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Exploring the physiological efficiencies of promising rice (*Oryza sativa*) accessions for increasing grain yield

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ABSTRACT

High grain yield in rice (*Oryza sativa* L.) is a cumulative contribution of different morphological and physiological traits. However, the selection of high-yielding genotypes based on physiological traits is difficult where a large set of genotypes is used. Therefore, a study was carried out during rainy (*kharif*) seasons of 2019 and 2020 at research farm of ICAR-National Rice Research Institute, Cuttack, Odisha to assess the physiological efficiency of 211 elite rice genotypes having varying yield potential. The elite genotypes were classified into high, medium, and low categories based on their field performance. The results revealed that 29, 41, 34, 31, 49, 35, 39, 29, and 30 genotypes showing high values for FLA (>51.51 cm^2), TCC (>3.99 mg/g fresh weight), P_N (>20.79), g_s (>0.97), E (>9.03), TB (>15.95 t/ha), GY (>6.27 t/ha), PR (>0.29 kg/cm), and CS (>42.12 g/stem) respectively. Among them, 3 genotypes i.e. IG-020, IG-211 and IG-010 were identified to be highly efficient in 4 traits, 2 genotypes i.e., IG-044 and IG-186 in 5 traits, and 2 genotypes; IG-008 and IG-161 were found to be superior in 7 traits along with high grain yield. The selection of these genotypes with superior morphological and physiological traits could be beneficial in the breeding programme in terms of increasing yield potential in rice.

Keywords: Grain yield, New generation rice, Photosynthetic rate, Physiological efficiency

Rice (*Oryza sativa* L.) is one of the oldest cultivated and most consumable food crops, feeding two-thirds of the global population, notably in Asian countries, which produce and consume 90% of the rice (Saju and Thavaprakaash 2020). India has the most rice farming land and is second in production behind China (FAO 2018). However, the existing pace of rice production is insufficient to satisfy the rising population's need for food. So, it is necessary to develop high-yielding rice varieties with limited land resources. In this regard, many high-yielding rice varieties have been developed having around 10 t/ha yield potential. However, most of these genotypes were improved morphologically to increase grain yield (Dash *et al*. 2018). However, physiological traits still need to be tapped to maximize yield potential (Singh *et al*. 2014). Rice grain yield strongly relies on the chlorophyll content as well as the photosynthetic efficiency of flag leaf (activist leaf) during grain filling, which increases grain weight by 41–43% by contributing 60–80% of photosynthates (Lin *et al*. 2018). According to Kalyan *et al*. (2017), the direct selection of rice genotypes based on leaf area can benefit in increasing grain yield. The required CO_2 supply for photosynthesis is governed by stomatal conductance, which has increased in the last 50–80 years and is crucial for obtaining high yields. It also regulates the transpiration rate in plants. Mining rice resources for high biomass is also important, as it is a precondition for obtaining high grain yield by remobilizing photosynthates for grain development during the grain filling period (Qu *et al*. 2017). A further increase in grain yield requires an increase in culm strength to support the heavy panicle and withstand plant lodging to prevent yield loss (Kashiwagi and Ishimaru 2004). By looking into the relevance of the aforementioned physiological traits, the present study was carried out with the objectives – (i) to characterize rice genotypes based on superior physiological traits and (ii) to identify elite accessions having high yield along with superior physiological traits. These elite genotypes can be used as donors having high yields with superior physiological traits for further enhancement of grain yield in rice.

MATERIALS AND METHODS

Location, plant material and experimental design: A field experiment was conducted during rainy (*kharif*)

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seasons of 2019 and 2020 at research fram of ICAR-National Rice Research Institute, Cuttack, Odisha, taking 211 genotypes of rice which were selected from the set of 654 rice accessions based on grain yield potential. All the genotypes were evaluated for morpho-physiological and yield-related traits during both the season and the pooled data of 211 genotypes is presented in supplementary Table 1. The panel of 211 genotypes consisted of high, medium, and low-yielding genotypes along with 7 checks (Heera, Anjali, Swarna, Maudamani, IR-64, CR-Dhan-206, and CR-Dhan-304) and 47 new-generation rice genotypes (Dash *et al*. 2018). These genotypes excelled in one or more attributes. So, the entire panel of genotypes was designated as elite/improved genotype (IG). The genotypes were raised in the nursery bed and transplanted in the main field at 25 days after sowing (DAS) in two replications in a complete randomized design (CRD).

Phenotyping for morphological traits: Three plants were randomly selected and observed from each replication at 15 days after anthesis for measurement of flag leaf area and at 35 days after anthesis for measurement of pushing resistance and culm strength. The flag leaf area (cm^2) was measured using a portable leaf area meter (LI-COR, LI-3050c). Pushing resistance (kg/cm) and culm strength (g/stem) were measured in standing plants in field conditions using a prostrate tester (DIK-7401, Tokyo, Japan) following the procedure of Kashiwagi and Ishimaru (2004). The culm strength of individual culms was worked out by the formula given by Hai *et al*. (2005).

Phenotyping for physiological traits: Physiological traits such as total chlorophyll content and photosynthetic gas exchange parameters were analyzed at 15 days after anthesis. For total chlorophyll content analysis, 25 mg of a freshly cut flag leaf sample was immersed in 10 ml of 80% acetone (v/v) for 48 h in the dark. Then the extract was filtered, and absorbance was taken at 645 and 663 nm wavelengths using a UV visible spectrophotometer (UV 2600, Shimadzu, Japan). The total chlorophyll content (mg/g FW) was calculated using the formula given by Arnon (1949). Photosynthetic rate, stomatal conductance and transpiration rate were measured in the intact flag leaf using a portable infrared gas analyzer (LICOR6400XT, USA) from 9 am to 12 noon following the procedure of Mohanty *et al.* (2023). The same leaf was used for photosynthetic gas exchange parameters and also used for the measurements of leaf area and total chlorophyll content.

Phenotyping for yield and yield attributes: Total biomass and grain yield were measured during the maturity stage when the grain reached full ripeness. Plants were cut from the base, straw, and panicles were separated, air dried for sometimes and then oven dried at 80ºC till a constant weight was attained. Straw and panicle dry weight were added to get the total biomass (t/ha). Panicles were threshed and chaffs were removed to get grain yield (t/ha).

Statistical analysis: DSAASTAT was used to do an analysis of variance (ANOVA) on the recorded data (Onfri 2007). Rice genotypes were classified into high, medium, and low categories based on variation in their values from the average for the traits, viz. FLA, TCC, P_N, g_s, E, TB, GY, PR, and CS following the standard procedure described by Gill *et al.* (2004), Singh *et al.* (2014) and Irfan *et al.* (2017) with minor modification. Briefly, the genotypes were categorized into the high group when Xi > Xp + SDp, into the low group when Xi < Xp - SDp, and the medium group when Xi was < Xp + SDp but > Xp - SDp; where Xi represents the mean of a single genotype, Xp stands for the mean of the entire population, and SDp is the overall population standard deviation. The cluster analysis was carried out by using SRplot in 211 genotypes to categorize the genotypes based on GY and P_N. Clusters were formed using the Euclidian distance algorithm by the Ward method and represented as circular dendrograms.

RESULTS AND DISCUSSION

Study of genotypic variation for morphophysiological and yield traits: The analysis of variance was conducted between the genotypes for the morpho-physiological and yield-attributing traits such as FLA, TCC, P_N, g_s, E, TB, GY, PR, and CS. For all the measured variables, the results showed a substantial difference between the genotypes with a highly significant mean square value (Table 1). The mean value of the above-mentioned traits of each genotype along with their original name is presented in Supplementary Table 1. The high level of variation in the panel for the

Table 1 Genotypic variations for morphophysiological and yield traits of rice genotypes

	DF	FLA	TCC	P_N	g_s	E	TB	GY	PR	CS
Genotype	210	326.540**	1.751**	29.721**	0.260**	18.426**	24.036**	6.051**	0.015**	317.782**
Residual	211	20.916	0.241	3.707	0.006	0.658	1.449	0.312	0.001	10.018
Total	421	173.365	0.994	16.683	0.133	9.521	12.715	3.175	0.008	163.534
CV (%)		11.806	16.072	11.370	12.894	13.534	9.645	12.337	13.138	10.723
SEM (±)		3.233	0.346	1.361	5.519	0.573	0.851	0.394	1.880	2.238
$LSD_{0.05}$		9.015	0.966	3.795	0.153	1.598	2.372	1.101	5.243	6.239
$LSD_{0.01}$		11.887	1.274	5.004	0.202	2.108	3.129	1.451	0.069	8.227

FLA, flag leaf area (cm^2); TCC, total chlorophyll content (mg/g fresh weight); P_N, photosynthetic rate (µmol $CO_2/m^2/s$); g_s, stomatal conductance ($mmol/m^2/s$); E, transpiration rate (mmol $H_2O/m^2/s$); TB, total biomass (t/ha); GY, grain yield (t/ha); PR, pushing resistance (kg/cm); CS, culm strength (g/stem); DF, degree of freedom; CV, coefficient of variation; SEM, standard error of mean; LSD, least significant difference; **- statistically significant values at 1% probability level.

concerned traits provides adequate opportunity for the efficient selection of genotypes for crop improvement. As reported by Singh *et al*. (2014), a wide amount of variation in a population is a prerequisite in the breeding program to get contrasting parents with diverse characters.

Categorization of genotypes based on phenotypic performance: Of the numerous factors affecting grain yield, flag leaf area is one of the most important as it provides a photosynthetically active surface area (Lin *et al*. 2018). In the current study, a large amount of variation was observed in the flag leaf area of 211 genotypes of rice ranging from 15.19 (IG-126) to as high as 89.07 (IG-201) cm^2 with an average of 38.74 cm^2 (Table 2 and Supplementary Table 2). The results indicated that 29, 146, and 36 genotypes belonged to high, medium, and low for the flag leaf area, whereas 41, 137, and 33 genotypes were classified into high, medium, and low categories for total chlorophyll content of the flag leaf (Fig 1). A high chlorophyll concentration in flag leaves during the grain-filling stage has been linked to higher grain production in rice as it plays a crucial part in photosynthesis. In the present study, TCC ranged from 0.82 (IG-105) to 5.50 mg/g FW (IG-067) with a mean of 3.05 mg/g FW (Table 2 and Supplementary Table 2).

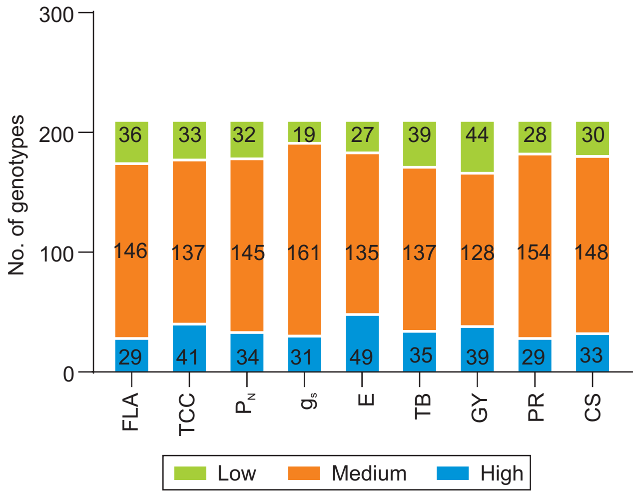

Fig 1 Distribution of genotypes in high, medium, and low category based on morphophysiological and yield traits.
FLA, flag leaf area (cm^2); TCC, total chlorophyll content (mg/g fresh weight); P_N, photosynthetic rate (µmol CO_2/m^2/s); g_s, stomatal conductance (mmol/m^2/s); E, transpiration rate (mmol H_2O/m^2/s); TB, total biomass (t/ha); GY, grain yield (t/ha); PR, pushing resistance (kg/cm); CS, culm strength (g/stem).

One way to improve biomass production and consequently grain yield is to improve the photosynthetic capability of the source leaf, which is a crucial component of source strength (Qu *et al*. 2017). A positive correlation has been found between the photosynthetic efficiency of flag leaf and the grain yield of rice. But, the assessment of photosynthetic traits in a large set of genotypes, particularly in natural variation is an unexplored area as conducting this kind of experiment is very tedious in many instances (Singh *et al*. 2014). The photosynthetic rate across the genotypes varied from 7.55 (IG-021) to 28.69 (IG-112) µmol/m^2/s with an average of 16.93 µmol/m^2/s. The results showed that 34, 145, and 32 genotypes were showing high, medium, and low P_N respectively. (Table 2 and Fig 1). While working with the global mini-core panel and elite rice lines, Qu *et al*. (2017) discovered photosynthetic rates ranging from 13.65 to 28.19 µmol/m^2/s, which also showed a positive relationship with plant biomass. The large diversity in P_N in the current study shows, a higher possibility for adopting P_N in future breeding programmes to improve biomass and productivity in rice. Similarly, genotypes were categorized based on g_s and E. g_s and E ranged from 0.12 (IG-167)–2.07 (IG-204) mmol/m^2/s and 0.94 (IG-192)–12.85 (IG-008) mmol/m^2/s respectively with a mean of 0.36 mmol/m^2/s and 5.99 mmol/m^2/s respectively (Table 2 and Supplementary Table 2). The results revealed that 31, 161, and 19 genotypes in g_s and 49, 135, and 27 genotypes in E belonging to high, medium, and low categories respectively (Fig 1).

Grain yield is a function of biomass accumulated from flowering to physiological maturity and translocation of biomass stored before flowering from straw to panicle (Laza *et al*. 2003). Above-ground biomass is used to predict the productivity of many plants. It has a direct positive effect on grain yield in rice. Wu *et al*. (2008) reported that the high grain yield of super rice hybrid resulted from high dry matter accumulation after the elongation period. The results show that the total biomass produced within the range of 3.76 (IG-062) to 21.62 (IG-161) t/ha with an average biomass of 12.48 t/ha and categorized 35, 137, and 39 genotypes into high, medium, and low TB categories. However, grain yield varied from 1.39 (IG-062) to 8.84 (IG-161) t/ha with a mean of 4.53 t/ha. 39, 128, and 44 genotypes were identified

Table 2 Classification of rice genotypes according to their morphophysiological and yield traits

Trait	FLA	TCC	P_N	g_s	E	TB	GY	PR	CS
Threshold value for considering efficient genotype (mean + SD)	51.51 cm^2	3.99 mg/g fresh weight	20.79 µmol CO_2/m^2/s	0.97 mmol/m^2/s	9.03 mmol H_2O/m^2/s	15.95 t/ha	6.27 t/ha	0.29 kg/cm	42.12 g/stem
Number of genotypes in efficient category	29	41	34	31	49	35	39	29	30

FLA, flag leaf area (cm^2); TCC, total chlorophyll content (mg/g fresh weight); P_N, photosynthetic rate (µmol CO_2/m/s); g_s, stomatal conductance (mmol/m^2/s); E, transpiration rate (mmol H_2O/m^2/s); TB, total biomass (t/ha); GY, grain yield (t/ha); PR, pushing resistance (kg/cm); CS, culm strength (g/stem); SD, standard deviation.

as high, medium, and low-yielding genotypes respectively (Table 2, Supplementary Table 2, and Fig 1).

Lodging causes yield and quality loss in rice. Therefore, culm strength (CS) should be increased to support heavy panicles, particularly in long culm high-yielding rice genotypes (Kashiwagi and Ishimaru 2004). Pushing resistance (PR) and culm strength in 211 genotypes ranged from 0.03 (IG-162) to 0.59 (IG-102) kg/cm and 3.87 (IG-162) to 73.59 (IG-082) g/stem respectively with a mean of 0.20 kg/cm and 29.51 g/stem respectively (Table 2 and Supplementary Table 2). 29, 154, and 28 genotypes showed high, medium, and low PR. While, 33, 148, and 30 genotypes belonged to low, medium, and high CS groups respectively (Fig 1).

Identification of promising genotypes: After classifying genotypes into high, medium, and low categories based on their morpho-physiological and yield-attributing traits such as, FLA, TCC, P_N, g_s, E, TB, GY, PR, and CS, the high-performance genotypes in more than one character were identified and grouped (Table 3). Out of the total set of genotypes, 50 genotypes were reported to be highly efficient in 2 traits, 21 genotypes in 3 traits, 11 genotypes in 4 traits, and 5 genotypes in 5 traits. IG-186 and IG-044 were quite efficient having high values in 6 traits. However, from the lot of 211 genotypes, the results showed 2 highly promising genotypes IG-008 and IG-161 which exhibited high value in 8 traits. IG-008 reported high FLA, TCC, P_N, g_s, E, GY, PR, and CS and IG-161 exhibited high TCC, P_N, g_s, E, TB, GY, PR, and CS. These genotypes are superior in most significant morphophysiological features, which are the primary determinants of grain yield, so they can be considered in future breeding programmes for varietal improvement, particularly for high grain yield.

Identification of genotypes with contrasting traits: Photosynthesis is the most important physiological trait that directly affects the grain yield of rice plants (Panda *et al*. 2023). Based on the simulation analysis performed by Gu *et al*. (2014) a 25% increase in single-leaf photosynthesis can increase biomass production up to 22–29% and thereby increase the grain yield. So, to group the genotypes based on their photosynthetic ability and yield potential, a hierarchical cluster analysis was performed on 211 genotypes based on GY and P_N. Euclidean distance was used as a measure of dissimilarity, and genotypes were sorted into distinct clusters using Ward's minimum variance approach. The genotypes were classified into 6 major clusters at an Euclidean distance of 10 (Fig 2). As observed from cluster analysis 35, 28, 24, 40, 48, and 36 genotypes belonged to cluster I, II, III, IV, V, and VI respectively. The outcome of the cluster analysis demonstrated the substantial level of diversity present in the genotypes for grain yield and photosynthetic rate. As genetic diversity is a critical aspect of parent selection (Tuhina-Khatun *et al*. 2015), the current panel of genotypes can be exploited to get parents with contrasting traits. Previously many reports have been published, where a positive correlation had been established between photosynthetic rates and grain yield (Haritha *et al*. 2019). However, from the cluster analysis, results revealed that 26 genotypes showed 4 different combinations for photosynthetic rate and grain yield and they belonged to 4 different clusters. Eight varieties were identified as high P_N and high GY genotypes belonging to cluster III and 7 varieties showing low P_N and low GY belonged to cluster VI. Interestingly, 7 genotypes were identified as high P_N but low GY (IG-027,

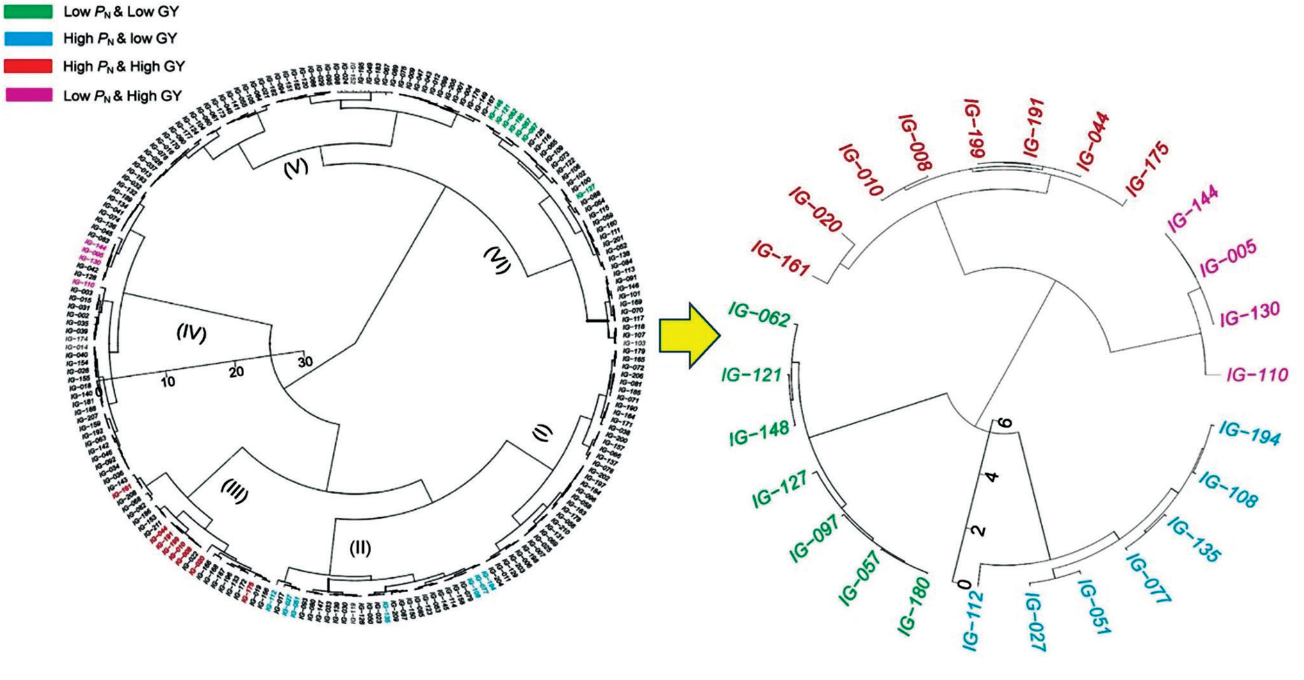

Fig 2 Hierarchical cluster analysis of rice genotypes based on grain yield and photosynthetic rate, using Euclidean distance and Ward's algorithm.

Table 3 High-performance genotypes based on morphophysiological and yield traits

Traits with high values	Genotype with high efficiencies	Total
FLA, E	IG-180	1
FLA, TB	IG-090	1
TCC, P_N	IG-017, IG-027, IG-112, IG-137, IG-187, IG-196	6
TCC, E	IG-053, IG-101, IG-169	3
TCC, GY	IG-140	1
TCC, PR	IG-054, IG-103	2
TCC, CS	IG-210	1
P_N, g_s	IG-078, IG-156	2
P_N, E	IG-108, IG-150	2
P_N, GY	IG-191	1
g_s, E	IG-021, IG-025, IG-028, IG-070, IG-106, IG-177, IG-189, IG-198	8
E, PR	IG-190	1
TB, GY	IG-002, IG-003, IG-026, IG-031, IG-035, IG-039, IG-063, IG-068, IG-083, IG-110, IG-130, IG-142, IG-143, IG-154, IG-174	15
TB, PR	IG-034, IG-046	2
PR, CS	IG-004, IG-098, IG-102, IG-145	4
FLA, P_N, GY	IG-199	1
FLA, g_s, E	IG-193, IG-195, IG-205, IG-207	4
FLA, E, PR	IG-050	1
FLA, E, CS	IG-202	1
FLA, TB, GY	IG-128	1
FLA, PR, CS	IG-037	1
TCC, P_N, g_s	IG-051, IG-157, IG-172	3
TCC, E, CS	IG-127	1
TCC, TB, GY	IG-155	1
P_N, g_s, E	IG-077	1
P_N, PR, CS	IG-087	1
g_s, E, CS	IG-203	1
E, TB, GY	IG-153	1
E, PR, CS	IG-181, IG-197	2
TB, GY, CS	IG-005	1
FLA, TCC, P_N, g_s	IG-019	1
FLA, TCC, g_s, E	IG-178	1
FLA, P_N, E, GY	IG-175	1
FLA, P_N, PR, CS	IG-022, IG-023	2
FLA, g_s, E, CS	IG-201	1
FLA, TB, GY, CS	IG-018	1
TCC, TB, GY, CS	IG-208	1
P_N, E, PR, CS	IG-066	1
g_s, E, TB, GY	IG-042	1
TB, GY, PR, CS	IG-082	1
FLA, TCC, P_N, g_s, CS	IG-209	1
FLA, g_s, E, PR, CS	IG-204	1
TCC, P_N, TB, GY, CS	IG-010	1
TCC, g_s, GY, PR, CS	IG-211	1
P_N, E, TB, GY, PR	IG-020	1
FLA, g_s, E, GY, PR, CS	IG-186	1
TCC, P_N, TB, GY, PR, CS	IG-044	1
FLA, TCC, P_N, g_s, E, GY, PR, CS	IG-008	1
TCC, P_N, g_s, E, TB, GY, PR, CS	IG-161	1

FLA, flag leaf area (cm^2); TCC, total chlorophyll content (mg/g fresh weight); P_N, photosynthetic rate (µmol $CO_2/m^2/s$); g_s, stomatal conductance (mmol/m^2/s); E, transpiration rate (mmol $H_2O/m^2/s$); TB, total biomass (t/ha); GY, grain yield (t/ha); PR, pushing resistance (kg/cm); CS, culm strength (g/stem).

IG-051, IG-077, IG-108, IG-110IG-112, IG-135, and IG-194) genotypes and belonged to cluster II, and 4 genotypes reported low P_N but high GY (IG-005, IG-110, IG-130, and IG-144) belonging to cluster IV. These genotypes with contrasting features could be studied further to uncover the mechanistic difference between genotypes with high grain yield despite low photosynthesis and genotypes with low grain yield despite high photosynthesis. This could offer important details about grain yield constraints.

From the phenotypic evaluation of 211 rice genotypes, the results revealed that 2 rice genotypes IG-161 and IG-008 were highly efficient in multiple traits. Whereas, 7 genotypes showed low grain yield even with a high photosynthetic rate, and 4 genotypes reported high grain yield despite a low photosynthetic rate. As photosynthesis is one of the bases of grain yield, these genotypes showing contrasting grain yield and photosynthetic behaviour, may be studied further and used in future breeding programmes suitably.

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