PLANT SCIENCE TODAY
Vol 13(sp1): 1-11
https://doi.org/10.14719/pst.14021

eISSN 2348-1900

RESEARCH ARTICLE

Multivariate analysis of morpho-physiological traits in rice (*Oryza sativa* L.)

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Received: 06 February 2026; Accepted: 07 March 2026; Available online: Version 1.0: 08 April 2026

Cite this article: Srimathi K, Jeyaprakash P, Vanniarajan C, Raveendran M, Senthil A, Raju M, Williams M, Bharathi A, Sudha M. Multivariate analysis of morpho-physiological traits in rice (*Oryza sativa* L.). Plant Science Today. 2026; 13(sp1): 1-11. https://doi.org/10.14719/pst.14021

Abstract

Rice is a highly water-demanding crop and climate change–driven water scarcity is making sustainable production increasingly difficult. Enhancing water-use efficiency through improved photosynthesis and reduced transpiration is therefore a key breeding objective. In this study, 70 rice genotypes were evaluated for 16 morpho-physiological traits under non-stressed conditions. Analysis of variance revealed significant genotypic differences for most traits. High genotypic and phenotypic coefficients of variation were recorded for stomatal conductance, transpiration rate (TR), photosynthetic rate (PR), intrinsic water-use efficiency (iWUE) and single plant yield, accompanied by high heritability (>97 %) and genetic advance, indicating strong selection potential. Single plant yield showed significant positive correlations with plant height, days to 50 % flowering, panicle length, spikelet fertility and harvest index, demonstrating that yield is governed by growth, physiological and agronomical components. Photosynthetic rate increased with stomatal conductance, whereas iWUE declined, reflecting a carbon–water trade-off and suggesting an optimal range of moderate conductance. Path coefficient analysis identified plant height (0.38), days to 50 % flowering (0.34), harvest index (0.33), spikelet fertility (0.27), iWUE (0.12) and stomatal density as major direct contributors to yield. Principal component analysis showed that the first 2 components explained 35.94 % of total variation, while cluster analysis grouped genotypes into 5 clusters, indicating substantial genetic divergence. The results suggest that moderate stomatal conductance, high iWUE, panicle length, spikelet fertility and harvest index are important selection criteria for improving yield and water-use efficiency in rice breeding programmes.

Keywords: intrinsic water-use efficiency; rice; stomatal conductance; yield

Abbreviations: SC: Stomatal conductance; PR: Photosynthetic rate; TR: Transpiration rate; iWUE: Intrinsic water-use efficiency; RWC: Relative water content; SPAD: Chlorophyll index; DFF: Days to 50 % flowering; PL: Panicle length; S_ABA: Abaxial stomatal density; S_ADA: Adaxial stomatal density; GCV: Genotypic coefficient of variation; PCV: Phenotypic coefficient of variation.

Introduction

Rice (*Oryza sativa* L.) is the staple food for a large proportion of the global population. In previous reports, paddy production increased substantially from 182.7 to 217.9 million tonnes in 2020-2024 (1). However, with the global population projected to increase markedly by 2050, further enhancement of rice productivity will be essential to meet the growing food demand and ensure global food security (2). Rice is a water-intensive crop and under changing climatic conditions, sustaining rice production has become increasingly challenging for farmers. Climate change is intensifying water scarcity, making improvement of water use efficiency (WUE) in rice essential for sustaining agricultural productivity. Alongside the development of improved agronomic practices, global research efforts increasingly focus on breeding rice varieties with enhanced WUE (3, 4).

Leaves play a central role in regulating plant water use, as they are the primary sites of carbon dioxide uptake and water loss through transpiration. Stomata are key regulators of these processes, controlling the balance between transpiration and carbon assimilation and thereby strongly influencing plant water status, photosynthetic efficiency and yield formation, particularly under stress conditions (5, 6). Consequently, improvement in WUE has traditionally focused on stomatal traits such as stomatal density, size and conductance. However, emerging evidence suggests that WUE is not governed by stomatal regulation alone; non-stomatal leaf traits, including photosynthetic efficiency, leaf anatomical features and biochemical characteristics, also play a significant role in determining intrinsic water-use efficiency (iWUE) (4). Under drought and salinity stress, rice productivity is governed by coordinated stomatal and non-stomatal physiological processes. Optimised stomatal regulation reduces transpirational water loss, while efficient non-stomatal mechanisms sustain carbon assimilation, resulting in higher iWUE. Thus, stomatal traits and iWUE serve as key physiological indicators linking water conservation with grain productivity under stress conditions.

Recent advances in molecular breeding have further highlighted the importance of stomatal regulation as a viable target for improving water-use efficiency in rice. The ICAR-IARI developed Pusa Rice DST1 (Drought and Salt Tolerant 1*)* using CRISPR-Cas9 genome editing in the MTU1010 genetic background to enhance adaptation to drought and saline environments. Pusa Rice DST1 exhibits reduced stomatal density, leading to lower transpirational water loss and improved iWUE under stress. Targeted editing of stomatal regulatory genes such as *OsEPF1* enables improved water conservation without compromising photosynthesis, resulting in up to 30 % higher grain yield under stress conditions (7). Recent genome-editing studies have demonstrated that targeted manipulation of stomatal density using CRISPR/Cas9 can effectively regulate transpiration and photosynthetic traits in rice (8). Therefore, examining stomatal traits and iWUE in relation to yield is crucial for understanding stress management mechanisms and identifying key physiological traits for developing climate-resilient, water-efficient rice cultivars.

Although individual physiological traits influencing water-use efficiency have been studied extensively, their integrated contribution to yield under field conditions remains poorly understood. In particular, the combined influence of stomatal traits, gas-exchange parameters and yield components has not been systematically evaluated across diverse rice genotypes. It was hypothesised that genotypic differences in stomatal regulation modulate gas-exchange efficiency, thereby influencing iWUE and grain yield in rice and that integrative morpho-physiological traits underlying this regulation can be identified as effective selection criteria for breeding water-efficient, high-yielding cultivars. Accordingly, the present study aimed to (i) quantify genetic variability for morpho-physiological traits related to WUE and yield, (ii) dissect trait interrelationships using correlation and path coefficient analyses and (iii) identify major contributors to yield variation through multivariate techniques, including principal component analysis (PCA).

Materials and methods

The experiment was conducted during the kharif 2024 season using 70 rice genotypes grown under non-stress conditions at the Department of Rice, Centre for Plant Breeding and Genetics, Tamil Nadu Agricultural University (11° N, 77° E). The trial was laid out in an augmented design with 63 test genotypes from the 3K RG panel, released varieties and landraces and 7 checks (CBMAS 14065, CO 51, Nagina 22, APO, Way Rarem, Norungan and PMK 3) arranged in 3 blocks. The experimental field, characterised by clay loam soil, was maintained under normal irrigation and 25-day-old seedlings were transplanted at 20 × 20 cm spacing with a fertiliser application of 150:50:50 kg ha^{-1}(N:P:K) following recommended agronomic and standard crop management practices.

Agronomical traits

For each genotype, 3 randomly selected plants from the middle rows were utilised for the observations to reduce border effects. Data were recorded for different agronomical traits at different stages of vegetative and reproductive growth, viz., days to 50 % flowering (DFF), plant height (PH), panicle length (PL), spikelet fertility (SF %), chlorophyll index using SPAD (SPAD reading), harvest index (HI %), thousand grain weight (TGW), single plant yield (SPY).

Physiological traits

Measurement of stomatal density

To measure stomatal density, a fully expanded leaf was sampled after anthesis and both the abaxial and adaxial leaf surfaces were gently cleaned using tissue paper. Then, the stomatal impressions were made from the middle of the leaves using a transparent nail polish. Adequate care was taken to prepare impressions on both the sides of the midrib to avoid the bias in measuring the stomata number. After 10 min, the stomatal imprints were gently peeled off and immediately mounted on the glass slide. The number of stomata in both abaxial and adaxial surfaces of the leaf was counted using the images captured at 40 × magnification, in a field of ≈ 0.993 × 0.748 = 0.742 mm^2 using a fluorescence microscope (Radical RXLr-5, Ambala Cantt, India). The stomatal density was calculated using the formula: (Eqn. 1)

$$\text{Stomatal density} = \frac{\text{Number of Stomata}}{\text{Area in view}} \qquad \text{(Eqn.1)}$$

A total of ten fields of view were randomly observed in each impression and counted as abaxial (S_ABA) and adaxial (S_ADA) stomatal density per each genotype.

Measurement of gas exchange parameters

A portable photosynthesis analyser (LCpro SD, ADC Bio Scientific, Hoddesdon, UK) was used for the measurement of all the gas exchange parameters, such as photosynthetic rate (PR), stomatal conductance (SC) and transpiration rate (TR). All the measurements were recorded at the middle of the fully expanded 3rd leaf from the top. All the measurements were taken after the instrument reached the stability (2–10 min). The CO_2 concentration was 400 µmol m^{-2} s^{-1} and the photosynthetic photon flux density (PPFD) was 1500 µmol m^{-2} s^{-1}. The parameters measured are as follows: PR (A, µmol CO_2 m^{-2} s^{-1}), stomatal conductance (gs mol H_2O m^{-2} s^{-1}) and TR (E, mmol H_2O m^{-2} s^{-1}). All the measurements were taken under light-saturated conditions. The WUE was derived from the measured photosynthetic parameters. The ratio of photosynthetic CO_2 assimilation (A) to stomatal conductance (gs) was calculated as the intrinsic iWUE.

Relative water content

Relative water content (RWC) was measured on leaf sections from the same plant used for measuring gaseous exchange parameters. A 10 cm segment was excised from the middle of the leaf blade and its fresh weight was immediately taken. Segments were floated 24 hr on pure water in a Petri dish and reweighed after gently blotting away surface moisture. A third weight was taken after drying in a forced convection oven at 60 °C for 48 hr. The RWC was calculated as: (Eqn. 2)

$$\text{RWC} = \frac{\text{FW- DW}}{\text{TW-DW}} \times 100 \qquad \text{(Eqn.2)}$$

where FW, TW and DW represent fresh weight, turgid weight and dry weight, respectively.

Statistical analysis

The required statistical analysis was performed using the R-Studio (R version 4.5.2). Descriptive statistics, including mean, standard deviation, range, variance and coefficient of variation (CV), were computed for all traits using R software. Estimates of genetic parameters, including genotypic variance (Vg), phenotypic variance (Vp), genotypic coefficient of variation (GCV), phenotypic coefficient of variation (PCV), broad-sense heritability (H^2) and genetic advance as a percentage of the mean (GAM), were computed using the augmented randomized completely block design (RCBD) package in R. Pearson's pairwise correlation coefficients were estimated to examine linear relationships among traits using the corrplot package. Cluster analysis was performed using agglomerative hierarchical clustering based on Euclidean distance and Ward's D^2 minimum variance method using the ape, dendextend and cluster packages. Principal component analysis was conducted to identify major sources of variation among germplasm accessions using the factoextra, ggplot2 and ggbiplot packages in R software.

Results and Discussion

ANOVA revealed highly significant ($p \leq 0.01$) genotypic differences for PH, DFF, S_ADA, S_ABA, TR, SC, PR, iWUE, PL, SF % and TGW, indicating substantial genetic variability. Moderate significance ($p \leq 0.05$) was observed for SPAD chlorophyll index and single plant yield, suggesting detectable but comparatively lower genotypic variation (Table 1). In contrast, relative water content, number of productive tillers and harvest index showed non-significant differences, implying a stronger influence of environmental factors and limited genetic variability for these traits under experimental conditions. To further characterise the magnitude and distribution of variation among genotypes, descriptive statistics were computed for all traits.

Descriptive statistics

Descriptive statistics for the 16 traits are presented in Table 2, which provides detailed numerical values and extreme observations. Considerable variation was observed among genotypes for physiological and yield-related traits. Traits such as stomatal conductance, TR, PR, intrinsic water-use efficiency and single plant yield exhibited high coefficients of variation, indicating substantial phenotypic variability and strong selection potential. In contrast, days to flowering, SPAD chlorophyll index, relative water content and panicle length showed comparatively lower variability, suggesting greater stability across genotypes. While descriptive statistics reveal phenotypic variation, estimates of genetic parameters provide insight into the heritable component of this variation.

Genetic variability

The GCV for 16 traits ranged from 2.43 % (RWC) to 39.63 % (SC) and the PCV ranged from 5.53 % (RWC) to 44.65 % (SPY) (Table 3). All traits showed higher PCV than GCV, indicating the influence of environmental factors. The traits plant height, stomatal density S_ADA, S_ABA, panicle length and spikelet fertility % exhibited moderate GCV and PCV. High GCV and PCV were recorded in TR, stomatal conductance, PR, iWUE, thousand grain weight and single plant yield. Relative water content had low GCV and PCV. Heritability broad sense ranged from 19.37 to 99.76 % and GAM genetic advance ranged from 2.21 to 81.67 %. The traits TR, SC, PR, iWUE, PL and SF % showed high values of GCV, PCV, heritability and GAM. Medium to high heritability coupled with moderate to high GAM observed for HI and SPY indicates the predominance of additive gene action, suggesting good prospects for improvement through selection. Low heritability and GAM for RWC indicate limited scope for improvement through direct selection. In contrast to the moderate heritability of RWC (0.42) reported under severe stress conditions by previous researchers (9), the low heritability observed in the present study suggests stronger environmental influence under non-stress field conditions. These results indicate that RWC expression is highly environment-dependent and may vary with stress intensity.

Although high heritability was observed for stomatal and gas-exchange traits in the present study, earlier reports indicate that TR is weakly heritable and highly environment-dependent (10), suggesting strong genotype × environment interactions. Such discrepancies likely reflect differences in genetic background and environmental uniformity, implying that gas-exchange traits may be effectively selected under stable conditions but require multi-environment validation before deployment in breeding programmes. In addition, these traits vary with leaf age and developmental stage, with younger leaves exhibiting higher physiological activity (11), potentially inflating phenotypic variance independent of genetic control. The substantial variation detected for PR, TR and SC aligns with findings under severe moisture stress, where significant phenotypic and genotypic variability for PR, TR and RWC was reported (9), reinforcing the genetic basis of physiological regulation linked to water-use efficiency and yield. Collectively, while gas-exchange traits contribute to genetic divergence, their breeding utility depends on cross-environment validation and standardised phenotyping. Correlation analysis was therefore conducted to clarify trait interactions governing yield.

Correlation analysis

Correlation analysis (Table 4; Fig. 1) revealed strong associations among morpho-physiological and yield-related traits. Plant height showed positive correlations with iWUE (0.365**), panicle length (0.521**), thousand grain weight (0.375**) and single plant yield (0.32**), but negative associations with S_ABA, SC and SPAD. Days to flowering was positively associated with panicle length (0.444**) and yield (0.458**). Gas-exchange traits exhibited strong interrelationships: TR was positively correlated with stomatal conductance (0.836**) and PR (0.707**), while iWUE showed significant negative correlations with transpiration (-0.438**) and SC (-0.555**), reflecting the trade-off between carbon assimilation and water loss. Yield was positively associated with panicle length (0.508**), SF (0.425**), harvest index (0.416**), plant height and days to flowering, indicating that grain yield is governed by coordinated interactions among growth, reproductive efficiency and physiological regulation. Yield-related traits, including grain weight, spikelet fertility, grain number and harvest index, showed positive associations with PR, chlorophyll content and iWUE, indicating that yield improvement is closely linked to efficient carbon assimilation and water-use strategies. The positive association between yield and stomatal conductance and density observed in the present study is supported by previous findings (12), which showed that longer flag leaves and reduced stomatal density enhance grain yield under specific conditions. This suggests that improved canopy photosynthetic efficiency combined with reduced transpirational loss is critical for sustaining

Table 1. Analysis of variance (treatment-adjusted) using 70 genotypes for morpho-physiological and yield-related traits in rice

Source	Df	Mean.Sq															
		PH	DFF	S_ADA	S_ABA	TR	SC	PR	iWUE	SPAD	RWC	NPT	PL	SF %	HI %	TGW	SPY
Block (ignoring Treatments)	2	892.51**	92.35**	115.19**	244.93**	0.77**	0.00**	3.37**	332.75**	12.34^{ns}	10.36^{ns}	20.99^{ns}	15.87**	138.66**	391.13^{ns}	9.93**	54.98^{ns}
Treatment (eliminating Blocks)	69	321.86**	69.60**	55.15**	107.04**	1.26**	0.00**	5.72**	398.82**	20.86*	28.25^{ns}	23.96^{ns}	7.84**	114.46**	185.87^{ns}	23.12**	54.36*
Treatment: Check	6	366.21**	117.01**	129.30**	505.97**	0.36**	0.00**	12.63**	802.05**	48.21**	39.54^{ns}	35.41^{ns}	20.33**	204.65**	250.30^{ns}	67.52**	84.94*
Treatment: Test and Test vs. Check	63	317.64**	65.09**	48.08**	69.04**	1.35**	0.00**	5.06**	360.42**	18.25*	27.17^{ns}	22.87^{ns}	6.65**	105.87**	179.73^{ns}	18.89**	51.45*
Residuals	12	30.61	6.40	0.49	2.23	0.01	0.00	0.05	10.18	6.84	20.79	12.56	1.18	9.12	125.71	0.15	21.03

ns (non – significant) at $p > 0.05$; *:significant at $p \leq 0.05$; **:significant at ≤ 0.01 ***PH - Plant height; DFF- Days to 50 % flowering; S_ADA- Adaxial stomatal density; S_ABA- Abaxial stomatal density; TR- Transpiration rate; SC- Stomatal conductance; PR- Photosynthetic rate; iWUE- Intrinsic water-use efficiency; SPAD- Chlorophyll index; RWC- Relative water content; NPT- Number of productive tillers; SF %- Spikelet fertility; HI %- Harvest index; TGW- Thousand grain weight; PL- Panicle length; SPY- Single plant yield.

Table 2. Descriptive statistics of morpho-physiological and yield-related traits for 70 genotypes

Traits	Mean	SD	Min	Max	Variance	CV %
PH	106.04	18	74	151	324.1	16.97
DFF	78.8	7.89	64	101	62.25	10.01
S_ADA	39.3	7.1	21	62	50.42	18.07
S_ABA	52.97	9.26	33	73	85.74	17.48
TR	3.26	1.12	1.42	5.76	1.25	34.36
SC	0.1	0.04	0.04	0.19	0.001	40
PR	6.81	2.25	2.79	11.64	5.08	33.04
iWUE	70.69	18.96	32.82	116.7	359.34	26.82
SPAD	42.02	4.27	34.1	54.09	18.25	10.16
RWC	91.84	5	69.99	99.92	25.02	5.44
NPT	14.72	4.54	4.67	25.67	20.61	30.84
PL	21.98	2.64	13.47	28.93	6.98	12.01
SF %	78.28	10.11	46.17	92.51	102.15	12.92
HI %	44.9	13.62	14.68	69.86	185.58	30.33
TGW	20.56	4.37	10.5	32.19	19.11	21.25
SPY	15.83	6.96	5.63	48.3	48.43	43.97

***PH- Plant height; DFF- Days to 50 % flowering; S_ADA- Adaxial stomatal density; S_ABA- Abaxial stomatal density; TR- Transpiration rate; SC- Stomatal conductance; PR- Photosynthetic rate; iWUE- Intrinsic water-use efficiency; SPAD- Chlorophyll index; RWC- Relative water content; NPT- Number of productive tillers; SF %- Spikelet fertility; HI %- Harvest index; TGW- Thousand grain weight; PL- Panicle length; SPY- Single plant yield.

Table 3. Genetic variability estimated using morpho-physiological and yield-related traits of 70 genotypes

Trait	GCV	PCV	ECV	h²	GAM
PH	16.80	17.59	5.22	91.20	33.10
DFF	9.57	10.10	3.21	89.89	18.72
S_ADA	18.26	18.35	1.78	99.06	37.50
S_ABA	16.41	16.65	2.82	97.13	33.36
TR	35.82	35.89	2.36	99.57	73.73
SC	39.63	39.68	1.93	99.76	81.67
PR	33.44	33.59	3.12	99.14	68.69
iWUE	27.03	27.41	4.52	97.28	55.00
SPAD	8.20	10.30	6.22	63.48	13.49
RWC	2.43	5.53	4.97	19.37	2.21
NPT	19.65	31.07	24.06	40.01	25.64
PL	11.03	12.09	4.94	83.28	20.77
SF %	12.43	13.01	3.86	91.21	24.49
HI %	17.99	30.68	24.85	34.37	21.75
TGW	21.02	21.10	1.86	99.22	43.19
SPY	33.99	44.65	28.96	57.93	53.36

***PH- Plant height; DFF- Days to 50 % flowering; S_ADA- Adaxial stomatal density; S_ABA- Abaxial stomatal density; TR- Transpiration rate; SC - Stomatal conductance; PR- Photosynthetic rate; iWUE- Intrinsic water-use efficiency; SPAD- Chlorophyll index; RWC- Relative water content; NPT- Number of productive tillers; SF %- Spikelet fertility; HI %- Harvest index; TGW- Thousand grain weight; PL- Panicle length; SPY- Single plant yield.

Table 4. Correlation analysis of morpho-physiological and yield-related traits for 70 genotypes

Traits	PH	DFF	S_ADA	S_ABA	TR	SC	PR	iWUE	SPAD	RWC	NPT	PL	SF %	HI %	TGW	SPY
PH	1	-0.005	-0.201	-0.251*	-0.067	-0.257*	-0.043	0.365**	-0.306*	0.125	0.108	0.521**	-0.029	-0.032	0.375**	0.32**
DFF	-0.005	1	0.099	0.281*	-0.166	-0.092	-0.067	-0.006	-0.09	0.03	0.038	0.444**	0.129	-0.007	0.025	0.458**
S_ADA	-0.201	0.099	1	0.66**	0.003	0.024	0.084	0.003	0.182	-0.008	-0.145	0.036	0.271*	0.107	-0.171	0.219
S_ABA	-0.251*	0.281*	0.66**	1	-0.036	0.001	0.042	-0.055	0.304*	0.003	-0.115	0.072	0.266*	0.089	-0.092	0.217
TR	-0.067	-0.166	0.003	-0.036	1	0.836**	0.707**	-0.438**	0.12	-0.031	-0.006	-0.028	-0.175	-0.043	-0.172	-0.146
SC	-0.257*	-0.092	0.024	0.001	0.836**	1	0.765**	-0.555**	0.248*	-0.094	0.059	-0.018	-0.093	0.052	-0.181	-0.071
PR	-0.043	-0.067	0.084	0.042	0.707**	0.765**	1	0.055	0.111	-0.04	-0.02	0.099	-0.101	0.053	-0.141	0.008
iWUE	0.365**	-0.006	0.003	-0.055	-0.438**	-0.555**	0.055	1	-0.309**	0.051	-0.017	0.133	0	0.035	0.151	0.131
SPAD	-0.306*	-0.09	0.182	0.304*	0.12	0.248*	0.111	-0.309**	1	0.097	-0.271*	-0.091	0.108	-0.014	0.019	-0.137
RWC	0.125	0.03	-0.008	0.003	-0.031	-0.094	-0.04	0.051	0.097	1	-0.293*	0.278*	0.211	0.074	0.145	0.234
NPT	0.108	0.038	-0.145	-0.115	-0.006	0.059	-0.02	-0.017	-0.271*	-0.293*	1	-0.043	-0.182	0.181	-0.017	0.133
PL	0.521**	0.444**	0.036	0.072	-0.028	-0.018	0.099	0.133	-0.091	0.278*	-0.043	1	0.222	-0.047	0.231	0.508**
SF %	-0.029	0.129	0.271*	0.266*	-0.175	-0.093	-0.101	0	0.108	0.211	-0.182	0.222	1	0.173	0.13	0.425**
HI %	-0.032	-0.007	0.107	0.089	-0.043	0.052	0.053	0.035	-0.014	0.074	0.181	-0.047	0.173	1	0.055	0.416**
TGW	0.375**	0.025	-0.171	-0.092	-0.172	-0.181	-0.141	0.151	0.019	0.145	-0.017	0.231	0.13	0.055	1	0.047
SPY	0.32**	0.458**	0.219	0.217	-0.146	-0.071	0.008	0.131	-0.137	0.234	0.133	0.508**	0.425**	0.416**	0.047	1

*** PH- Plant height; DFF- Days to 50 % flowering; S_ADA- Adaxial stomatal density; S_ABA- Abaxial stomatal density; TR- Transpiration rate; SC - Stomatal conductance; PR- Photosynthetic rate; iWUE- Intrinsic water-use efficiency; SPAD- Chlorophyll index; RWC- Relative water content; NPT- Number of productive tillers; SF %- Spikelet fertility; HI %- Harvest index; TGW- Thousand grain weight; PL- Panicle length; SPY- Single plant yield.

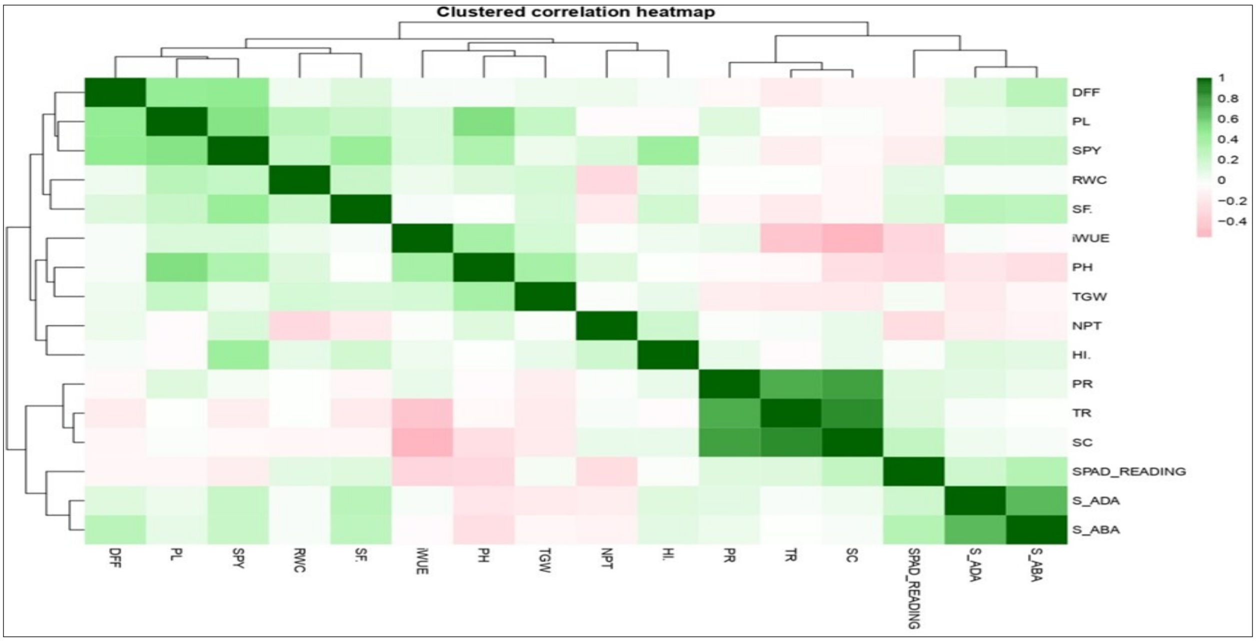

Fig. 1. Clustered correlation heatmap showing hierarchical relationships and pairwise correlations among morpho-physiological and yield-related traits in rice, where colour intensity indicates the strength and direction of correlation. ***PH: Plant height; DFF: Days to 50 % flowering; S_ADA: Adaxial stomatal density; S_ABA: Abaxial stomatal density; TR: Transpiration rate; SC: Stomatal conductance; PR: Photosynthetic rate; iWUE: Intrinsic water-use efficiency; SPAD: Chlorophyll index; RWC: Relative water content; NPT: Number of productive tillers; SF %: Spikelet fertility; HI %: Harvest index; TGW: Thousand grain weight; PL: Panicle length; SPY: Single plant yield.

yield under stress. Similarly, the positive relationships between PR, SC and yield-related traits agree with earlier reports of significant correlations between PR, SC and yield under severe water stress (11), reinforcing the value of gas-exchange traits as indirect selection criteria for yield improvement in water-limited environments.

The relationship between stomatal conductance and gas-exchange traits (Fig. 2) reveals a fundamental carbon–water trade-off in rice. The PR increased with SC, indicating enhanced CO_2 diffusion and assimilation, whereas iWUE declined at higher conductance, reflecting disproportionate water loss. Comparable associations between SC and photosynthesis have been reported under adequate moisture and heat stress (13, 15), while studies under elevated CO_2 show that reduced SC can improve iWUE without compromising assimilation (14), indicating environment-dependent stomatal optimisation. The wide genotypic variation observed supports an optimal moderate range of SC that balances carbon assimilation and water conservation. Mechanistically, high conductance increases transpirational demand and hydraulic risk, whereas very low conductance restricts carbon fixation. Thus, maintaining moderate SC ensures a balance between carbon gain and hydraulic safety, suggesting that optimising rather than maximising stomatal conductance is a more effective breeding strategy for improving productivity and water-use efficiency under variable environments.

Path coefficient analysis

Path coefficient analysis was performed to investigate the direct and indirect relationships among physiological and yield-related traits using 16 characters, with SPY as the dependent variable (Table 5). The diagonal (bold) values in the path matrix represent the direct effects of traits on SPY. Positive and substantial direct effects were observed for PH (0.3768), DFF (0.3441), PL (0.1094), SF % (0.2722), HI % (0.3292), NPT (0.0989), iWUE (0.1236), RWC (0.1421), S_ADA (0.1157), S_ABA (0.043). These traits may therefore be considered as important selection criteria for improving single plant yield. The TR, PR, SPAD chlorophyll index and thousand grain weight (TGW) exhibited negative direct effects on SPY and contributed mainly through indirect effects. Although SC (0.3826) showed a positive direct effect on yield, its biological interpretation requires caution. Higher conductance enhances CO_2 assimilation but also increases water loss, potentially reducing water-use efficiency. Therefore, maintaining

Table 5. Phenotypic path analysis of morpho-physiological and yield-related traits with dependent variable

Traits	PH	DFF	S_ADA	S_ABA	TR	SC	PR	iWUE	SPAD	RWC	NPT	PL	SF %	HI %	TGW	SPY
PH	0.377	-0.002	-0.023	-0.011	0.012	-0.098	0.007	0.045	0.013	0.018	0.011	0.057	-0.008	-0.011	-0.067	0.320
DFF	-0.002	0.344	0.011	0.012	0.029	-0.035	0.010	-0.001	0.004	0.004	0.004	0.049	0.035	-0.002	-0.004	0.458
S_ADA	-0.076	0.034	0.116	0.028	-0.001	0.009	-0.013	0.000	-0.008	-0.001	-0.014	0.004	0.074	0.035	0.030	0.219
S_ABA	-0.095	0.097	0.076	0.043	0.006	0.000	-0.006	-0.007	-0.013	0.000	-0.011	0.008	0.073	0.029	0.016	0.217
TR	-0.025	-0.057	0.000	-0.002	-0.176	0.320	-0.108	-0.054	-0.005	-0.004	-0.001	-0.003	-0.048	-0.014	0.031	-0.146
SC	-0.097	-0.032	0.003	0.000	-0.147	0.383	-0.117	-0.069	-0.010	-0.013	0.006	-0.002	-0.025	0.017	0.032	-0.071
PR	-0.016	-0.023	0.010	0.002	-0.125	0.293	-0.152	0.007	-0.005	-0.006	-0.002	0.011	-0.028	0.018	0.025	0.009
iWUE	0.137	-0.002	0.000	-0.002	0.077	-0.213	-0.008	0.124	0.013	0.007	-0.002	0.015	0.000	0.011	-0.027	0.131
SPAD	-0.115	-0.031	0.021	0.013	-0.021	0.095	-0.017	-0.038	-0.042	0.014	-0.027	-0.010	0.030	-0.004	-0.003	-0.137
RWC	0.047	0.010	-0.001	0.000	0.005	-0.036	0.006	0.006	-0.004	0.142	-0.029	0.031	0.057	0.024	-0.026	0.234
NPT	0.041	0.013	-0.017	-0.005	0.001	0.023	0.003	-0.002	0.011	-0.042	0.099	-0.005	-0.050	0.060	0.003	0.133
PL	0.196	0.153	0.004	0.003	0.005	-0.007	-0.015	0.016	0.004	0.040	-0.004	0.109	0.060	-0.016	-0.041	0.508
SF %	-0.011	0.044	0.031	0.011	0.031	-0.035	0.015	0.000	-0.005	0.030	-0.018	0.024	0.272	0.057	-0.023	0.425
HI %	-0.012	-0.002	0.012	0.004	0.008	0.020	-0.008	0.004	0.001	0.011	0.018	-0.005	0.047	0.329	-0.010	0.416
TGW	0.141	0.009	-0.020	-0.004	0.030	-0.069	0.022	0.019	-0.001	0.021	-0.002	0.025	0.035	0.018	-0.177	0.047
Residual effect = 0.5673																

******* PH: Plant height; DFF: Days to 50 % flowering; S_ADA: Adaxial stomatal density; S_ABA: Abaxial stomatal density; TR: Transpiration rate; SC: Stomatal conductance; PR: Photosynthetic rate; iWUE: Intrinsic water-use efficiency; SPAD: Chlorophyll index; RWC: Relative water content; NPT: Number of productive tillers; SF %: Spikelet fertility; HI %: Harvest index; TGW: Thousand grain weight; PL: Panicle length; SPY: Single plant yield.

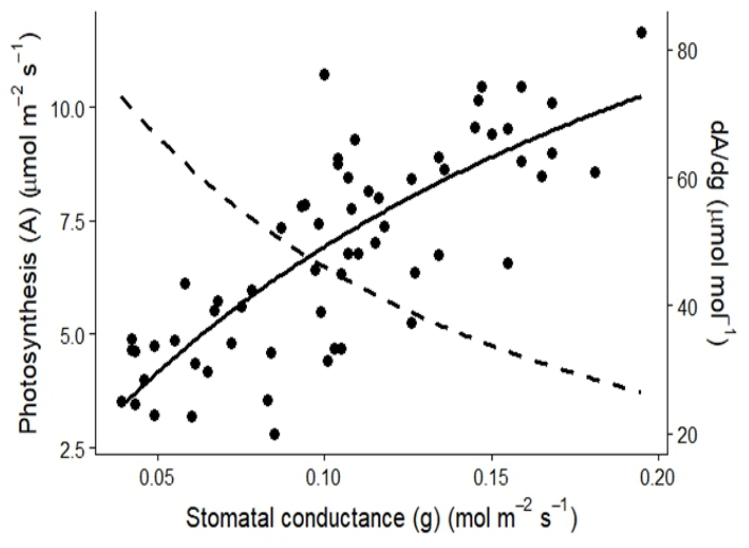

Fig. 2. Relationship between stomatal conductance (g) and photosynthetic rate (A) in rice genotypes. Solid line represents the positive relationship between stomatal conductance and photosynthesis, while the dashed line indicates the corresponding variation in intrinsic water-use efficiency (iWUE) across genotypes. Each point represents an individual genotype, highlighting the coordinated regulation of gas exchange and carbon assimilation.

moderate or optimal stomatal conductance, rather than maximising it, is more desirable for balancing carbon gain and water conservation in breeding programs. The moderate residual effect (0.5673) indicates that approximately 43 % of yield variation was explained by the studied traits, while the remaining 57 % was influenced by unmeasured factors, highlighting the complex nature of grain yield determination.

Path coefficient analysis partitions correlation coefficients into direct and indirect effects, enabling clearer interpretation of trait interactions and facilitating indirect selection for complex traits such as grain yield (16). However, it does not establish true causal relationships; the observed direct effects indicate relative contributions of traits to yield rather than definitive cause–effect mechanisms. In the present study, key yield-determining traits identified through path analysis, particularly harvest index and productive tiller number, were consistent with earlier reports highlighting their major contribution to grain yield (17). The positive influence of harvest index on yield agrees with previous studies, including Green Super Rice, where higher harvest index was associated with improved yield under drought conditions (18, 19). Physiological traits also played an important role in yield regulation. Lower stomatal density and improved water-use efficiency have been reported to enhance yield under stress conditions by reducing transpirational water loss. Similarly, the positive association of yield with water consumption under non-stress conditions suggests that yield expression depends on the plant's ability to efficiently utilise available water, as reported under well-watered environments (20). Previous studies have identified Quantitative trait loci (QTLs) and genes regulating drought-responsive physiological traits such as stomatal behaviour and WUE (21, 22). Although no molecular analysis was performed in this study, the observed trait associations are consistent with these reports and support the genetic basis of physiological regulation in rice. Collectively, these findings highlight the importance of integrating physiological phenotyping with molecular breeding strategies to improve WUE and productivity in rice (11).

Principal component analysis

Principal component analysis with the integration of physiological and yield-attributing traits enabled us to estimate the correlations involving components and therefore identified 16 principal components (PC). Out of the 16 quantitative variables examined in this study, PCA analysis indicated that the first six PCs (PC1, PC2, PC3, PC4, PC5 and PC6) had cumulative variability of 73.26 % across each attribute and demonstrated an eigenvalue greater than one (>1) (Table 6). The first 2 PCs (PC1 and PC2) accounted for 20.04 % and 15.89 % of the variation, respectively, meaning that they explained 35.93 % of the variation collectively. This suggests a high correlation between the traits that were the subject of the study. According to the PCA variable plot (Fig. 3) and PCA biplot (Fig. 4), four agronomical traits, viz., PH, iWUE, PL and SPY, contributed to the utmost variations in PC1, whereas S_ADA, S_ABA, SF, SPY contributed to the maximum variations in PC2. The PC3 with PH, PL, PR, TR and PC4 with NPT, HI, SPY showed maximum variation. The PC5 was associated with HI, SF, RWC and PC6 explained only ~7 % variance but its eigenvalue exceeded unity and it was strongly associated with iWUE, indicating its physiological relevance. The PC1 contains strong negative loadings for TR (-0.768), SC (-0.821), PR (-0.575). The PCA variable plot depicts the interaction among the characters; the length of each trait vector indicates its contribution to the total divergence, with longer vectors representing greater contributions. Traits exhibiting longer vectors namely SPY, PL, SF, DFF, iWUE, PH and TGW contribute substantially to the overall variability captured by the first 2 principal components, whereas traits with shorter vectors, such as NPT, are weakly represented and has lesser variation. Like earlier reports in rice, the first principal component was largely influenced by yield and yield-associated traits, whereas physiological and gas-exchange parameters contributed substantially to subsequent components (23). This separation indicates that yield formation is primarily driven by sink-related traits, while physiological traits modulate yield indirectly through their influence on photosynthetic efficiency and water-use dynamics. These results provide valuable insights into cause-effect relationships among traits and aids in identifying key attributes for indirect selection in breeding programs, particularly for complex traits like grain yield.

Cluster analysis

Cluster analysis based on Mahalanobis (D^2) statistics grouped the seventy rice genotypes into 5 distinct clusters (Table 7) and their inter- and intra-cluster distances presented in Table 8. Cluster III contained the highest number of genotypes (21), followed by Cluster I (20) and Cluster IV (13), whereas Clusters V and II comprised 9 and 7 genotypes, respectively. The clustering pattern was illustrated through a dendrogram using Ward's method (Fig. 5), reflecting genetic relationships among genotypes based on morpho-physiological and yield traits. Physiological traits, particularly SC, TR and iWUE, contributed higher genetic divergence, highlighting their importance in selection programs. Cluster mean performance indicated that

Table 6. Principal component analysis (PCA) of morpho-physiological and yield-related traits for 70 genotypes

PC	Eigenvalue	SD	Percentage of variance	Cumulative percentage of variance
PC 1	3.21	1.79	20.05	20.05
PC 2	2.54	1.60	15.89	35.94
PC 3	2.09	1.45	13.05	48.99
PC 4	1.53	1.24	9.59	58.57
PC 5	1.20	1.10	7.52	66.09
PC 6	1.15	1.07	7.18	73.27
PC 7	0.92	0.96	5.78	79.04
PC 8	0.72	0.85	4.47	83.51
PC 9	0.66	0.81	4.13	87.64
PC 10	0.55	0.74	3.46	91.10
PC 11	0.51	0.72	3.19	94.29
PC 12	0.30	0.55	1.89	96.18
PC 13	0.28	0.53	1.74	97.92
PC 14	0.20	0.44	1.23	99.15
PC 15	0.11	0.34	0.71	99.86
PC 16	0.02	0.15	0.14	100.00

Table 7. Cluster mean values of different traits and percent contribution of traits to total genetic divergence estimated using Mahalanobis D^2 trait-ranking method

Traits	C I	C II	C III	C IV	C V	Contribution (%)
PH	97.4	109.29	106.38	118.69	103.67	5.22
DFF	75.95	73	84.33	80.31	74.56	5.47
S_ADA	40.5	34	43.14	38	33.67	4.47
S_ABA	53.9	43.86	58.29	51.92	47.11	4.64
TR	4.18	2.22	3.01	2.17	4.22	7.04
SC	0.14	0.06	0.1	0.06	0.13	18.26
PR	7.73	4.86	7.16	4.75	8.47	11.39
iWUE	56.4	84.61	72.38	86.51	64.83	9.73
SPAD	44.07	39.28	42.23	39.68	42.53	4.93
RWC	92.72	92.29	93.58	91.52	85.92	4.55
NPT	12.93	14.38	14.46	15.54	18.41	3.23
PL	21.19	19.15	23.55	23.34	20.34	5.71
SF %	81.1	69.58	82.49	82.55	62.81	4.22
HI %	47.3	35.47	47.4	45.03	40.88	3.44
TGW	19.42	20.29	20.52	23.45	19.23	3.11
SPY	14.36	9.03	21.29	17.01	9.97	4.6

C I – cluster I; C II – cluster II; C III – cluster III; C IV – cluster IV; C V – cluster V.

Table 8. Mean inter- and intra cluster distances using Mahalanobis D^2 approach

Cluster	Name of the genotype	No. of genotypes	C I	C II	C III	C IV	C V
I	IRG 203, IRG 253, IRG 218, IRG 260, ADT 37, ADT 53, IRG 215, CBMAS 14110, IRG 288, IRG 271, IRG 297, IRG 258, ASD 16, ADT 43, IRG 256, IRG 233, IRG 273, ADT 45, IRG 240 and IRG 287	20	4.66	5.90	5.25	6.15	5.58
II	IRG 219, IRG 263, IRG 204, IRG 266, IRG 222, IRG 276 and Nagina 22	7	5.90	4.01	5.95	5.14	5.71
III	IRG 212, IRG 286, PMK 3, IRG 231, Dhaksha, IRG 243, Kuliyadichan, APO, CO 51, TPS 5, CO 53, IRG 205, CBMAS 14065, CO 55, Norungan, Anna 4, IRG 241, Way Rarem, IRG 246, ASD 21 and IRG 285	21	5.25	5.95	4.79	5.36	6.39
IV	IRG 244, IRG 293, IRG 227, IRG 209, IRG 228, IRG 223, IRG 268, IRG 225, IRG 248, IRG 277, IRG 264, IRG 249 and IRG 296	13	6.15	5.14	5.36	4.93	6.72
V	IRG 216, IRG 235, IRG 217, IRG 290, IRG 270, IRG 265, IRG 284, IRG 274 and IRG 279	9	5.58	5.71	6.39	6.72	5.06

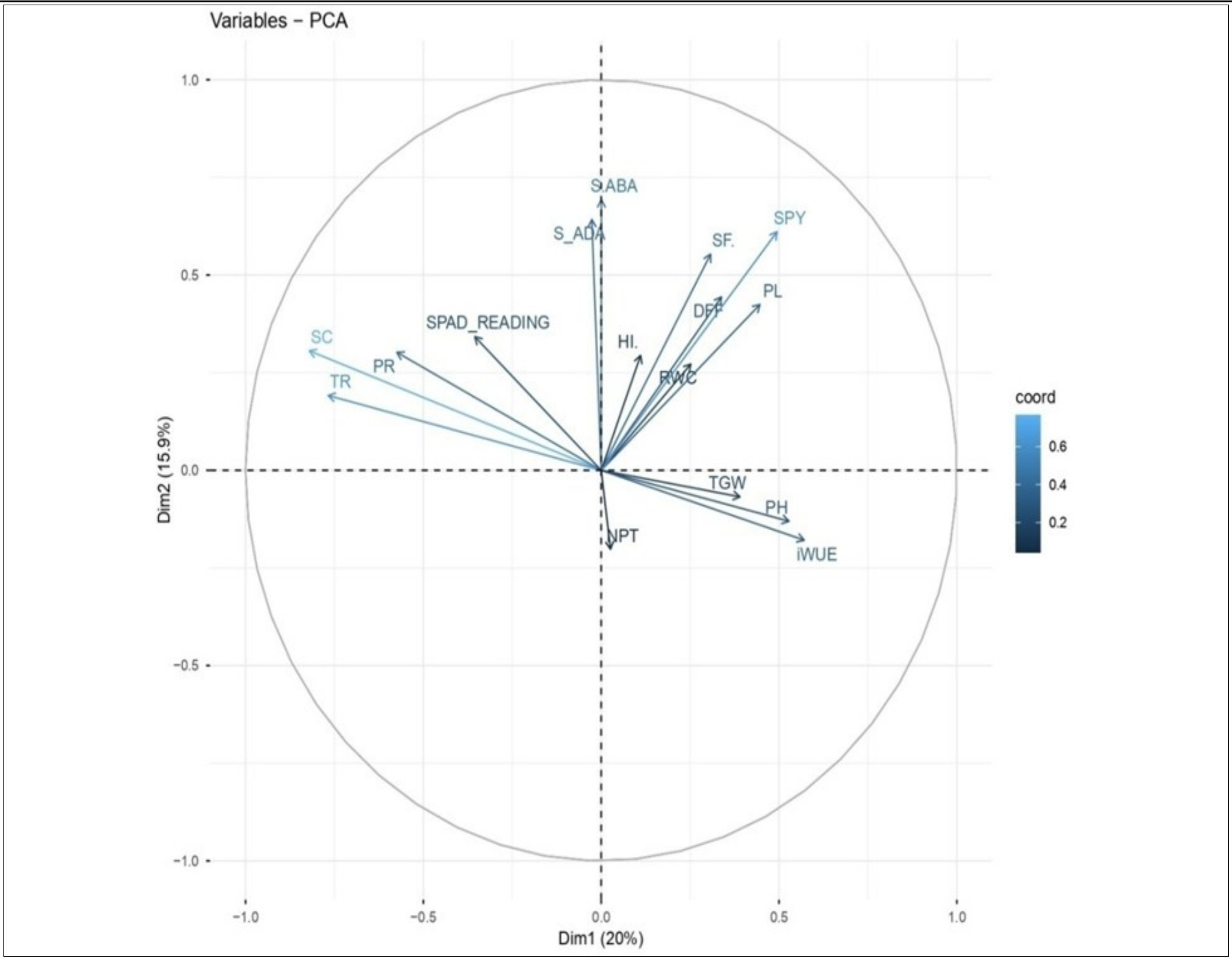

Fig. 3. Principal component analysis variable biplot showing relationships among morpho-physiological and yield traits in rice. The PC1 and PC2 explain 20.0 % and 15.9 % of the total variation, respectively; vector length and direction indicate trait contributions and correlations.

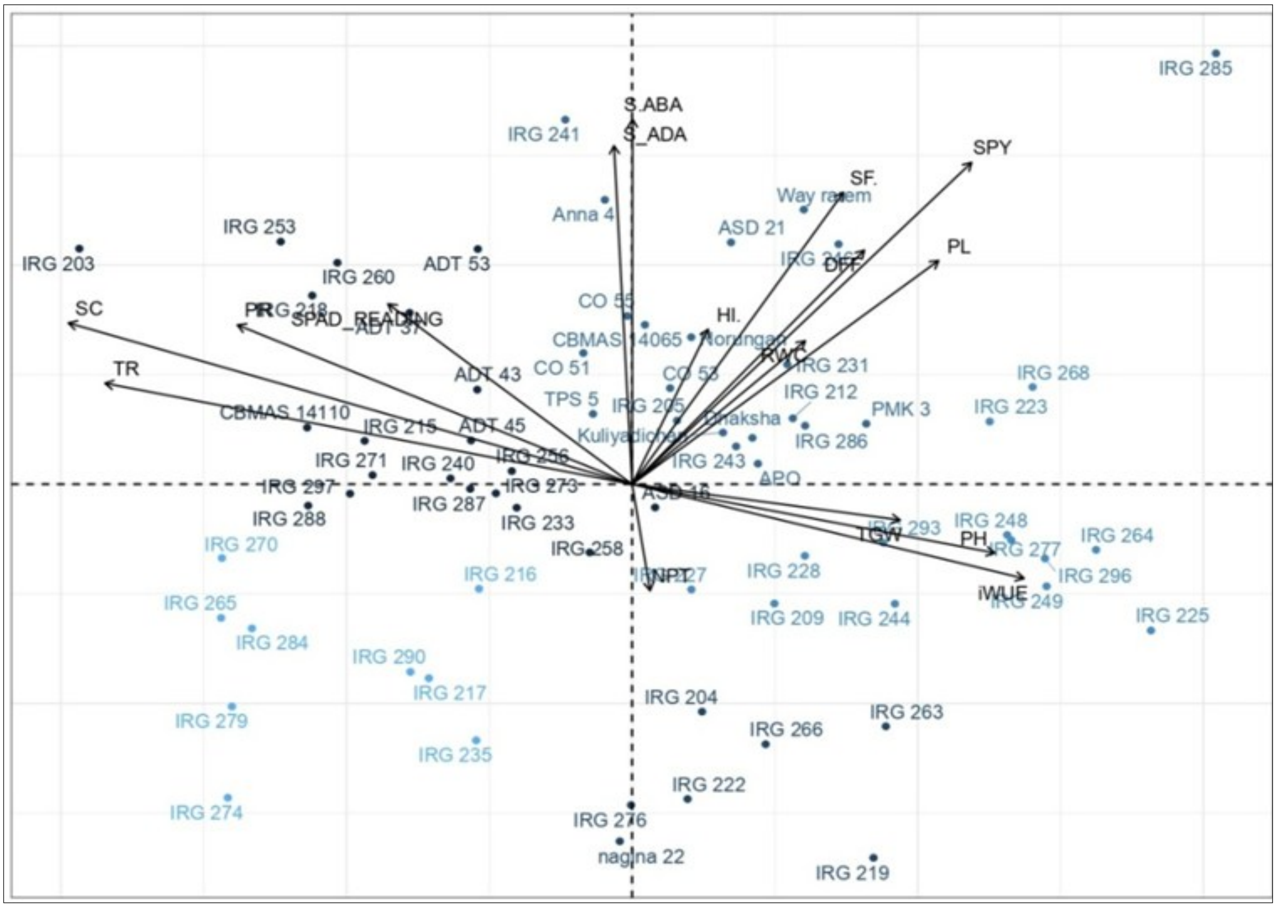

Fig. 4. Principal component analysis biplot showing the distribution of rice genotypes and the association of morpho-physiological and yield-related traits along the first 2 principal components.

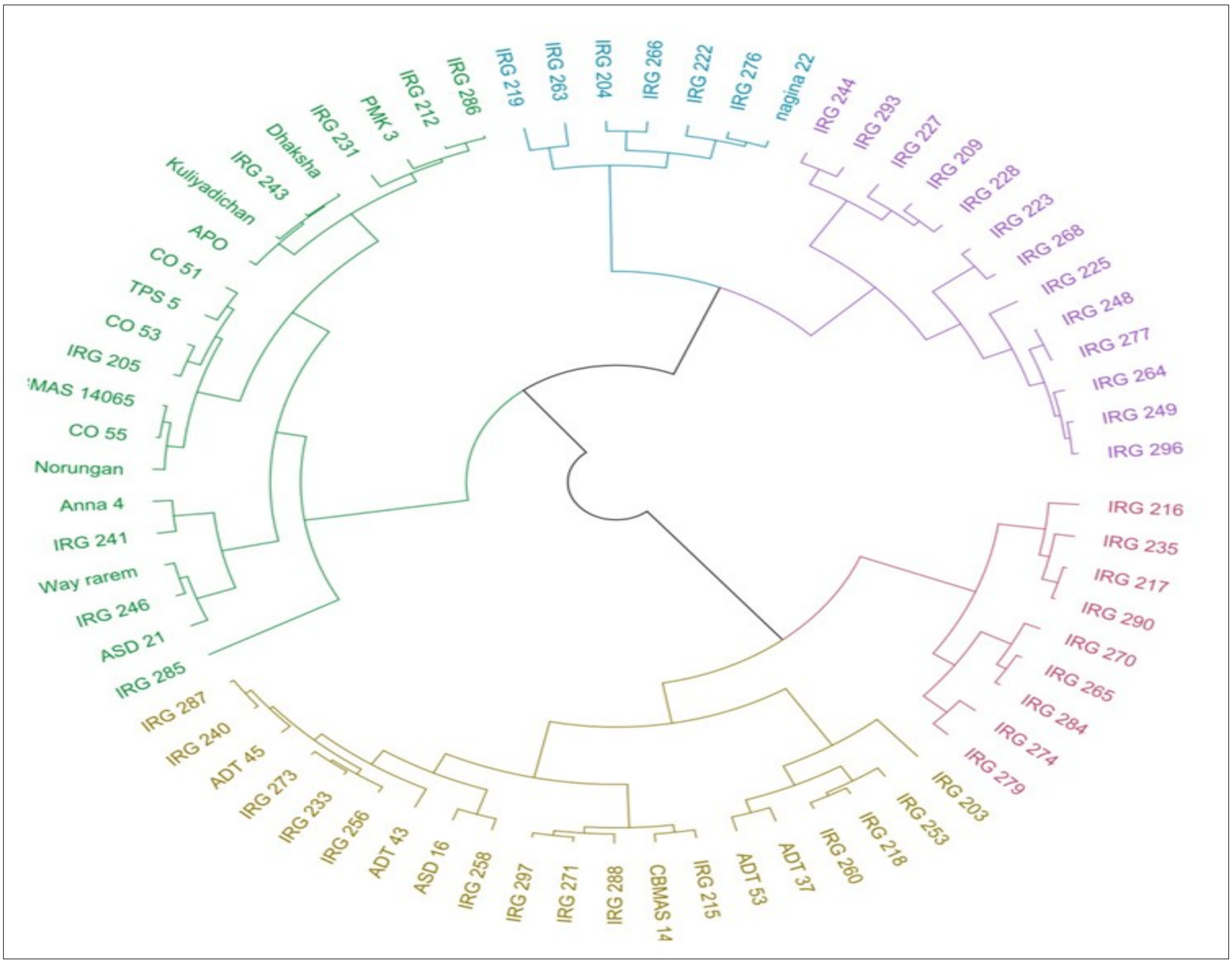

Fig. 5. Circular dendrogram showing hierarchical clustering (Ward's method) based on morpho-physiological and yield-related traits.

Cluster III recorded the highest single plant yield, spikelet fertility and panicle length, suggesting its suitability as a donor for yield improvement, whereas Cluster IV exhibited superior iWUE and thousand grain weight, indicating its potential for improving physiological efficiency. The greatest genetic divergence was observed between Clusters IV and V, followed by Clusters III and V. However, considering both performance and divergence, crosses between Cluster III and Cluster IV genotypes are expected to generate superior recombinants combining high yield and improved water-use efficiency. Promising genotypes include IRG 285, Anna 4, APO and CO 51 (Cluster III) and IRG 296 and IRG 223 (Cluster IV). Similar ward clustering patterns had been observed in the study performed using rice germplasms (20, 24). Although the present study provides important insights into morpho-physiological traits associated with yield and water-use efficiency, the experiment was conducted under non-stress field conditions. Therefore, the relevance of these traits for drought tolerance and stress adaptation should be interpreted with caution. The relationships observed in this study reflect inherent genetic differences under optimal moisture availability and may not fully represent genotype performance under water-deficit environments. Since physiological responses such as stomatal regulation and water-use efficiency are highly environment-dependent, further validation under controlled drought or stress conditions is required to confirm their role in improving stress tolerance. Hence, the identified traits provide a useful basis for selecting potential genotypes for future stress evaluation and breeding programs.

The integrated analysis of morpho-physiological, stomatal and yield-related traits highlights the central role of optimised stomatal regulation and iWUE in determining rice productivity. The observed trade-off between SC, PR and iWUE indicates that genotypes maintaining moderate SC achieve a more efficient balance between carbon assimilation and water conservation. Multivariate and path analyses further demonstrate that yield formation is governed not by single traits but by coordinated interactions among plant height, panicle architecture, spikelet fertility, harvest index and iWUE. These findings emphasise that physiological efficiency, rather than maximum gas-exchange capacity, underpins sustainable yield expression. Consequently, integrating stomatal traits and iWUE into selection strategies provides a robust physiological framework for breeding climate-resilient, water-efficient rice cultivars.

Conclusion

Rice genotypes showed significant genetic variability in stomatal, physiological and yield traits, with intrinsic water use efficiency emerging as a key factor linking carbon assimilation and water conservation. Grain yield was driven by coordinated interactions among stomatal regulation, gas exchange and yield components. Genotypes with moderate stomatal conductance and higher iWUE demonstrated superior performance. These findings support integrating physiological traits with modern breeding to develop climate-resilient, water-efficient rice cultivars.

Acknowledgements

The authors acknowledge support from the Department of Biotechnology, Ministry of Science and Technology, India (No. BT/INF/22/SP45584/2022).

Authors' contributions

All authors contributed to the conception and conceptualisation of the study and the overall experimental design. SK conducted the experiments, collected and analysed the data and prepared the first draft of the manuscript. WM and BA contributed to the development and refinement of the methodology and experimental protocols. JP, VC, RM[1], SA, RM[2] and SM critically reviewed, edited and commented on earlier versions of the manuscript. All authors read and approved the final manuscript [RM[1]- Raveendran Muthurajan; RM[2]- Raju Marimuthu].

Compliance with ethical standards

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

Ethical issues: None

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT for assistance with language refinement, restructuring of text and improving readability. After using this tool, the authors reviewed and edited the content as needed and takes full responsibility for the content of the publication.

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Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

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