leaf length, flag leaf width, panicle length, third leaf length, third leaf breadth, third leaf weight, leaf area, specific leaf weight, wet biomass, dry matter produced, harvest index and single plant yield (**Table 1**). The dry matter production and grain yield has increased in N22-CC-M4-HT-1333 than N22 in both the seasons. This showed that the parent selected was efficient. This mutant parent needs to be evaluated more for the identification of dry matter produced. The dry matter accumulation increase may be attributed by crop growth rate and increased duration of crop growth (Yoshida, 1983). The biomass production during vegetative and grain filling stages contributed significantly for biomass (Ying, 1998). The higher biomass production may be due to prolonged growth duration in super hybrid rice (Zhang, 2009).

The phenotypic and genotypic coefficient of variation, heritability, genetic advance as percentage of mean are given in **Table 1**. In  $F_2$ , the variability analysis for the characters like number of tillers, productive tillers per plant,

**Table 1. Range, mean, PCV, GCV, heritability(H), genetic advance as percentage of mean (GAM) in  $F_2$  and  $F_3$  population of N22 x N22-CC-M4-HT-1333**

Traits	N22	N22-CC- M4-HT- 1333	$F_2$					$F_3$								
			Min	Max	Mean	PCV (%)	GCV (%)	H (%)	GAM (%)	Min	Max	Mean	PCV (%)	GCV (%)	H (%)	GAM (%)
PH	95.05	105.4	76	120.5	100.5	7.41	6.29	72.11	11	61.4	129.4	96.24	11.5	11.2	95.14	22.57
NT	20	28	5	30	13	40.8	21.2	26.92	22.61	4	34	14	37.2	32	74.28	56.84
NPT	14	17	2	27	10	49.7	33.5	45.35	46.42	1	23	9	35.3	25.3	51.41	37.35
FLL	27.6	31.4	23.5	46	33.1	12.3	11.7	91.33	23.1	15.4	48.5	26.6	31.3	29.8	90.8	58.45
FLW	1.1	1.4	1.1	2	1.5	13.1	11.8	80.69	21.82	0.6	1.8	1.2	22.7	21.2	87.32	40.81
PL	16.4	20.3	17.5	30.5	22	11.5	7.34	40.91	9.67	1.6	30.5	19.7	19	17.3	83.03	32.41
TLL	27	34.4	21	62.5	39.3	15.4	10.6	47.57	15.1	9	45.1	23.3	21.8	21	92.81	41.76
TLB	1	1	0.8	2.1	1.4	20.6	20.1	95.02	40.28	0.4	1.2	0.8	20	16.1	64.8	26.65
LA	21.34	24.77	16.63	76.5	39.53	22.4	16.5	54.53	25.12	3.86	28.86	12.82	15.1	11	53.32	16.55
TLW	24.1	75.62	0.08	0.52	0.21	33.7	30.8	83.11	57.75	20.72	231.62	89.03	31	24.4	61.71	39.46
SLA	195.61	120.77	102.37	449.2	193.6	34.2	31.6	85.52	60.17	88.25	249.22	150.85	40.5	40.4	99.5	83.04
SLW	5.11	8.72	2.23	9.77	5.52	27.9	26.9	92.76	53.3	4.01	11.33	6.81	16.4	13.2	64.62	21.83
WB	49.9	75.44	18	147	66.72	25.3	22.8	81.37	42.36	5.5	53.91	17.56	16.2	10.7	43.63	14.57
DMP	31.56	69.8	12	125	54.54	41.6	40.4	94.16	80.68	5.09	49.62	15.94	34	32.5	91.49	64.11
HI	0.44	0.49	0.26	0.51	0.43	45.3	42.8	89.32	83.28	0.12	0.83	0.47	34.4	33.4	94.06	66.66
GY	16.5	43.64	5	56.2	23.6	11.5	9.6	69.94	16.54	1.79	67.47	14.84	17	16.9	98.8	34.55



**Fig. 1. PCV, GCV of seventeen characters in F<sub>2</sub> and F<sub>3</sub> population of N22 x N22-CC-M4-HT-1333**

third leaf length, leaf area, leaf weight, specific leaf area, specific leaf weight, wet biomass, dry matter produced and grain yield showed high PCV and GCV. The narrow variation of PCV and GCV in traits like leaf area, leaf weight, specific leaf area, specific leaf weight, wet biomass, dry matter produced and grain yield (Fig. 1). In F<sub>3</sub>, number of tillers, productive tillers per plant, efficient tillering per cent, flag leaf length, panicle length, leaf area, leaf weight, wet biomass, dry matter produced and grain yield showed high PCV and GCV. Similar reports of high PCV and GCV were given by Tiwari (2015) and Singh *et al.* (2016) for productive tillers per plant, Priyanka *et al.* (2019) and Mamtha *et al.* (2018) for single plant yield in F<sub>2</sub> population, Khatun *et al.* (2015) for dry matter produced. These results make us to understand that these traits having variability contributed by genetic factors and less influenced by environment, hence selection for these traits

may be fruitful. In F<sub>2</sub>, the traits like efficient tillering percentage, flag leaf length and panicle length registered moderate PCV and GCV, whereas flag leaf width and harvest index showed moderate PCV and low GCV. This revealed that the former traits had comparatively less environmental influence than the later. In F<sub>3</sub>, plant height, flag leaf width, third leaf length, third leaf breadth, specific leaf area, specific leaf weight, harvest index showed moderate PCV and GCV. Selection of these traits can be done based on heritability. The plant height in F<sub>2</sub> has low PCV and GCV showing that the variation for plant height is less and selection may not be rewarding. The traits viz., number of tillers, productive tillers, third leaf length, leaf breadth, leaf area, specific leaf area and weight, wet biomass and dry matter produced showed higher variability in F<sub>2</sub> compared to F<sub>3</sub> generation.

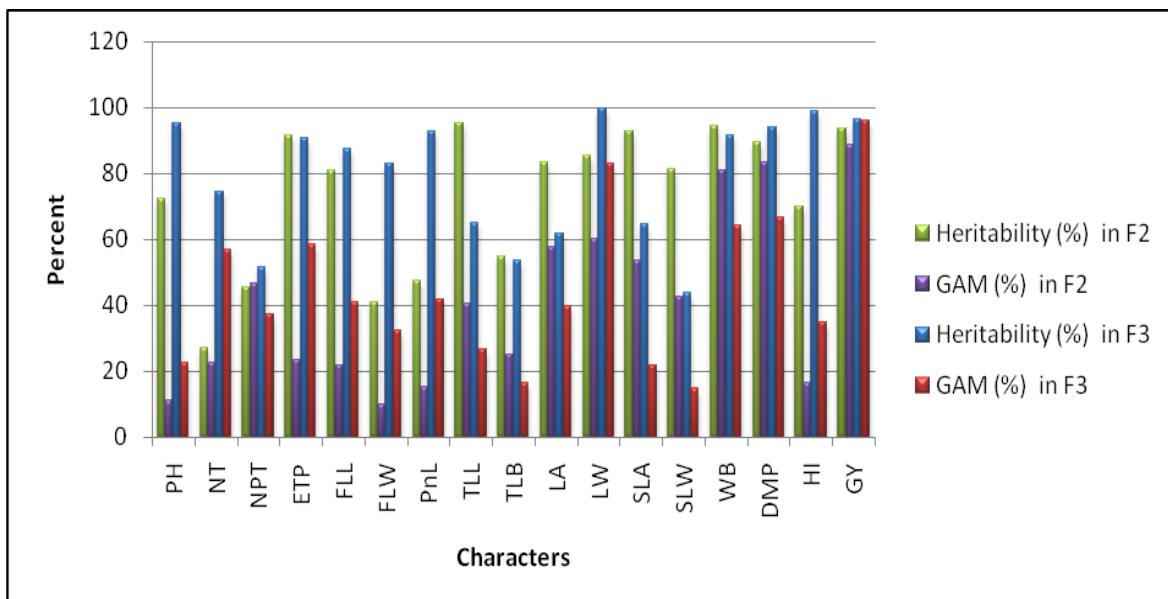
**Table 2. Correlation coefficient in F<sub>2</sub> generation of population of N22 x N22-CC-M4-HT-1333**

	PH	NT	NPT	FLL	FLW	PL	TLL	TLB	LW	WB	DMP	HI	GY
PH	1.000												
NT	<b>0.827**</b>	1.000											
NPT	<b>0.855**</b>	<b>0.961**</b>	1.000										
ETP	0.677*	0.418	0.600*										
FLL	0.636*	<b>0.696**</b>	<b>0.728**</b>	1.000									
FLW	0.532	0.507	0.574*	0.503	1.000								
PL	<b>0.758**</b>	<b>0.770**</b>	<b>0.829**</b>	<b>0.685**</b>	0.627	1.000							
TLL	-0.239	-0.306	-0.311	-0.219	-0.121	-0.283	1.000						
TLB	-0.481	-0.515	-0.500	-0.309	-0.260	-0.596	0.239	1.000					
LW	-0.058	-0.064	-0.040	-0.009	0.039	-0.089	<b>0.722**</b>	0.453	1.000				
WB	<b>0.866**</b>	<b>0.917**</b>	<b>0.916**</b>	<b>0.718**</b>	0.588*	<b>0.864**</b>	-0.329	-0.560	-0.104	1.000			
DMP	<b>0.881**</b>	<b>0.926**</b>	<b>0.929**</b>	<b>0.742**</b>	0.610	<b>0.897**</b>	-0.299	-0.578	-0.089	<b>0.966**</b>	1.000		
HI	0.014	-0.085	-0.061	-0.091	0.049	-0.020	0.081	-0.031	0.004	-0.078	-0.066	1.000	
GY	<b>0.852**</b>	<b>0.860**</b>	<b>0.877**</b>	<b>0.691**</b>	0.620*	<b>0.869**</b>	-0.235	-0.574	-0.067	<b>0.909**</b>	<b>0.947**</b>	0.231	1.000

\* $r_{0.05} = 0.552$ , \*\* $r_{0.01} = 0.683$

Heritability and genetic advance as percentage of mean gives a picture of additive or non-additive gene action, thus it may be helpful in selection procedures. In this study, many traits showed high heritability and genetic advance. The traits like plant height, efficient tillering percent, flag leaf length, third leaf length, leaf area, specific leaf area, specific leaf weight, wet biomass, dry matter produced and grain yield showed high heritability and genetic advance in  $F_2$  generation (Table. 1, Fig. 2). In  $F_3$ , plant height, number of tillers, efficient tillering per cent, flag

leaf length, flag leaf width, third leaf length, leaf weight, specific leaf area, wet biomass, dry matter produced, harvest index and grain yield expressed high heritability and genetic advance. This shows that these traits controlled by additive gene action and selection may be effective. Priyanka *et al.* (2019) and Mamtha *et al.* (2018) for single plant yield and Khatun *et al.* (2015) for dry matter produced had reported high heritability and genetic advance.



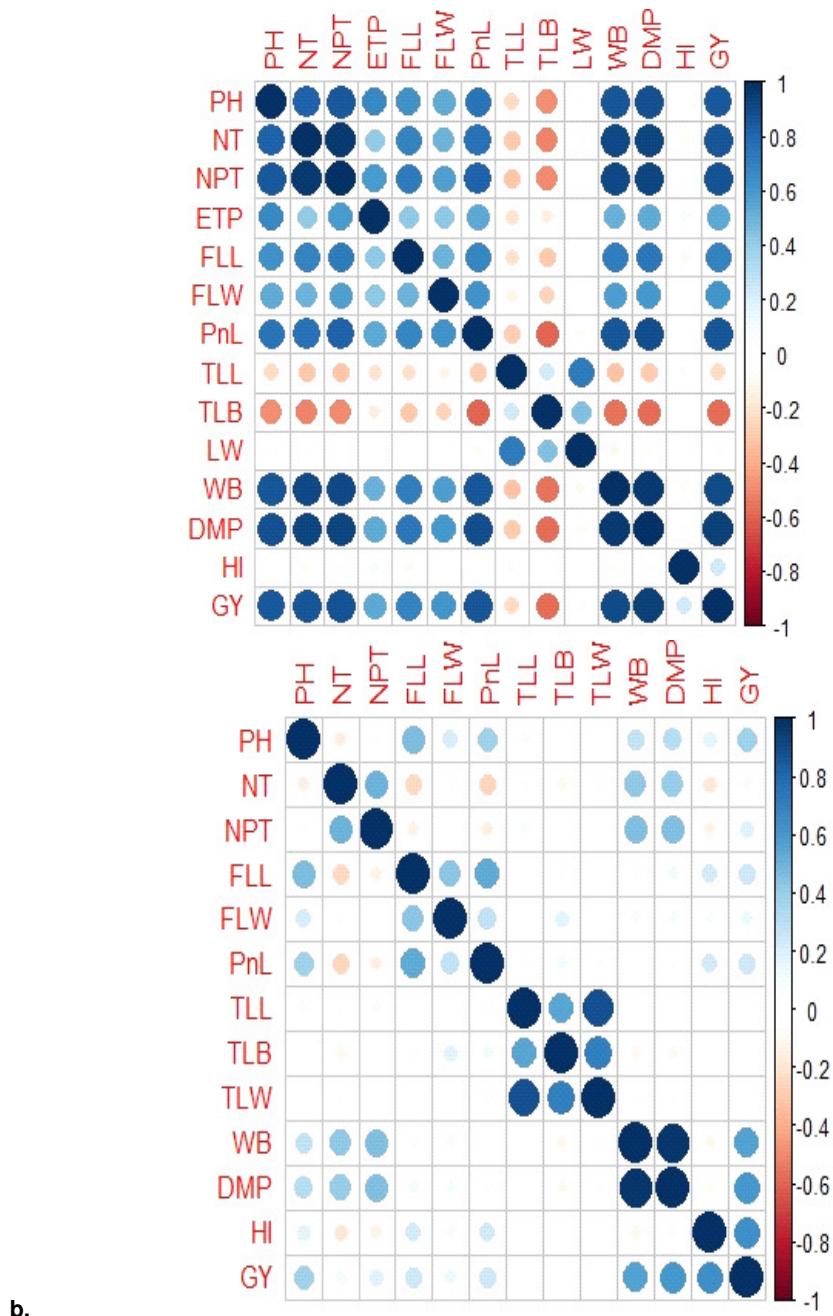
**Fig. 2. Heritability and genetic advance of seventeen characters in  $F_2$  and  $F_3$  population of N22 x N22-CC-M4-HT-1333**

The simple linear correlation was performed in  $F_2$  and  $F_3$  generations for single plant yield with twelve traits (Table. 2 ; Fig. 3). The results of  $F_2$  correlation showed that the single plant yield was significantly positively correlated with plant height ( $r = 0.852$ ,  $r_{0.01} = 0.683$ ), number of tiller ( $r = 0.860$ ,  $r_{0.01} = 0.683$ ), number of productive tillers ( $r = 0.877$ ,  $r_{0.01} = 0.683$ ), flag leaf length ( $r = 0.691$ ,  $r_{0.01} = 0.683$ ), flag leaf width ( $r = 0.620$ ,  $r_{0.05} = 0.552$ ), panicle length ( $r = 0.869$ ,  $r_{0.01} = 0.683$ ), wet biomass ( $r = 0.909$ ,  $r_{0.01} = 0.683$ ) and dry matter produced ( $r = 0.947$ ,  $r_{0.01} = 0.641$ ). Third leaf breadth showed significant negative correlation with grain yield. In  $F_3$  the tiller per plant had significant positive correlation with grain yield wet biomass ( $r = 0.567$ ,  $r_{0.05} = 0.552$ ), dry matter produced ( $r = 0.605$ ,  $r_{0.05} = 0.552$ ) and harvest index ( $r = 0.644$ ,  $r_{0.05} = 0.552$ ) (Table. 3; Fig. 3). Based on correlation analysis in  $F_2$  and  $F_3$ , it was observed that the key contributor for grain yield was dry matter produced and wet biomass. This showed that the mutant N22-CC-M4-HT-1333 selected for altered biomass contributing grain yield was efficient. Among all the traits, wet biomass and dry matter produced showed highest correlation coefficient showing strong correlation

of trait with dry matter produced with grain yield. This was supported by Wu *et al.* (2008) where they studied the correlation of grain yield with dry matter accumulation at different growth stages of super hybrid rice. They found that the biomass yield was key in improvement of super hybrid rice rather than harvest index. Bueno and Lafarge (2009) reported that the biomass accumulation and harvest index were significantly correlated to grain yield. Chen *et al.* (2012) found that grain per  $m^2$  quadratically correlated with stem dry matter at heading stage and suggested that the dry matter accumulation during heading was more contributing for grain yield and dry matter produced prior to heading may have negative effect. Plant height was reported to have positive correlation with biomass in *Indica* hybrids by Li *et al.* (2019). Yield improvement can be done by increasing harvest index by reducing plant height especially in semi dwarf rice varieties (Khush, 1999). In this study, even though plant height showed significant correlation with grain yield, dry matter produced, number of tillers and productive tillers in  $F_2$  generation, it showed no significance correlation with grain yield, dry matter

produced, number of tillers and productive tillers in  $F_3$  generation. Lakshmi *et al.* (2014), Kishore *et al.* (2015) and Kahani and Hittalmani (2016) have reported

significant positive correlation of number of productive tillers, panicle length, and plant height.



**Fig. 3. Heatmap of correlation coefficient in N22 x N22-CC-M4-HT-1333 of a.  $F_2$  generation; b.  $F_3$  generation**

**Table 3. Correlation coefficient in  $F_3$  generation of population of N22 x N22-CC-M4-HT-1333**

	PH	NT	NPT	FLL	FLW	PnL	TLL	TLB	TLW	WB	DMP	HI	GY
PH	1.000												
NT	-0.151	1.000											
NPT	0.061	0.506	1.000										
FLL	0.467	-0.243	-0.136	1.000									
FLW	0.213	-0.053	-0.008	0.436	1.000								
PnL	0.384	-0.254	-0.150	0.539	0.290	1.000							
TLL	0.071	-0.044	0.085	0.038	0.039	0.058	1.000						
TLB	0.029	-0.095	-0.013	0.062	0.170	0.117	0.557*	1.000					
TLW	-0.015	-0.063	0.040	0.007	0.040	0.058	0.884**	0.709**	1.000				
WB	0.280	0.426	0.453	0.063	0.087	0.028	-0.028	-0.106	-0.063	1.000			
DMP	0.314	0.405	0.453	0.100	0.093	0.063	-0.001	-0.093	-0.045	0.976**	1.000		
HI	0.168	-0.187	-0.127	0.224	0.096	0.235	-0.016	0.018	-0.005	-0.109	-0.087	1.000	
GY	0.390	0.096	0.183	0.245	0.130	0.244	0.015	-0.038	-0.018	0.567*	0.605*	0.644*	1.000

\* $r_{0.05} = 0.552$ , \*\* $r_{0.01} = 0.683$

Grain yield is a complex trait governed by quantitative trait loci and environmentally influenced (Wang *et al.*, 2012, Zeng *et al.*, 2017 and Li *et al.*, 2019). In rice, yield increase is explored in many ways for crop improvement. Ideotype breeding by altering plant architecture is an established strategy for yield improvement (Jeon *et al.*, 2011). Based on this study, it was found that the mutant parent N22-CC-M4-HT-1333 was efficient parent in increasing grain yield through altered biomass and dry matter production. Upon exploring the genomic regions contributing for altered plant type, it can be concluded that the key factor for increasing grain yield is increase in

biomass production. This mutant parent is good source for studying functional genomics of altered plant architecture, biomass production and grain yield to serve in future breeding programs.

#### ACKNOWLEDGEMENT

We would like to acknowledge DBT for providing fund and material under the scheme "Maintenance, characterization and use of EMS mutants of upland variety Nagina 22 for functional genomics in Rice – Phase II" for conducting research.

#### REFERENCES

Bueno, C. S., and Lafarge, T. (2009). Higher crop performance of rice hybrids than of elite inbreds in the tropics: 1. Hybrids accumulate more biomass during each phenological phase. *Field Crops Research*, **112**(2-3), 229–237.

Burton, G.W. (1952) Quantitative inheritance in grasses. *Proceedings of 6th International Grassland Congress*, **1**, 277-283

Chen, S., Zhang, X., Zhang, G., Wang, D., and Xu, C. (2012). Grain yield and dry matter accumulation response to enhanced panicle nitrogen application under different planting methods (*Oryza sativa* L.). *Australian Journal of Crop Science*, **6**(12), 1630–1636.

FAO. (2015). *The future of food and agriculture: Trends and challenges*. Food and Agriculture Organization of the United Nations.

Fischer, R. (1983). *Growth and Yield of Field Crops (Wheat)*. Symposium on Potential Productivity of Field Crops Under Different Environments.

GRISP. (2013). *Rice Almanac*. IRRI, Los Baños, Philippines.

Jeon, J.S., Jung, K.-H., Kim, H.-B., Suh, J.P., and Khush, G. S. (2011). Genetic and Molecular Insights into the Enhancement of Rice Yield Potential. *Journal of Plant Biology*, **54**(1), 1–9.

Kahani, F., and Hittalmani, S. (2016). Identification of  $F_2$  and  $F_3$  segregants of fifteen rice crosses suitable for cultivation under aerobic situation. *Sabrao Journal of Breeding and Genetics*, **48**(2), 219–229.

Katsura, K., Maeda, S., Horie, T., and Shiraiwa, T. (2007). Analysis of yield attributes and crop physiological traits of Liangyoupeiji, a hybrid rice recently bred in China. *Field Crops Research*, **103**(3), 170–177.

Khush, G. S. (1995). Breaking the yield frontier of rice. *GeoJournal*, **35**(3), 329–332.

Kishore, N., Srinivas, T., Nagabhushanam, U., Pallavi, M., and Sameera, S. (2015). Genetic variability, correlation and path analysis for yield and yield components in promising rice (*Oryza sativa* L.) genotypes. *SAARC Journal of Agriculture*, **13**(1), 99–108.

Lakshmi, L., Rao, M.V.B, Raju, Ch.S. and Reddy, S.N. (2017). Variability, Correlation and Path Analysis in Advanced Generation of Aromatic Rice. *Int.J.Curr.Microbiol.App.Sci.* **6**(7): 1798-1806.

Li, R., Li, M., Ashraf, U., Liu, S., and Zhang, J. (2019). Exploring the relationships between yield and yield-related traits for rice varieties released in China from 1978 to 2017. *Frontiers in Plant Science*, **10** (543).

Lush, J. L. (1940). Intra – sire Correlation and regression of offspring in rams as a method of estimating heritability of characters. *Proc. American Soc. Animal Product.*, **33**: 292 – 301.

Mamata, K., Rajanna, M. and Savita. S. (2018). "Assessment of genetic parameters for yield and its related traits in  $F_2$  populations involving traditional varieties of rice (*Oryza sativa* L.)." *Int.J.Curr.Microbiol.App.Sci.* **7** (1):2210-2217.

Peng, S., Laza, R. C., Visperas, R. M., Sanico, A. L., and Cassman, K. G. (2000). Grain Yield of Rice Cultivars and Lines Developed in the Philippines since 1966. *Crop Science*, **40**(2), 307–314.

Peng, S., Khush, G. S., Virk, P., Tang, Q., and Zou, Y. (2008). Progress in ideotype breeding to increase rice yield potential. *Field Crops Research*, (108), 32–38.

Singh, N., Choudhury, D. R., Tiwari, G., Singh, A. K., Kumar, S., Srinivasan, K., Tyagi, R., Sharma A., Singh, N. and Singh. R. (2016). "Genetic diversity trend in Indian rice varieties: an analysis using SSR markers." *BMC genetics* **17** (1):127.

Tiwari, G. C. (2015). "Variability, heritability and genetic advance analysis for grain yield in rice." *International Journal of Engineering Research and Applications* **5** (7):46-49.

Tuhina-Khatun, M., Hanafi, M. M., Rafii Yusop, M., Wong, M. Y., Salleh, F. M., and Ferdous, J. (2015). Genetic Variation, Heritability, and Diversity Analysis of Upland Rice (*Oryza sativa* L.) Genotypes Based on Quantitative Traits. *BioMed Research International*, **2015**, 1–8.

Wang, S., Wu, K., Yuan, Q., Liu, X., Liu, Z., Lin, X., Zeng, R., Zhu, H., Dong, G., Qian, Q., Zhang, G., and Fu, X. (2012). Control of grain size, shape and quality by OsSPL16 in rice. *Nat. Genet.* **44**, 950–954.

Wu, W.ge, Zhang, H. cheng, Qian, Y. Fei, Cheng, Y., Wu, G. cheng, Zhai, C. qun, and Dai, Q. gen. (2008). Analysis on Dry Matter Production Characteristics of Super Hybrid Rice. *Rice Science*, **15**(2), 110–118.

Ying, J., Peng, S., He, Q., Yang, H., Yang, C., Visperas, R. M., and Cassman, K. G. (1998). Comparison of high-yield rice in tropical and subtropical environments I. Determinants of grain and dry matter yields. *Field Crops Research*, **57**(1), 71–84.

Zeng, D., Tian, Z., Rao, Y., Dong, G., Yang, Y., Huang, L., et al. (2017). Rational design of high-yield and superior-quality rice. *Nat. Plants* **3**:17031.

Zhang, Y., Tang, Q., Zou, Y., Li, D., Qin, J., Yang, S., Chen, L., Xia, B., Peng, S. (2009). Yield potential and radiation use efficiency of "super" hybrid rice grown under subtropical conditions. *Field Crops Research*, **114**(1), 91–98.