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INTEGRATED EVALUATION OF YIELD–PROTEIN–AMYLOSE TRADE-OFFS UNDER NITROGEN LIMITED DIRECT SEEDED AND NITROGEN SUFFICIENT TRANSPLANTED RICE SYSTEMS

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ABSTRACT

The coordinated expression of grain yield, protein content, and amylose under contrasting nitrogen and establishment systems remains poorly characterized in rice. Most studies evaluate these traits independently or under uniform nitrogen supply, limiting understanding of their integrated response under low-input direct-seeded systems. This study systematically compared yield, grain protein content, and amylose content across nitrogen-deficient direct-seeded rice (DSR;0 kg N ha^{-1}) and nitrogen-sufficient transplanted rice (TR; 80 kg N ha^{-1}) over two wet seasons using 117 genotypes from the 3K Rice Genome Panel. Grain yield under TR was nearly three-fold higher than under DSR, reflecting strong establishment and nitrogen effects on productivity. In contrast, pooled mean AC and GPC remained comparable between systems despite wide genetic variation. Correlation analysis revealed a strong positive association between yield and biomass in both systems. A pronounced negative yield–protein relationship was observed under TR, consistent with dilution effects at higher yield potential, whereas this trade-off was weaker under DSR. Amylose content showed negligible associations with yield or protein under both systems, indicating independence of starch composition from productivity and nitrogen allocation. Principal component analysis demonstrated system-specific trait coordination, with productivity traits dominating variation under DSR and phenology contributing more strongly under TR. Differential genotype responses across systems indicate genotype × establishment × nitrogen interactions for grain quality expression. These results indicate that trait relationships are system-dependent, and therefore grain quality must be evaluated under the specific nitrogen and establishment conditions targeted for varietal deployment, especially in low-input direct-seeded systems.
***Keywords*:** Direct seeded rice, Transplanted rice, Amylose content, Grain protein content.

Introduction

Rice is a primary staple food for a large proportion of the global population, and its value is determined by both grain yield and grain quality attributes that influence consumer preference and nutritional intake. Among grain quality traits, amylose content is a key determinant of cooking and eating quality, affecting textural properties such as firmness, stickiness, and gelatinization behaviour of cooked rice (Juliano, 1992; Fitzgerald *et al*., 2009). In parallel, grain protein content contributes to the nutritional value of rice, particularly in regions where rice constitutes a major dietary energy and protein source (Bhattacharya, 2011). Grain yield remains the principal agronomic trait governing varietal adoption and productivity. Therefore, simultaneous consideration of yield and grain quality traits is essential in rice improvement programs.

Amylose content exhibits substantial quantitative variation among rice genotypes and is influenced by both genetic background and environmental conditions during grain filling. Grain protein content and grain yield are similarly complex quantitative traits, governed by multiple physiological processes including nitrogen uptake, assimilation, partitioning, and carbon–nitrogen interactions during grain development. Evaluating these traits independently provides limited insight into overall varietal performance, whereas their integrated assessment enables identification of trade-offs or complementarities among eating quality, nutritional quality, and productivity. In particular, understanding how yield, protein, and amylose are coordinately expressed under contrasting resource environments is critical for breeding rice varieties that satisfy both market and agronomic demands.

Rice cultivation systems can substantially influence the expression of both yield and grain quality traits. In many rice-growing regions, including central India, there is a gradual shift from conventional transplanted rice to direct-seeded rice due to increasing labour scarcity, water limitations, and rising production costs. These establishment systems differ markedly in water regime, nitrogen availability, soil redox conditions, and early-season growth dynamics. DSR under rainfed, nitrogen-deficient conditions often expose plants to intermittent stress and limited nitrogen supply, whereas transplanted systems typically receive assured irrigation and fertilizer inputs. Such differences can alter biomass accumulation, grain filling dynamics, nitrogen remobilization, and starch biosynthesis, thereby influencing both yield and grain composition.

Despite the growing adoption of DSR, systematic research explicitly comparing grain yield, amylose content, and grain protein content simultaneously under nitrogen-deficient DSR versus nitrogen-sufficient TR remains limited. Most studies examine nitrogen effects on yield or protein alone, or assess grain quality traits without explicitly contrasting establishment methods under divergent nitrogen regimes. The coordinated response of yield, starch composition, and protein accumulation under nitrogen limitation relative to nitrogen sufficiency is therefore insufficiently characterized. In particular, whether nitrogen deficiency in DSR alters the balance between carbon allocation to starch synthesis and nitrogen partitioning to grain protein, compared with N-replete transplanted systems, remains underexplored. Multi-season evaluation is essential for reliable characterization of such interactions, as it captures both genetic variation and environmental modulation across years with differing climatic conditions. Integrating multi-season data with trait association and multivariate analyses enables identification of stable and system-specific genotype responses, as well as clarification of how trait relationships shift across contrasting environments.

In the present study, amylose content, grain protein content, grain yield, and related agronomic traits were evaluated in a panel of 117 rice genotypes across two consecutive kharif seasons under two contrasting crop establishment systems: rainfed direct-seeded rice without external nitrogen application (N0) and irrigated transplanted rice with sufficient nitrogen application (N80). The objectives were to: (i) quantify the extent of phenotypic variation for yield and grain quality traits under contrasting establishment and nitrogen regimes, (ii) assess their consistency across seasons, (iii) examine how associations among yield, protein, and amylose differ between DSR and TR systems

Materials and Methods

Plant material and experimental site

Field experiments were conducted during the 2022 and 2023 wet (kharif) seasons at the research farm of Indira Gandhi Krishi Vishwavidyalaya (IGKV), Raipur, India (21.2514° N, 81.6296° E). A total of 117 rice accessions representing diverse genetic backgrounds from the 3K Rice Genome Panel were evaluated (Supplementary File 1). The accessions were evaluated under two contrasting crop establishment systems designed to represent divergent nitrogen and water regimes: DSR grown under rainfed, nitrogen-deficient conditions without external nitrogen application (N0, 0 kg N ha^{-1}), and TR grown under irrigated, nitrogen-sufficient conditions with 80 kg N ha^{-1} (N80) applied, using a planting spacing of 20 × 20 cm. The two systems were managed as independent experiments in each season. Within each system, genotypes were arranged in a randomized block design (RBD) and standard agronomic practices appropriate for each establishment method were followed. In the N80 treatment, phosphorus and potassium were applied as basal doses at 50 kg P ha^{-1} and 50 kg K ha^{-1}, respectively, while no nitrogen fertilizer was applied in the N0 treatment.

Soil nitrogen characterization and meteorological data

The available soil nitrogen under the experimental systems was quantified prior to sowing in each season. Soil samples were collected from five locations per plot, composited, air-dried, and analysed in the Soil Testing Laboratory, Department of Soil Science, IGKV. Meteorological data for the crop-growing periods were obtained from the Department of Agricultural Meteorology, IGKV, Raipur. Seasonal variation in rainfall, temperature, relative humidity, and sunshine duration was observed between years, providing contrasting yet representative wet-season environments. Seasonal trends in meteorological parameters are summarized in table (Table 1).

Table 1: Meteorological parameters recorded during the Kharif seasons of 2022–2023 and 2023–2024 at IGKV, Raipur (Source: Department of Agricultural Meteorology, IGKV)

Weather parameter	2022-23	2023-24
Mean Max. Temperature (°C)	32.5	31.1
Mean Min. Temperature (°C)	22.9	21.7
Total Rainfall (mm)	1083.2	1359.2
Mean Relative Humidity (%)	71.2	72.9
Mean Sunshine duration(hr/day)	5.2	4.9

Agronomic traits and amylose content estimation

Agronomic parameters, such as plant height (PH), days to maturity (DTM), panicle length (PL), grain yield (GY), and biological yield (BY), were measured according to the IRRI Standard Evaluation System for Rice (2013). Amylose content (AC) in percentage (%) was estimated using the iodine colorimetric method following the Juliano method (Juliano, 1971). Dehusked and polished rice grains were milled to fine flour, starch was dispersed under alkaline conditions, and the iodine–potassium iodide reagent was added to form a coloured complex. Absorbance was measured using a spectrophotometer, and amylose concentration was quantified using a standard calibration curve. Results were expressed as a percentage on a dry weight basis.

Estimation of grain protein content

Grain protein content (GPC) was determined using the Kjeldahl method (Nelson and Sommers, 1980). Finely ground grain samples were digested in concentrated sulfuric acid with catalyst (K_2SO_4, $CuSO_4$) to convert organic nitrogen to ammonium. After alkalization, ammonia was distilled and quantified by titration. Total nitrogen content was converted to protein percentage using a nitrogen-to-protein conversion factor of 5.95 and expressed on a dry weight basis (Tkachuk, 1977).

Statistical analysis

Descriptive statistics, including mean, range, standard deviation, and coefficient of variation (CV%), were calculated for the measured traits separately for each establishment system (DSR and TR), for each season, and for pooled data, to assess overall phenotypic variability as well as condition-specific trait expression. The effects of genotype, establishment system, season, and their interactions were evaluated using mixed-model analysis. Genotype, establishment system, and season were treated as fixed effects, while replications were considered as blocks nested within each season × establishment system combination, consistent with the randomized block design. Genotype-wise performance across seasons and establishment systems was summarized using best linear unbiased estimates (BLUEs), which were subsequently used for pooled as well as system-specific analyses. Associations among traits were quantified using Pearson's correlation coefficients, calculated separately for DSR and TR conditions as well as using pooled BLUEs. Pairwise trait relationships were visualized using scatterplots with fitted linear regression lines.

Multivariate patterns of trait variation were examined using principal component analysis (PCA) based on standardized BLUE values of amylose content, grain protein content, and grain yield, conducted separately for DSR and TR systems. PCA was used to identify major axes of variation and visualize genotype distribution under contrasting conditions.

Results

Phenotypic Variation and Analysis of Variance Across Establishment Systems

Soil N content differed between management conditions, with 125 kg N ha^{-1} in N0 plots and 176 kg N ha^{-1} in N80 plots. Two-year pooled means of the traits in each cultivation condition are represented in Fig 1. Significant genotypic effects were detected for all traits under both systems ($p < 0.001$; Supplementary File 2), indicating substantial inherent variability among accessions.

Vegetative growth traits exhibited moderate establishment effects. PH averaged 89.3 cm under DSR compared with 112.4 cm under TR. PL followed a similar trend, with pooled means of 21.9 cm in DSR and 24.0 cm in TR, indicating modest but consistent elongation of panicle architecture under transplanted management. AC maintained comparable pooled means under DSR (19.52%) and TR (19.14%) despite wide genetic ranges in both systems (4.28–25.45% and 4.65–25.35%, respectively in DSR and TR). GPC similarly showed stable pooled means (6.43% in DSR; 6.41% in TR), although greater dispersion under TR in 2023 suggests seasonal effects on N allocation.

In contrast, productivity traits (GY and BY) were strongly system-dependent. GY under TR (0.293 kg m^{-2}) was nearly three-fold higher than under DSR (0.105 kg m^{-2}), with substantially broader upper ranges in TR. BY also followed the same pattern (0.901 vs. 0.448 kg m^{-2}), reflecting approximately twofold greater biomass accumulation under transplanted conditions. These shifts indicate pronounced establishment effects on biomass production and yield realization. Days to maturity showed comparatively minor differences between systems (119 vs. 122 days), suggesting limited phenological plasticity relative to yield traits

ANOVA results supported these patterns. Productivity traits exhibited significant main effects of year and establishment system along with strong genotype × year, genotype × establishment, and three-way interaction terms, indicating environment-dependent genotypic performance. Plant height and panicle length displayed highly significant genotypic effects with moderate but significant interaction components, reflecting some environmental modulation yet greater structural stability relative to yield traits. GPC showed significant genotype and interaction effects consistent with moderate environmental sensitivity. In contrast, AC exhibited nonsignificant year and establishment main effects despite strong genotypic control, reinforcing its overall environmental stability. Phenological traits showed comparatively weaker interaction effects across seasons and systems.

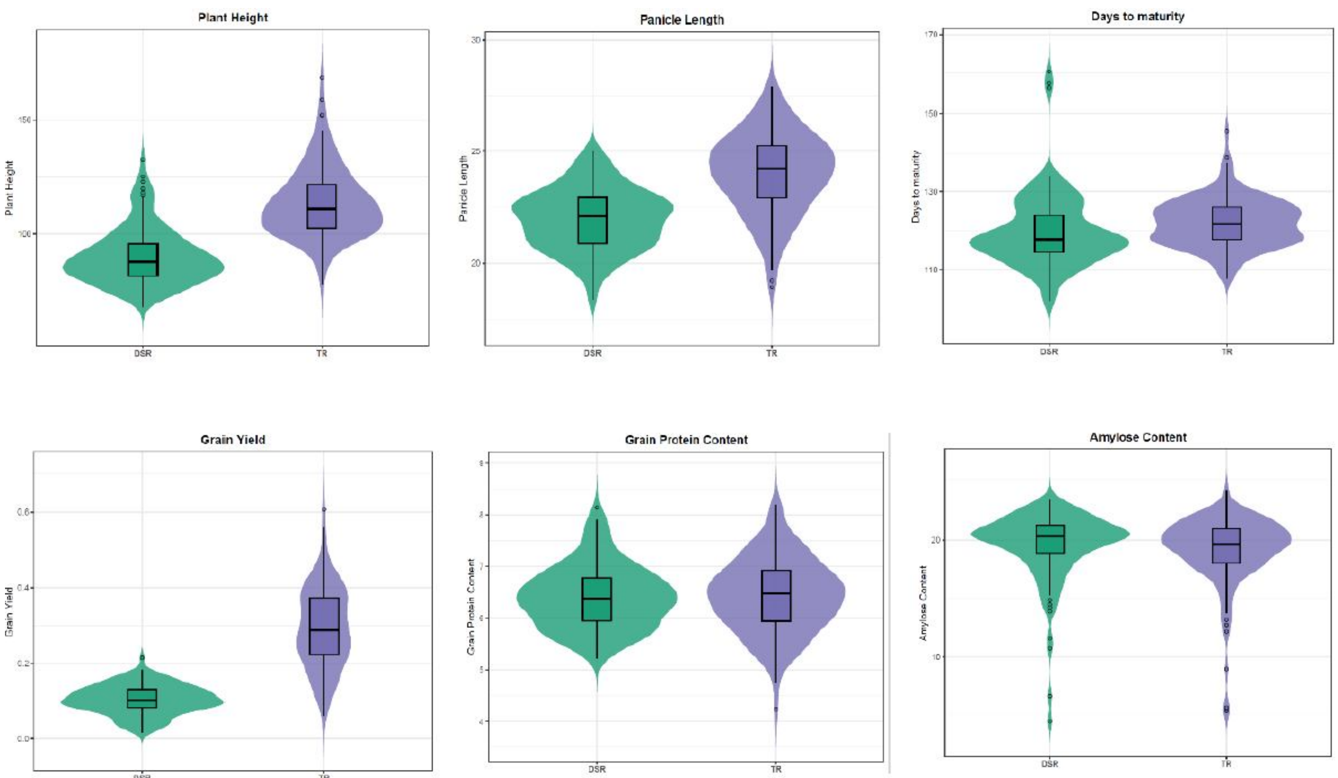

Fig. 1 : Violin–boxplot distributions of plant height, panicle length, days to maturity, grain yield, grain protein content and amylose content under DSR and TR systems (pooled across years).

Correlation analysis

Correlation analysis based on genotype BLUEs revealed clear and quantifiable system-dependent relationships among productivity, grain quality, and supporting agronomic traits. Across both systems, GY showed a very strong positive association with BY, confirming that biomass production was the principal determinant of yield variation (Fig. 2, Supplementary file 3). Under DSR, the correlation between GY and BY was $r = 0.91$ ($p < 0.001$), while under TR it was similarly strong at $r = 0.94$ ($p < 0.001$). These consistently high coefficients indicate that differences in grain yield among genotypes were primarily driven by total assimilate production rather than structural or phenological traits alone.

PH and PL showed moderate associations with productivity traits, with clearer patterns under TR. Under DSR, PH exhibited a weak to moderate positive correlation with GY ($r = 0.24$, $p < 0.05$) and BY ($r = 0.27$, $p < 0.01$), while PL showed similar modest positive associations with GY ($r = 0.22$, $p < 0.05$) and BY ($r = 0.25$, $p < 0.05$). Under TR, these relationships strengthened, with PH positively correlated with GY ($r = 0.38$, $p < 0.001$) and BY ($r = 0.41$, $p < 0.001$), and PL showing significant positive associations with GY ($r = 0.35$, $p < 0.001$) and BY ($r = 0.39$, $p < 0.001$). These results indicate that taller plants and longer panicles contributed more substantially to yield formation under irrigated, nitrogen-sufficient conditions than under DSR.

The role of phenology differed between establishment systems. Under DSR, DTM showed only a weak and nonsignificant association with GY ($r = 0.12$, $p > 0.05$) and BY ($r = 0.18$, $p > 0.05$), indicating that extended duration did not translate into yield advantage under aerobic, nitrogen-limited conditions. In contrast, under TR, DTM was positively correlated with both GY ($r = 0.42$, $p < 0.001$) and BY ($r = 0.46$, $p < 0.001$), suggesting that longer-duration genotypes benefited from favourable water and nitrogen availability, allowing extended growth to enhance biomass accumulation and yield.

GPC exhibited a contrasting pattern relative to yield. In DSR, GPC showed a moderate negative correlation with GY ($r = –0.31$, $p < 0.01$) and BY ($r = –0.28$, $p < 0.01$). Under TR, these negative associations were stronger, with correlations of $r = –0.48$ ($p < 0.001$) for GY and $r = –0.44$ ($p < 0.001$) for BY. This pattern indicates a more pronounced dilution effect under transplanted conditions, where increased biomass and grain production were associated with reduced protein concentration in the grain. Additionally, GPC was negatively correlated with DTM under TR ($r = –0.37$, $p < 0.001$), whereas the relationship was weak under DSR ($r = –0.15$, $p > 0.05$), further supporting the idea that longer-duration, high-yielding genotypes accumulated proportionally less nitrogen in the grain under non-limiting conditions. Associations between GPC and structural traits (PH and PL) were weak and generally nonsignificant across systems, indicating limited direct linkage between plant architecture and grain nitrogen concentration.

In contrast, AC showed consistently weak or negligible associations with productivity and phenological traits in both systems. Under DSR, correlations between AC and GY ($r = 0.05$, $p > 0.05$), BY ($r = 0.03$, $p > 0.05$), and DTM ($r = –0.08$, $p > 0.05$) were nonsignificant. Similar patterns were observed under TR, where correlations with GY ($r = –0.04$, $p > 0.05$) and BY ($r = –0.02$, $p > 0.05$) remained negligible. Moreover, the association between AC and GPC was weak under both DSR ($r = 0.07$, $p > 0.05$) and TR ($r = 0.09$, $p > 0.05$), indicating independence between starch composition and nitrogen partitioning.

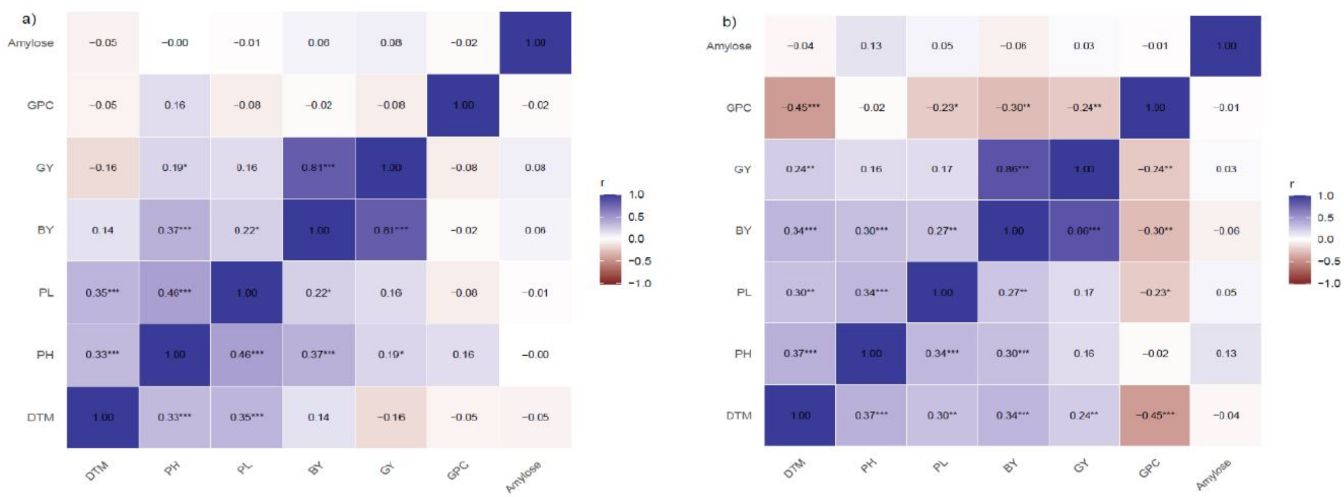

Fig. 2 : Heatmaps of Pearson correlation coefficients among yield, grain quality, and associated agronomic traits under a) direct-seeded and b) transplanted rice systems. Significance levels are indicated by asterisks.

Principal Component Analysis of trait variation under DSR in relation to TR

Principal component analysis (PCA) based on genotype BLUEs revealed clear multivariate structuring of agronomic, productivity, and grain quality traits under both establishment systems (Fig. 3; Supplementary File 4). Under DSR, the first two principal components explained 52.93% of the total phenotypic variation, with PC1 accounting for 31.66% and PC2 for 21.27%, indicating that the multidimensional trait dataset could be effectively summarized within a two-dimensional space.

Under DSR, PC1 represented the primary productivity axis, showing strong positive loadings for GY and BY, with additional contributions from PH and PL. DTM showed relatively weak loading on PC1, indicating that phenological duration contributed minimally to yield variation under rainfed, nitrogen-deficient conditions. PC2 was primarily associated with GPC and, to a lesser extent, DTM, and was largely orthogonal to the productivity axis. This separation indicates that variation in grain protein content was largely independent of biomass accumulation and grain yield under DSR. AC displayed low loadings on both PC1 and PC2, occupying a distinct position in the multivariate space and reflecting weak associations with yield, protein, and phenological traits.

In comparison, PCA under TR showed broadly similar trait groupings but differences in trait coordination. The first two principal components under TR explained 54.19% of the total variation, with PC1 contributing 36.94% and PC2 contributing 17.25%. Under TR, PC1 was again dominated by productivity-related traits (GY and BY), but unlike DSR, DTM showed stronger alignment with the productivity axis, indicating that longer-duration genotypes tended to achieve higher biomass and yield when water and nitrogen were non-limiting. GPC under TR was separated from the productivity axis and oriented opposite to grain yield, consistent with a dilution effect under higher yield potential. As observed under DSR, AC showed small loadings on the major principal components, indicating relative independence from yield and protein-related traits.

Overall, PCA results demonstrate that under DSR, grain yield variation was driven primarily by biomass accumulation with limited contribution from phenological duration, whereas under TR, phenology played a more prominent role in structuring productivity-related variation. Across both systems, grain protein content varied largely independently of yield, and amylose content remained consistently decoupled from agronomic and nitrogen-related traits.

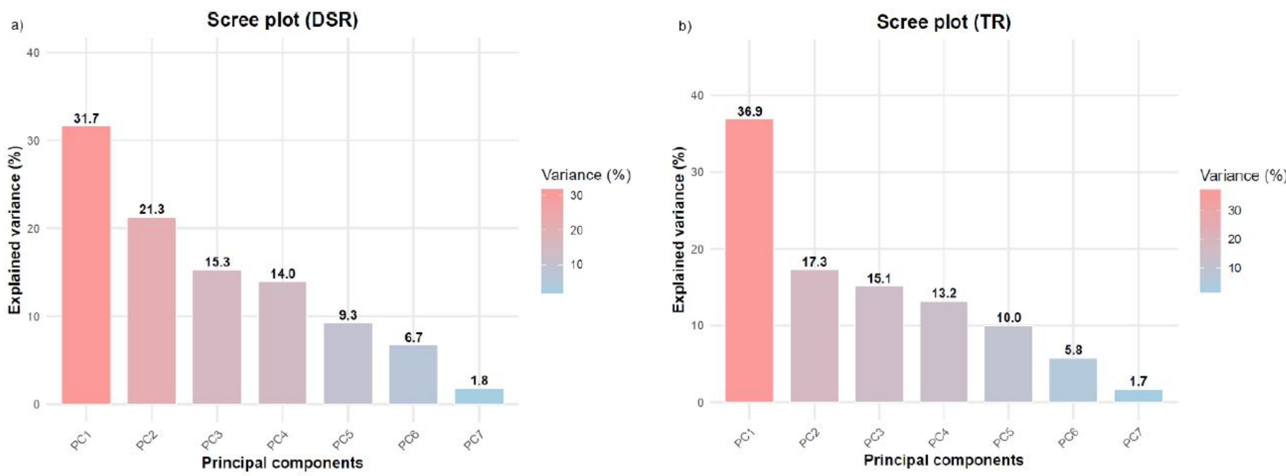

Fig. 3 : Scree plots illustrating the proportion of total variance explained by each principal component under a) DSR and b) TR systems, with the first two components accounting for 52.93% (DSR) and 54.19% (TR) of the total phenotypic variation.

Discussion

Across two wet seasons, establishment system and seasonal environment were the dominant drivers of mean performance, with rainfed, N-deficient DSR showing a ~3-fold yield penalty relative to irrigated, N-sufficient TR (Chowdhury *et al.*, 2024; Chowdhury *et al.*, 2025). This aligns with known constraints in DSR, poorer early stand establishment, greater stress exposure, and reduced capacity to sustain biomass accumulation whereas transplanted flooded rice benefits from buffered early growth and more predictable water and N supply (Chaudhary *et al.*, 2023; Kiranmai *et al.*, 2025). Despite large productivity shifts, amylose and protein means were comparatively stable across systems, reinforcing that quality traits can be less plastic than yield under contrasting establishment environments, even though dispersion can increase in specific seasons (Vandna *et al.*, 2025).

A consistent outcome across systems was the tight coupling between grain yield and biological yield, indicating that biomass accumulation remains the primary proximate determinant of yield under both resource-limited DSR and favourable TR conditions (Qin *et al.*, 2025; Ma *et al.*, 2025). However, phenology contributed differently by system: days to maturity showed little association with yield under DSR, suggesting that stress and resource limitation constrain the ability of longer-duration genotypes to translate extended growth into added biomass; under TR, longer duration supported higher biomass and yield, consistent with resource-sufficient environments allowing phenological differences to express as yield advantages (Chowdhury *et al.*, 2024; Baite *et al.*, 2025).

Trait inter-relationships further revealed system-dependent trade-offs. The yield-protein dilution effect was stronger under TR, where high biomass and grain production likely outpaced proportional grain-N accumulation, intensifying negative GY-GPC associations; under DSR the trade-off weakened, consistent with co-limitation by water and N restricting both carbon gain and N acquisition (Padhan *et al*., 2023; Ma *et al*., 2025; Jiang *et al*., 2026). By contrast, amylose content remained largely decoupled from yield and protein, supporting its relative genetic autonomy from source–sink and N-partitioning processes and indicating scope to improve eating quality without inherent yield penalties (Prez-Almeida *et al*., 2025; Fujita *et al*., 2022; Reis *et al*., 2025). Nonetheless, because starch synthesis can respond to grain-filling environment, multi-environment screening remains important for ensuring amylose stability across establishment methods and seasons.

Implications for breeding and deployment. These results support (i) biomass-based selection as a robust route to yield improvement across systems; (ii) DSR-targeted ideotypes emphasizing stress tolerance and efficient biomass production rather than longer duration; (iii) TR ideotypes that maintain grain-N allocation to mitigate protein dilution through improved N partitioning/remobilization and management synergies; and (iv) independent selection for amylose profiles using starch biosynthesis loci while validating stability across environments (Hu *et al*., 2024; Zhang *et al*., 2025; Zhang *et al*., 2024).

Conclusion

This study underscores the necessity of multivariate evaluation for balanced rice improvement. Grain yield, grain protein content, and amylose content exhibited distinct environmental sensitivities and genetic architectures, with yield strongly influenced by establishment system and nitrogen availability, protein showing a system-dependent dilution effect, and amylose remaining largely independent of productivity traits. These differential responses highlight that simultaneous optimization of yield and grain quality requires system-specific evaluation rather than uniform selection environments. The results indicate that improving biomass production is central to yield enhancement, while mitigating protein dilution under high-input systems will depend on improved nitrogen uptake and partitioning. Importantly, the genetic independence of amylose from yield provides flexibility to enhance eating quality without inherent productivity penalties, provided stability is validated across environments. Overall, achieving high yield without compromising nutritional and cooking quality will require integrated breeding strategies that combine physiological understanding of trait trade-offs with targeted selection under both transplanted and direct-seeded systems. Such an approach is critical for developing rice varieties adapted to both high-input and resource-efficient production environments.

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