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GENETIC ARCHITECTURE OF NEW PLANT TYPE RICE (*ORYZA SATIVA* L.) LINES BASED ON A 12-YEARS MULTI-EXPERIMENT

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SUMMARY

New plant-type (NPT) rice can increase grain yield globally. Although many studies have shown the association between harvest and yield-related traits in rice, it remains obscure in the case of NPT rice. This study aimed to elucidate the relationship between agronomic and yield features in new plant-type rice based on a 12-years multi-experiment. A large dataset of 704 NPT rice lines of various generations (F_4 to F_{10}), derived from 24 different populations, underwent study. The analysis of variance showed a highly significant population effect ($P < 0.01$) on all traits studied. The NPT rice populations had groupings into four clusters, with a highly substantial cluster effect ($P < 0.01$) on the number of total tillers (NTT), number of total grains (NTG), number of filled grains (NFG), and thousand-grain weight (TGW). Standard best NPT lines from each experiment achieved an average of 1.67 t ha^{-1} or 26% higher yield than the Ciherang variety. Determining the yield advantage of NPT lines was by higher plant height (PH) ($r = 0.37$), panicle length (PL) ($r = 0.15$), NTG ($r = 0.28$), NFG ($r = 0.28$), TGW ($r = 0.10$), and lower days to harvest (DTH) ($r = -0.10$). The principal component analysis biplot revealed that NFG could better serve as a selection characteristic for enhancing grain yield in developing NPT rice adapted to irrigated tropical ecosystems.

Keywords: Cluster analysis, combined analysis, genotype × trait, grain yield, Pearson correlation, rice breeding

Key findings: The new plant-type rice architecture allows a higher yield (26%) than the green revolution rice type represented by the Ciherang variety. Genetic diversity among the NPT lines is prevalent; therefore, breeding-improved NPT rice varieties are promising.

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INTRODUCTION

The development of new plant-type rice started in the late 1980s to break the yield barriers in the stalemate of semi-dwarf varieties. Since then, a study on the reason for the yield advantages of NPT rice has evolved. The NPT design sought a higher yield from fewer tillers and heavy panicle architecture (Peng *et al*., 1999). Poor grain filling and low biomass production in NPT rice are due to apical dominance and early leaf senescence, respectively (Ladha *et al*., 1998; Parida *et al*., 2022). The backcrossing to superior indica varieties, such as IR64, has enhanced grain-filling (Sasaki *et al*., 2017). Moreover, the large, dark green, long-flag leaf could facilitate higher photosynthesis at the late-growth stage (Murchie *et al*., 1999). As a result, major NPT lines produced a higher yield potential range, i.e., 9–13 t ha^{-1} (Abdullah *et al*., 2008).

The initial NPT rice architecture was for irrigated and favorable rainfed tropical lowlands. Correspondingly, it remains important to regionalize the criteria based on local climatic and cultivation conditions (Feng *et al*., 2013). The release of NPT rice varieties went on in many countries. A few examples are as follows: Pusa 1266 in India (Marathi *et al*., 2012); Takanari in Japan (Horie, 2001); Fatmawati (Abdullah *et al*., 2008) and IPB3S in Indonesia. In China, the NPT rice variety, namely, Shennong265, began its release in 1997 and has reached a yield potential of 11–11.8 t ha^{-1}. This variety, along with others, such as Shennong174 and Shennong606, has farmers widely adopting them (Chen *et al*., 2001). On the other hand, the rice's theoretical yield potential in tropical regions estimates at 15.9 t ha^{-1} (Yoshida, 1981). It implies that more improvement can proceed for NPT to achieve a higher yield potential.

Developing new plant-type rice varieties through the ideotype breeding approach hopes to enhance the achievement already attained by green-revolution-type selections (Peng *et al*., 2008). The ideotype breeding approach tries to improve complex traits by changing simpler ones highly correlated with them. Several ideotype traits, such as, panicle number and grain weight, served as target selection in most cereal breeding programs (Rasmusson, 1991). Yield is the most important and complex trait of rice. Rice yield has the number of productive tillers, filled grains per panicle, and thousand-grain weight directly determining it (Peng *et al*., 2000; Gaballah *et al*., 2021; Syahril *et al*., 2022). Meanwhile, plant height, panicle length, and growth period influence it indirectly (Khush, 1999). Understanding the relationship among traits could push the limit of rice yield.

Many studies have revealed that the relationship pattern between agronomic and yield traits gained influences from genetics, environment, and the ecotype level (Li *et al*., 2019). However, it is still obscure for the case of NPT rice, with its development by crossing the *indica* and *javanica* subspecies. This study aimed to elucidate the relationship between agronomic and yield traits in new plant-type rice based on a 12-years multi-experiment.

MATERIALS AND METHODS

Twenty experiments on NPT rice lines progressed from 2010 to 2020, coordinated by the NPT rice breeding program at the Department of Agronomy and Horticulture, Faculty of Agriculture, IPB University, led by the first author (Table 1). The NPT rice lines developed in this breeding program used the modified bulk breeding method. The details of each experiment, including the methods and results, have been written separately as a Bachelor of Science thesis by its respective authors (see citations in Table 1). All 20 experiments met the four following criteria: 1) the experiment requires execution in irrigated lowland agroecosystem, 2) the NPT rice lines used were above F_3 generation, 3) each studied trait must be measured by the same procedure among experiments, and 4) the Ciherang variety must serve as a check. Finally, this study used a large dataset of 704 NPT rice lines of various generations (F_4 to F_{10}) from 24 diverse populations (Table 2). Selecting and combining the NPT line with the highest grain yield from each experiment formed a subset called 'best lines.'

Table 1. Description of 20 experiments of NPT rice from 2010 to 2020.

Exp. No.	Year	Location	No. of lines	Gen.	No. of reps	Exp. design	Citation
1	2010	Bogor	8	F_9	3	RCBD	(Halimah, 2010)
2	2010	Bogor	30	F_8	3	RCBD	(Tiara, 2010)
3	2011	Lebak	8	F_9	3	RCBD	(Chirzin, 2011)
4	2012	Bogor	88	F_5	6[a]	A. RCBD	(Saniaty, 2012)
5	2012	Lebak	10	F_9	3	RCBD	(Haq, 2012)
6	2013	Bogor	30	F_6	3	RCBD	(Rahmah, 2013)
7	2013	Bogor	97	F_5	5[a]	A. RCBD	(Nurhidayah, 2013)
8	2014	Karawang	10	F_9	3	RCBD	(Septiani, 2014)
9	2015	Bogor	10	F_9	3	RCBD	(Zulkarnaen, 2015)
10	2015	Bogor	38	F_9	3	RCBD	(Nasution, 2015)
11	2016	Cianjur	10	F_{10}	3	RCBD	(Yusuf, 2016)
12	2017	Bogor	49	F_4	3[a]	A. RCBD	(Baharudin, 2017)
13	2018	Bogor	38	F_6	3	RCBD	(Alvianto, 2018)
14	2018	Bogor	36	F_6	3	RCBD	(Setiono, 2018)
15	2018	Bogor	38	F_6	3	RCBD	(Sari, 2018)
16	2019	Bogor	50	F_7	3	RCBD	(Pradana, 2019)
17	2019	Bogor	50	F_7	3	RCBD	(Gantina, 2019)
18	2019	Bogor	50	F_7	3	RCBD	(Romas, 2019)
19	2020	Bogor	26	F_9	3	RCBD	(Pangestu, 2020)
20	2020	Bogor	28	F_9	3	RCBD	(Putri, 2020)

[a]: replications for checks, Gen.: generation of the lines, A.: augmented, RCBD: randomized complete block design.

Table 2. Parents of the NPT rice populations studied.

Pop.	Parents	Pop.	Parents
97	Fatmawati/IPB6-d-10s-1-1-1	162	Cimelati/IPB97-F-44-2-1
102	IPB6-d-10s-1-1-1/Fatmawati	163	IPB117-F-5-1-1/Inpari 1
107	Fatmawati/Siam Sapat	165	IR64/IPB117-F-19-1-1
113	Fatmawati/Pare Bau	167	IPB113-F-2-1-1/IR64
115	Fatmawati/Lambau	168	IR64/IPB117-F-61-1-1
116	Fatmawati/Pinjan	175	IPB117-F-7-2-1/Inpari 13
117	Fatmawati/Pulu Mandoti	187	IPB160-F-36-4/IPB 3S
149	Sintanur/Lambau	189	IPB160-F-36-4/IPB93-F-8-1
158	IPB117-F-5-1-1/IR64	190	IPB160-F-36-4/IPB160-F-102-2-1
159	IPB98-F-5-1-1/IR64	191	IPB 4S/IPB160-F-7-1-1
160	Cimelati/IPB97-F-31-1-1	193	IPB 8G/IPB160-F-36-4
161	IR64/IPB98-F-5-1-1	194	IPB160-F-36-4/IPB 4S

Pop.: population

Traits analyzed were plant height (PH), number of total tillers per plant (NTT), number of productive tillers per plant (NPT), days to harvest (DTH), panicle length (PL), number of total grains per panicle (NTG), number of filled grains per panicle (NFG), and thousand-grain weight (TGW). The PH's measurement starts from the ground level to the tip of the tallest panicle while counting the total tillers per plant and the number of tillers that produced panicles for NTT and NPT, respectively. DTH recording comprised the days when 80%–90% of panicles in each plot matured. Measuring PL starts from the neck to the tip of the panicle. Counting the total grains per panicle and the number of filled grains per panicle served as the basis for NTG and NFG measurements, respectively, with TGW measured as the weight of 1,000 filled grains at 14% moisture content.

Adjusting the mean of each line in each experiment for a trait with the Ciherang variety's average ensued per investigation. The adjustment procedure was as follows: subtracting the mean of the Ciherang variety in

Table 3. Mean, standard deviation, and range of agronomic and yield traits of NPT rice across 20 experiments.

Trait	N	Mean	SD	CV (%)	Minimum	Maximum
Y	677	6.39	1.39	21.73	1.72	12.89
PH	694	117.11	9.98	8.52	79.75	157.75
NTT	566	12	2.73	22.49	5	29
NPT	607	12	2.21	18.86	4	20
DTH	704	111	3.75	3.38	91	126
PL	616	29.72	2.10	7.08	19.25	37.85
NTG	704	251	61.14	24.32	98	545
NFG	704	179	41.74	23.32	68	350
TGW	704	27.36	2.45	8.95	17.32	34.22

Y: yield, PH: plant height (cm), NTT: number of total tillers, NPT: number of productive tillers, DTH: days to harvest (d), PL: panicle length (cm), NTG: number of total grains per panicle, NFG: number of filled grains per panicle, TGW: thousand-grain weight (g), N: number of genotypes, SD: standard deviation, CV: coefficient of variation.

an experiment from the median of each NPT line presented in the research, then adding the resulting difference to the grand average of Ciherang across 20 experiments. It allows comparison of the lines across experiments because of excluding the experiment effect. The adjusted means continued for subsequent analyses. Descriptive statistics calculation included each trait's mean, standard deviation, and range across 20 experiments. The Pearson correlation analysis helped to understand the linear relationships between agronomic and yield features on the genotype mean basis. A cluster analysis based on quantitative traits based on Manhattan distance and neighbor-joining methods also classified the NPT populations into different clusters. Engaging the principal component analysis biplot visualized the interrelationship among all attributes studied. The analyses ran on SAS on Demand for Academics (welcome.oda.sas.com), R (R Core Team, 2022), and PBSTAT-CL 2.1.1 (www.pbstat.com).

RESULTS

Genetic variability among NPT rice lines

Descriptions of the overall characteristics of NPT rice lines are in Table 3. The phenotypic data obtained from 566 to 704 lines differed among traits because there were those not measured in a particular experiment. Nevertheless, an immense dataset was still available for analysis to meet the study objectives. The variations among lines were relatively higher (CV > 15%) for yield, number of total and productive tillers, and number of total and filled grains and somewhat smaller (CV < 10%) for plant height, days to harvest, panicle length, and thousand-grain weight (Table 3). Figure 1 displays the distributions of NPT lines for each trait.

Over 20 experiments, the yield of the best NPT lines ranged from 5.94 to 12.89 t ha^{-1}, while the Ciherang variety ranged from 4.69 to 7.76 t ha^{-1} (data not shown). The average yield of the best NPT lines was 8.08 t ha^{-1}, and for Ciherang was 6.41 t ha^{-1} (Table 4). Therefore, the average advantage of the NPT best lines was 1.67 t ha^{-1} or 26% over Ciherang. This difference was highly significant ($P < 0.01$) based on a paired two-sample t-test, and the 95% confidence interval of the difference was 0.67–2.66 t ha^{-1}.

To better understand the architecture of good NPT lines, selecting the best line from each experiment had their means calculated (Table 4). The explanation for the architecture of these lines could then be as follows: high yield potential (8 t ha^{-1}), relatively high plant stature (117 cm), few tillers (13 per hill), but all are productive, 111 days to harvest, comparatively long panicle (30 cm), numerous total grains (243) and filled grains (181) per panicle, and moderate grain size with an average 1000-grain weight of 28 g.

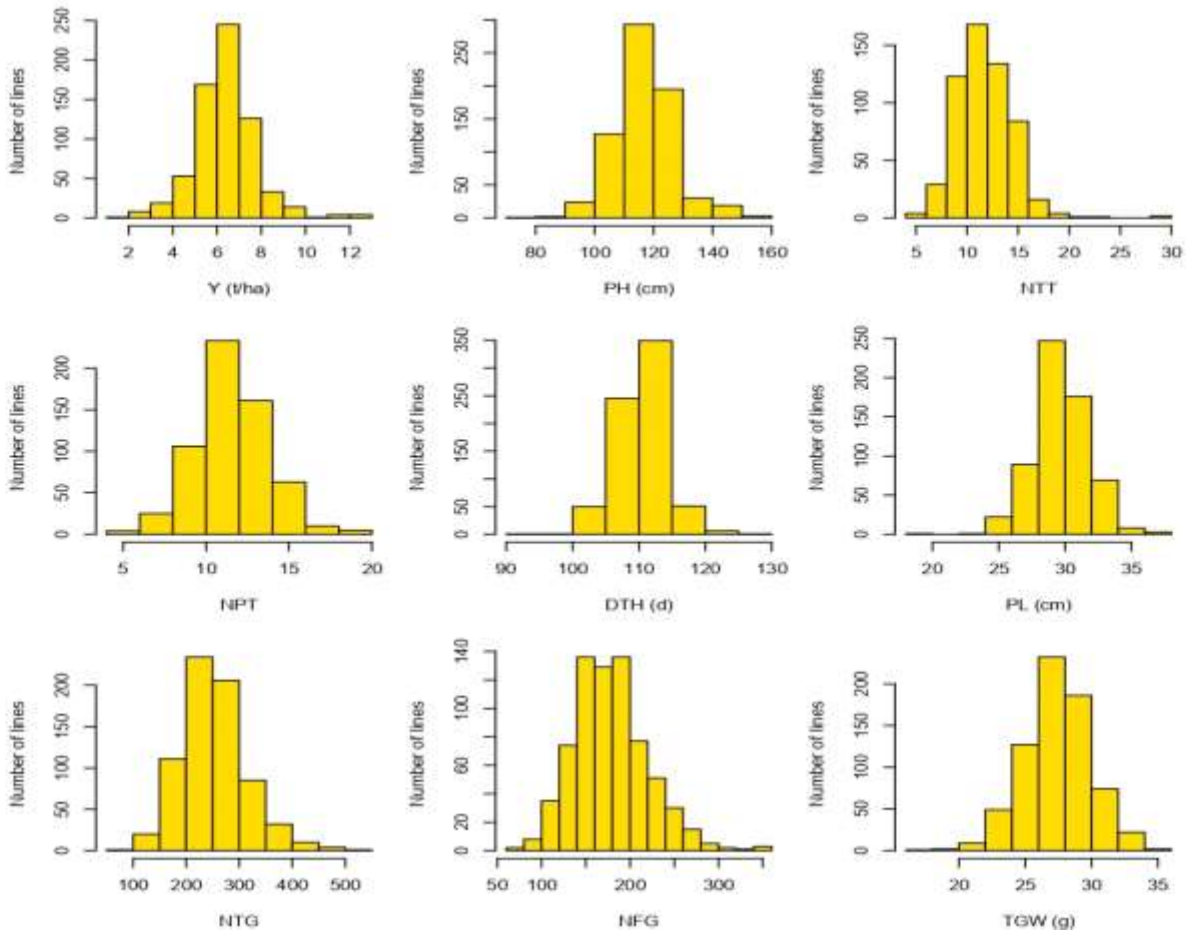

Figure 1. Distribution of yield and agronomic traits of 704 NPT rice lines across 20 experiments. Y: yield, PH: plant height (cm), NTT: number of total tillers, NPT: number of productive tillers, DTH: days to harvest (d), PL: panicle length (cm), NTG: number of total grains per panicle, NFG: number of filled grains per panicle, TGW: thousand-grain weight (g).

Table 4. Average of the best NPT lines compared with the Ciherang variety for agronomic and yield traits.

Trait	Average of best NPT lines	Average of Ciherang	Difference	%Difference
Y	8.08	6.41	1.67^{**}	26.00
PH	117.43	110.75	6.68^{*}	6.03
NTT	13	17	-4^{*}	-21.59
NPT	13	17	-4^{**}	-20.68
DTH	111	113	-2^{ns}	-1.96
PL	29.55	25.65	3.90^{**}	15.21
NTG	243	156	87^{**}	56.15
NFG	181	118	63^{**}	53.82
TGW	28.03	26.32	1.71^{*}	6.50

** Significant at $P < 0.01$, * significant at $P < 0.05$, ^{ns} not significant, Y: yield, PH: plant height (cm), NTT: number of total tillers, NPT: number of productive tillers, DTH: days to harvest (d), PL: panicle length (cm), NTG: number of total grains per panicle, NFG: number of filled grains per panicle, TGW: thousand-grain weight (g).

Grouping of NPT rice populations

The characteristics of NPT rice populations are available in Table 5. It is interesting to study the differences in the plant architecture among clusters (Table 6). The result of the cluster analysis of 24 diverse populations appears in Figure 2. The yield, days to harvest, and panicle length of the four clusters differ less significantly. Clusters 1 and 2 have a higher plant stature and fewer total tillers, and conversely, Clusters 3 and 4 have a shorter plant stature and more total tillers. A relatively high number of total and filled grains resulted in Cluster 2, contrasting with Cluster 3. The grain numbers in Clusters 1 and 4 are in between, but Cluster 4 has a higher filling rate (74.6%) than Cluster 1 (68.6%). Clusters 1, 2, and 3's grain size is larger than Cluster 4, as indicated by their thousand-grain weight (Table 6).

Table 5. Adjusted means of agronomic and yield traits of NPT rice populations.

Pop.	Clus.	Y	PH	NTT	NPT	DTH	PL	NTG	NFG	TGW
97	1	6.97	127.15	11	12+	109	29.25	261	204	28.52
102	4	6.30	117.42	14	13	114	29.72	278	198	25.98
107	4	6.02	114.59	14	13	114	30.39	303	228	23.77
113	4	5.23	115.75	15	14	105	31.65	249	183	26.32
115	3	4.90	110.25	11	11	110	29.65	228	147	28.32
116	4	5.29	104.97	14	13	109	29.57	249	179	26.18
117	2	5.35	118.65	11	11	112	32.00	286	206	29.72
149	4	5.70	110.75	13	13	112	29.65	274	182	26.32
158	3	7.20	107.45	15	12	112	27.45	212	161	26.22
159	3	6.14	111.65	-	12	111	28.46	235	173	27.89
160	3	5.94	109.92	17	11	113	28.26	178	140	27.27
161	4	6.31	114.77	13	12	114	28.47	242	199	25.15
162	3	6.57	118.95	15	14	117	27.77	225	167	29.17
163	4	6.72	116.88	12	12	113	28.74	247	201	26.09
165	4	6.39	114.94	12	12	115	28.94	241	184	26.03
167	3	5.88	107.42	-	14	103	26.08	190	146	27.98
168	3	5.09	109.93	16	13	107	27.51	186	144	26.86
175	3	6.46	131.89	15	-	114	32.72	198	139	26.72
187	1	6.39	117.53	12	12	109	30.67	271	180	28.95
189	1	6.57	123.07	12	12	108	30.07	283	183	27.77
190	2	6.55	123.02	12	11	110	30.35	297	205	27.45
191	2	6.25	121.52	11	11	110	30.31	312	218	27.02
193	1	6.60	118.81	11	11	110	30.02	279	190	27.76
194	1	6.79	123.35	11	12+	110	29.78	252	166	27.97
Sig.		**	**	**	**	**	**	**	**	**
LSD 0.05		1.63	10.28	3	3	4	2.31	59	43	2.56
CV		21.19	7.30	19.27	18.43	2.86	6.33	19.60	19.23	7.77

** significant at $P < 0.01$, Y: yield, PH: plant height (cm), NTT: number of total tillers, NPT: number of productive tillers, DTH: days to harvest (d), PL: panicle length (cm), NTG: number of total grains per panicle, NFG: number of filled grains per panicle, TGW: thousand-grain weight (g), Sig.: significancy (F-test), LSD: least significant difference, CV: coefficient of variation (%), Clus.: cluster number, + higher value of NPT compared with NTT were due to adjustments, and these values may be interpreted as 'similar.'

Table 6. Cluster means of agronomic and yield traits of NPT rice.

Clus.	Y	PH	NTT	NPT	DTH	PL	NTG	NFG	TGW
1	6.66	121.98[a]	11[b]	12[ab+]	109	29.96	269.21[b]	184.58[b]	28.19[a]
2	6.05	121.06[ab]	11[b]	11[b]	111	30.88	298.42[a]	209.37[a]	28.06[a]
3	6.02	113.43[c]	15[a]	12[a]	111	28.49	206.37[c]	152.20[c]	27.55[a]
4	6.00	113.76[bc]	13[a]	13[a]	112	29.64	260.31[b]	194.21[ab]	25.73[b]
Sig.	ns	*	**	*	ns	ns	**	**	**
CV	9.67	4.97	9.35	7.43	3.02	4.67	7.86	7.76	3.41

** significant at $P < 0.01$, * significant at $P < 0.05$, ns not significant, Clus.: cluster number, Y: yield, PH: plant height (cm), NTT: number of total tillers, NPT: number of productive tillers, DTH: days to harvest (d), PL: panicle length (cm), NTG: number of total grains per panicle, NFG: number of filled grains per panicle, TGW: thousand-grain weight (g), Sig.: significancy (F-test), CV: coefficient of variation (%). Numbers with the same letters in the same column are not significantly different based on LSD 0.05, + higher value of NPT compared with NTT was due to adjustments, and these values may be interpreted as 'similar.'

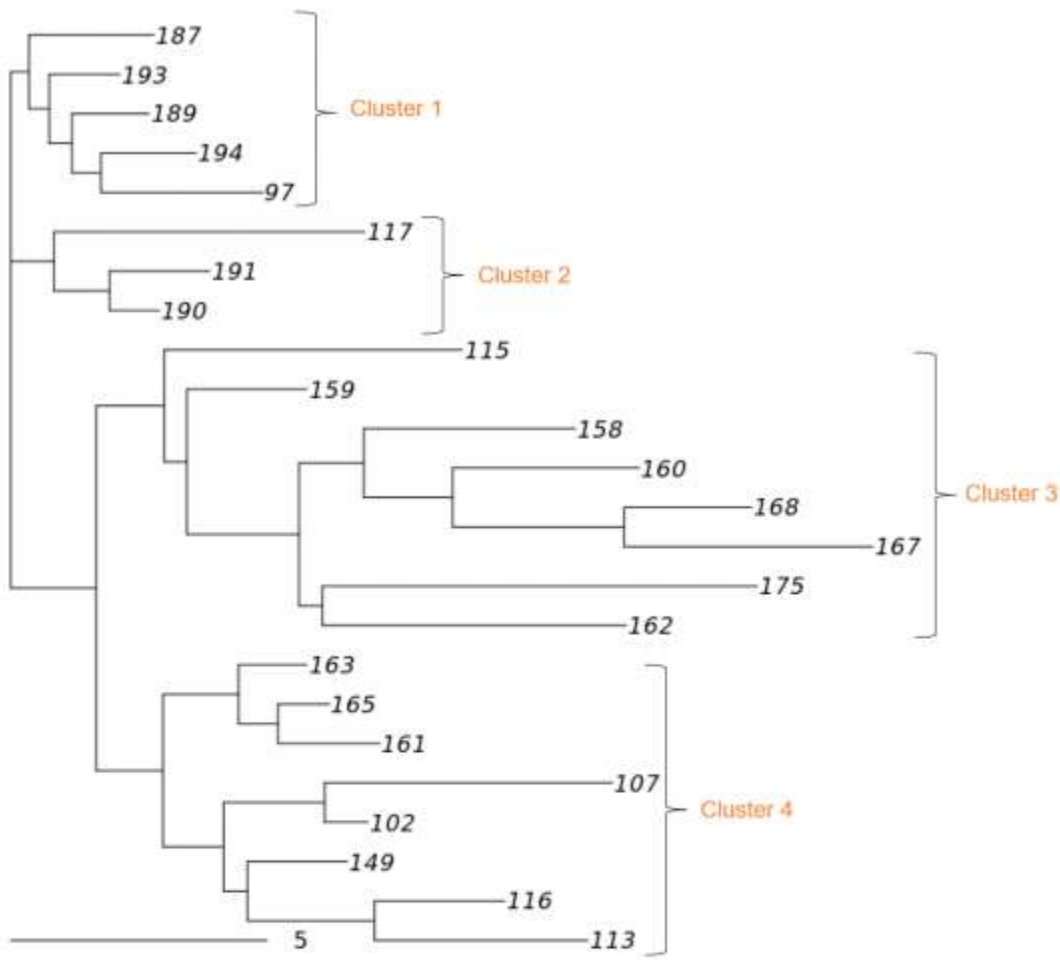

Figure 2. Neighbor-joining tree based on Manhattan distance of 24 populations of NPT rice lines based on adjusted agronomic and yield data in 20 experiments.

Correlation among traits of NPT rice

Grain yield was highly significantly correlated ($P < 0.01$) with plant height ($r = 0.37$), number of total tillers ($r = -0.13$), panicle length ($r = 0.15$), days to harvest (-0.10), number of total grain ($r = 0.28$), number of filled grains ($r = 0.28$), and thousand-grain weight ($r = 0.10$) (Table 7). Plant height was negatively correlated ($P < 0.01$) with the number of total tillers ($r = -0.40$), number of productive tillers ($r = -0.11$), and days to harvest ($r = -0.16$). Likewise, plant height was also highly significantly correlated with panicle length ($r = 0.47$), number of total grains ($r = 0.55$), number of filled grains ($r = 0.42$), and thousand-grain weight ($r = 0.22$). The correlation between the number of productive and total tillers was huge ($r = 0.90$, $P < 0.01$), and the number of productive tillers was also highly significantly correlated ($P < 0.01$) with the number of total grains ($r = -0.13$). A negative and highly significant correlation ($P < 0.01$) emerged between days to harvest with thousand-grain weight ($r = -0.17$). The correlation pattern of the number of total and filled grains for yield and the number of productive tillers were similar, with the correlation between the two at 0.84 ($P < 0.01$) (Table 7). Visualized interrelationships among all traits studied are in Figure 3.

Table 7. Pearson correlation coefficients among agronomic and yield traits of NPT rice across 20 experiments.

	Y	PH	NTT	NPT	DTH	PL	NTG	NFG	TGW
Y	1								
PH	0.37^{**}	1							
NTT	-0.13^{**}	-0.40^{**}	1						
NPT	0.02^{ns}	-0.11^{**}	0.90^{**}	1					
DTH	-0.10^{**}	-0.16^{**}	0.38^{**}	0.01^{ns}	1				
PL	0.15^{**}	0.47^{**}	-0.32^{**}	-0.26^{**}	-0.05^{ns}	1			
NTG	0.28^{**}	0.55^{**}	-0.47^{**}	-0.13^{**}	-0.22^{**}	0.44^{**}	1		
NFG	0.28^{**}	0.42^{**}	-0.37^{**}	-0.11^{**}	-0.12^{**}	0.29^{**}	0.84^{**}	1	
TGW	0.10^{**}	0.22^{**}	-0.24^{**}	-0.09^{*}	-0.17^{**}	0.28^{**}	0.09^{*}	-0.06^{ns}	1

^{ns} not significant, *, ** significant at $P < 0.05$ and $P < 0.01$, respectively. Y: yield, PH: plant height (cm), NTT: number of total tillers, NPT: number of productive tillers, DTH: days to harvest (d), PL: panicle length (cm), NTG: number of total grains per panicle, NFG: number of filled grains per panicle, TGW: thousand-grain weight (g).

DISCUSSION

It is understandable that although all experiments ran at irrigated lowlands, the phenotypes of these lines still had effects from the genetics, environment, and interaction between the two. Therefore, the adjusted mean value was chosen as a dataset rather than the actual one. The Ciherang variety, which became a check variety in each experiment, served well for correcting the environmental effects. As a result, the NPT lines in these 20 experiments can have comparative differentiation.

The average yield advantage of the best NPT lines over Ciherang, an Indonesian rice mega variety, was 0.67–2.66 t ha^{-1} (95% confidence interval). This gain is higher than that from the hybrid rice reported by Peng *et al*. (1999), Huang *et al*. (2018), and Xu *et al*. (2021). It indicated that the IPB's rice breeding program has successfully developed high-yielding genotypes, with the NPT architecture a prospect for adoption in a modern rice breeding program.

Cluster analysis is the most important tool for breeders to select the ideal parents for crossing. Among 24 populations, cluster analysis resulted in four clusters following the neighbor-joining method (Figure 2). Further assessing the different clusters' mean performance (Table 6) could improve various traits in NPT rice breeding. Population separation had the variation in PH, NTT, NPT,

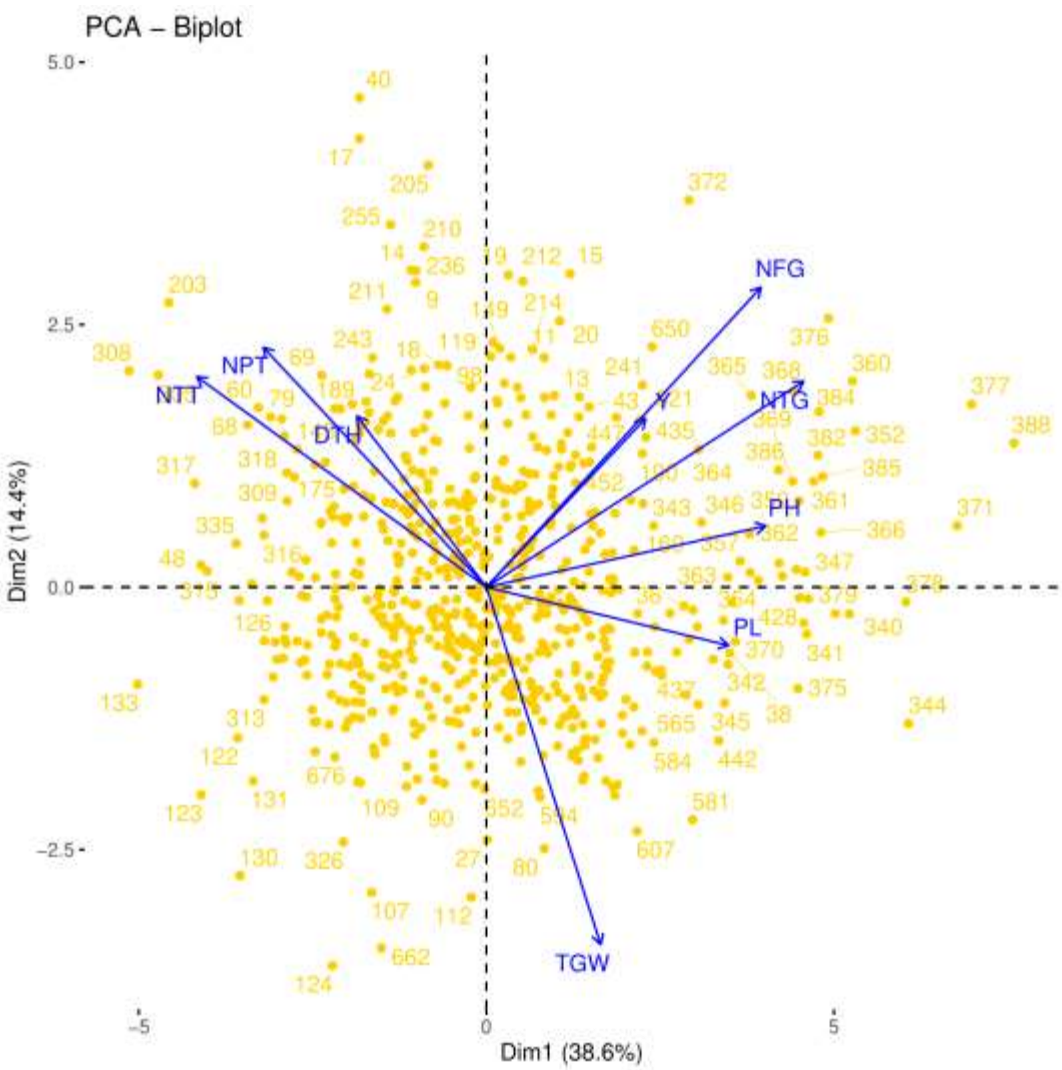

Figure 3. Principal component analysis biplot from 704 NPT lines and nine traits. Y: yield, PH: plant height (cm), NTT: number of total tillers, NPT: number of productive tillers, DTH: days to harvest (d), PL: panicle length (cm), NTG: number of total grains per panicle, NFG: number of filled grains per panicle, TGW: thousand-grain weight (g). Dim1 and Dim2 are the principal components axis 1 and 2, respectively.

NTG, NFG, and TGW, significantly affecting it. Cluster 2 has populations with the highest total and filled grain numbers, especially population 191 (Table 5). Moreover, Cluster 1 is characteristic of populaces with the tallest plant height. Populations with higher tillering capacity gained grouping into Clusters 3 and 4. Additionally, Cluster 4 also incorporated the smallest thousand-grain weight. The first, second, third, and fourth clusters comprised five, three, eight, and eight populations. Clusters that contained greater populations indicated a sufficient and large amount of genetic diversity (Nachimuthu *et al*., 2015). Based on the Manhattan distance, the highest inter-cluster interval exists between Cluster 1 and Cluster 4, indicating the presence of genetic dissimilarity (Shrestha *et al*., 2021). Consequently, the genotypes from those populations can serve better for hybridization to produce wide variability in segregating generations.

Selection plays a crucial role in plant breeding. Selecting merely based on unadjusted yield values across different experiments could be misleading. Consequently, defining traits as selection criteria through correlation analysis was crucial. The finding in this study confirmed that agronomic traits strongly affect yield. Therefore, enhancing and maintaining other related yield components was the ultimate prerequisite for implementing continuous selection.

The study found that plant height had a highly positive significant correlation with yield. Increasing PH became an effective way to escalate yield (Yuan, 2017). The desired genotypes are those with high yield but not excessively high plant stature to avoid lodging. However, the positive coefficient of plant height in the linear model presented herein was unfavorable from the selection standpoint. This positive coefficient reflected that several high-yielding lines in our breeding program have relatively high plant stature and vice versa. This finding indicates that stem diameter and strength need incorporation as essential selection characteristics.

The traits PL, NTG, NFG, and TGW resulted highly positively correlated with yield. Panicle length indirectly impacted yield, but may affect grain filling and weight (Bhatia *et al*., 2017). Large and compact panicle architecture can cause poor filling of the inferior spikelet (Parida *et al*., 2022). Based on Table 3, the average percentage of unfilled grains of NPT lines was 28.68%. This occurrence displayed the apical dominance phenomenon, i.e., the apical spikelets play as inhibitors in grain filling for the basal spikelets (You *et al*., 2016). Thus, a slightly open panicle without any change in length appeared to be advantageous for NPT rice improvement (Peng *et al*., 1999; Sahu *et al*., 2020).

NTG and NFG, along with branching, determined the panicle size. Based on Table 7, panicle size positively correlated with plant height. However, lodging will occur when tall plants have a large panicle size. Taller plants with low panicle height and stronger stems were important for NPT improvement (Breseghello and Coelho, 2013). Sink size is a function of the NTG and the number of productive tillers per plant. In this study, these two traits showed a negative correlation. Hence, their balance became a key factor for culminating the maximum sink size. Besides that, increasing sink capacity should go along with extended days to harvest.

The days to harvest are slightly negative but significantly correlated with yield. This correlation indicates that some NPT lines with earlier maturity had a higher yield, while others with later maturity had a lower harvest. Such a negative correlation may favor the breeding program, allowing it to select high-yielding lines with early ripeness. Plants with delayed harvest time may have a greater chance of exposure to pests, diseases, and abiotic stresses. On the contrary, plants with early maturity may escape unfavorable environmental conditions, such as drought or waterlogging, during a short rainy or dry season in the tropics.

The correlation coefficient only describes the relationship between two traits. Hence, using a biplot is beneficial to visualize the interrelationship among all attributes. A PCA biplot in Figure 3 depicts their affiliation and some genotypes possessing each trait. Another approach that could be better for such visualization is the genotype-by-trait (GT) biplot. The GT biplot applies the GGE biplot technique to display the genotype-by-trait data graphically (Yan and Rajcan, 2002). The GT determines the trait profile, which facilitates the identification of traits that can serve as a target selection (Samonte *et al*., 2013). The PCA biplot in Figure 3 explained 53% of the total variation of the adjusted mean dataset. As a result, it is not valuable to identify the superior genotypes. However, the fundamental patterns among traits need capturing. DTH and yield have a relatively short vector length, indicating traits' weak correlation with any characteristics, and the genotype variations were small. Traits positively correlated with grain yield show location on the right half of the biplot. The biplot suggests a close association between NFG and yield. Moreover, NFG is considered best for discriminating genotypes, as it has a long vector length. As a result, the selection for NFG was the most effective strategy for increasing yield in NPT rice breeding.

CONCLUSIONS

The study revealed that the NPT rice architecture allows a higher yield than the green revolution rice type represented by the Ciherang variety. The yield advantage is 1.67 t ha^{-1} or 26% based on the best-lines average. Therefore, the NPT architecture is potential for adoption in current and near-future rice breeding programs. Genetic diversity among the NPT lines is prevalent; thus, breeding-improved NPT rice varieties are promising.

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