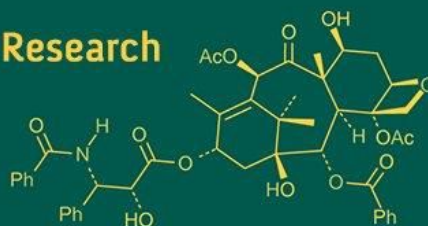
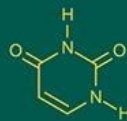
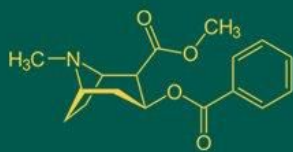


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Path analysis and correlation studies for identifying superior restorer lines in hybrid rice breeding

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Abstract

The present study evaluated 129 promising rice genotypes at the ICAR-Indian Institute of Rice Research, Hyderabad, during *Kharif* 2024 and *Rabi* 2024-2025, to investigate interrelationships and direct and indirect effects of yield component traits on grain yield. Eleven traits related to yield were assessed to understand their influence on rice grain production. Analysis of variance showed significant differences among genotypes for all traits studied. Grain yield was positively and significantly associated with panicle length (0.14), number of productive tillers (0.14), test weight (0.25), and per day productivity (0.99). Traits such as days to 50% flowering, panicle length, spikelet fertility, test weight, and per day productivity exerted positive effects on grain yield per plant. These results suggest that yield improvement in hybrid rice breeding can be achieved through selection targeting productive tillers, test weight, and panicle length.

Keywords: Path analysis, correlation studies, hybrid rice breeding, restorer lines, grain yield, yield components, *Oryza sativa* L.

Introduction

Rice (*Oryza sativa* L.) plays a pivotal role in global food security, serving as a primary staple food for over half of the world's population, especially across Asia and Africa (Maurya *et al.*, 2022) [23]. Given the increasing global population and shrinking arable land, there is an urgent demand to boost rice productivity sustainably. Hybrid rice technology has emerged as an important breakthrough to meet this challenge by harnessing hybrid vigor or heterosis. The superior performance of hybrid offspring compared to their parental lines in yield and other agronomic traits (Ashraf *et al.*, 2024) [4]. Extensive research and breeding efforts have shown that heterosis can significantly enhance grain yield, biomass accumulation, and tolerance to environmental stresses in rice and other cereal crops (Moll *et al.*, 1962; Liu *et al.*, 2020) [26, 22].

At the heart of commercial hybrid rice production is the successful exploitation of male sterility maintained by cytoplasmic male sterile (CMS) lines and the complementary fertility restoration function supplied by restorer lines. These two parental components enable large-scale hybrid seed production by preventing self-pollination and restoring fertility in hybrid progeny, respectively (Chang *et al.*, 2016; Xie & Zhang, 2018) [10, 48]. The classical three-line hybrid system consisting of the CMS line, a maintainer line retaining sterility, and a restorer line restoring fertility is widely adopted in hybrid rice breeding programs worldwide. Male sterility in CMS lines typically results from nuclear recessive genes interacting with cytoplasmic factors that are sensitive to photoperiod and temperature, contributing to environmental responsiveness of sterility expression.

Genetic divergence between parental lines is widely recognized as a critical factor influencing the magnitude of heterosis achieved in their hybrid progenies. Crosses between genetically distant parents tend to exhibit substantial heterotic effects and yield superiority (Sharma *et al.*, 2021) [43]. However, it is important to note that high heterosis does not guarantee superior yield performance in all hybrid combinations because gene interactions and environmental factors also modulate phenotypic outcomes. Therefore, maintaining and utilizing broad genetic diversity within germplasm pools is essential for introgressing

beneficial alleles and developing superior hybrid cultivars that exhibit both yield vigor and stability (Verma *et al.*, 2021; Khan *et al.*, 2021)^[46, 18].

Single plant grain yield is a complex quantitative trait governed by multiple genes and their interactions, as well as environmental influences. Its expression depends on both genetic architecture such as gene number, gene effects, and epistatic interactions and the environment in which plants are grown. Furthermore, single plant yield is closely influenced by various yield-contributing components including plant height, growth duration, panicle length, effective tiller number per plant, grain number per panicle, and panicle branching patterns (Asante *et al.*, 2019)^[3]. Understanding the phenotypic and genetic relationships among these component traits as well as their direct and indirect effects on grain yield is fundamental for formulating efficient selection strategies in breeding programs.

To dissect these complex relationships, statistical tools such as correlation and path coefficient analyses are instrumental. While correlation analysis reveals the strength and direction of associations among traits, path analysis partitions these relationships into direct and indirect effects, illuminating which traits have the most substantial causal influence on grain yield. This knowledge enables breeders to prioritize promising traits for selection to maximize genetic gain.

Considering these factors, the present study was undertaken with the objective to evaluate the performance and genetic variability of 129 promising rice genotypes with diverse genetic backgrounds, particularly focusing on their potential as restorer lines in hybrid rice production. The study aims to examine the phenotypic correlations and causal relationships among yield and yield-related traits, providing insights into the trait interactions that most significantly influence grain yield. Through this, we seek to identify superior genotypes and key traits that can be exploited for optimizing hybrid rice breeding programs toward enhanced yield and agronomic performance.

Materials and Methods

This study evaluated 129 promising rice lines, including two check varieties (AR-9-18 and PS 344), under irrigated conditions at ICAR-Indian Institute of Rice Research, Hyderabad, during Kharif 2024 and Rabi 2024-2025. The experiment was conducted using an Augmented Block Design (ABD) with a plant spacing of 20 × 15 cm and row spacing of 25 cm. Check varieties were replicated across blocks to control for environmental variation, while test genotypes were unreplicated.

Standard crop management practices and necessary precautions were followed to ensure optimal crop growth. Trait data were recorded on days to heading and days to 50% flowering on a plot basis by averaging observations across each plot. For other traits including plant height, panicle length, number of productive tillers, total grains per panicle, spikelet fertility (%), test weight (g), panicle weight (g), per day productivity (g), and single plant yield (g) data were collected from six randomly selected well-grown plants per genotype in each replication.

Phenotypic and genotypic correlation coefficients among traits were calculated following Falconer (1981). Direct and indirect effects of yield components on single plant yield were estimated through path coefficient analysis based on methods by Wright (1921) and Dewey and Lu (1959), using single plant yield as the dependent variable.

All statistical analyses were performed in R statistical software (Posit Team, 2025) utilizing packages such as 'agricolae' for analysis of variance, correlation, and path coefficient calculations.

Correlation analysis among yield-related traits provided insights into their relationships and facilitated the identification of key traits influencing grain yield. The trait single plant yield exhibited a significant positive association with the number of productive tillers, panicle length, test weight, and per-day productivity, with correlation coefficients of 0.142, 0.142, 0.259, and 0.999, respectively. Similarly, days to 50% flowering showed significant positive correlations with plant height, panicle length, and grain number per panicle, aligning with earlier findings by Bhadru *et al.* (2012)^[5] and Ravinder Babu *et al.* (2012)^[40].

The trait plant height was positively correlated with panicle length, test weight, panicle weight, days to heading, and days to flowering, consistent with reports by Ravinder Babu *et al.* (2012)^[40] and Soni *et al.* (2013)^[44]. Panicle length showed significant positive correlations with test weight, per-day productivity, and overall yield, as documented by Nandan *et al.* (2010)^[27]. Additionally, the number of productive tillers was positively related to per-day productivity and single plant yield, indicating their importance in yield optimization.

Path coefficient analysis revealed the magnitude and direction of direct and indirect effects of traits on grain yield. Per day productivity exhibited the highest positive direct effect (+0.994) on single plant yield, underscoring its importance as a key determinant of productivity. Traits such as days to 50% flowering and spikelet fertility also contributed positively through direct effects (+0.176 and +0.021, respectively). Conversely, traits like days to heading and plant height showed negative direct effects, indicating their complex indirect relationships with yield via other traits. Notably, the network of indirect effects highlighted the significance of traits like panicle length, panicle weight, and test weight, which mediated effects on yield through various pathways, echoing findings by Ravi *et al.* (2014)^[39] and Srijan *et al.* (2016)^[45].

The correlation matrix was visualized using heatmaps, illustrating the strength and significance of trait associations. The path analysis provided a clearer understanding of the causal relationships and prioritized traits for selection strategies. Traits with strong positive direct effects, such as per day productivity and spikelet fertility, emerged as prime targets for breeding programs aiming to enhance grain yield. Traits with negative or weak direct effects could be selectively improved indirectly through correlated traits with positive influences.

Results and Discussions

Correlation analysis provides valuable insights into the relationships between yield-related traits and grain yield, allowing breeders to identify important traits for selection to improve productivity. In the present study, the trait single plant yield exhibited positive and significant correlations with several key agronomic traits. Notably, single plant yield was positively associated with panicle length (correlation coefficient, $r = 0.1422$), number of productive tillers ($r = 0.1418$), test weight ($r = 0.2588$), and per day productivity ($r = 0.9999$). These correlations indicate that increases in these traits tend to be accompanied by increases

in grain yield, suggesting their critical role in yield determination.

Days to 50% flowering, an important phenological trait, showed positive significant associations with plant height ($r = 0.1789$), panicle length ($r = 0.127$), and total grains per panicle ($r = 0.1397$). These findings suggest that lines with later flowering tend to exhibit taller plants, longer panicles, and produce more grains, reflecting coordinated developmental patterns conducive to yield improvement. Similar relationships have been reported by earlier researchers such as Bhadru *et al.* (2012)^[5] and Ravinder Babu *et al.* (2012)^[40] for plant height, Sathish *et al.* and Srijan *et al.* (2016)^[45] for panicle length, and Eswara Reddy *et al.* (2013)^[12] and Rao *et al.* (2014)^[36] for grain number per panicle, confirming the consistency of these trait associations across rice genetic backgrounds.

Plant height itself showed strong positive and significant correlations with several traits including panicle length ($r = 0.3948$), test weight ($r = 0.1914$), panicle weight ($r = 0.1359$), days to heading ($r = 0.1834$), and days to 50% flowering ($r = 0.1798$). This suggests that taller plants tend to produce longer panicles with heavier grains and generally mature later. These results are in line with reports from Ravinder Babu *et al.* (2012)^[40] and Eswara Reddy *et al.* (2013)^[12] regarding panicle length, and Soni *et al.* (2013)^[44] and Mishra *et al.* (2014)^[24] regarding test weight, as well as Anis *et al.* (2016)^[1] and Rajendra Prasad *et al.* (2017)^[34] for panicle weight associations. The substantial positive association of plant height with yield-contributing traits underscores its potential as a key morphological trait in selection strategies.

Panicle length also demonstrated strong positive associations with test weight ($r = 0.1794$), per day productivity ($r = 0.1422$), and single plant yield ($r = 0.1422$). Positive associations were further observed between panicle length and days to heading ($r = 0.1258$), days to 50% flowering ($r = 0.127$), and plant height ($r = 0.3948$). These observations align with findings by Nandan *et al.* (2010)^[27], suggesting the importance of panicle traits in enhancing yield through their contribution to grain filling and productivity.

The number of productive tillers, directly influencing the number of panicles per plant, displayed positive significant relationships with per day productivity ($r = 0.1418$) and single plant yield ($r = 0.1418$). This indicates that genotypes with more productive tillers tend to have higher daily biomass accumulation and grain yield, factors critical for yield improvement. The total grains per panicle, another crucial yield component, showed positive significant correlations with spikelet fertility ($r = 0.1388$), panicle weight ($r = 0.1502$), days to heading ($r = 0.1343$), and days to 50% flowering ($r = 0.1397$). Supporting these findings, Mishra *et al.* (2014)^[24] and Naseer *et al.* (2015)^[49] documented similar positive relationships involving spikelet fertility.

Test weight is a direct indicator of grain size and weight, in turn exhibited positive significant correlations with panicle weight ($r = 0.2445$), per day productivity ($r = 0.2588$), single plant yield ($r = 0.2588$), plant height ($r = 0.1914$), and panicle length ($r = 0.1794$). The trait panicle weight correlated positively with plant height ($r = 0.1359$) and total grains per panicle ($r = 0.1502$), consistent with the results of Nandeshwar *et al.* (2010)^[28] and Ranwake and Amarasighe (2014). Per day productivity also showed strong positive

significant correlations with panicle length ($r = 0.1422$), number of productive tillers ($r = 0.1418$), test weight ($r = 0.2588$), and single plant yield ($r = 0.9999$), emphasizing the integrated nature of these yield components.

Path Analysis

Path analysis extends beyond correlation by partitioning the observed correlations between traits and yield into direct and indirect effects, clarifying the causal relationships among traits. This analytical approach is especially valuable in rice breeding, where numerous yield-contributing traits interact in complex ways. By quantifying these effects, breeders can focus on traits that directly elevate grain yield rather than those that are merely correlated indirectly.

In this study, days to heading exhibited a notable negative direct effect on single plant yield (path coefficient = -0.1530). Additionally, it showed negative indirect effects through plant height (-0.0019), total grains per panicle (-0.0002), spikelet fertility (-0.0002), test weight (-0.0011), and per day productivity (-0.0030). However, some low positive indirect effects were observed via days to 50% flowering (0.1753), panicle length (0.0008), number of productive tillers (0.0002), and panicle weight (0.0012). These complex interactions suggest that while days to heading negatively impacts yield directly, favorable influences via other traits partially compensate for this effect.

Days to 50% flowering positively influenced yield directly with a path coefficient of 0.1755 . Negative indirect effects through days to heading (-0.1528), plant height (-0.0019), total grains per panicle (-0.0002), spikelet fertility (-0.0001), and test weight (-0.0010) were observed, balanced by low positive indirect effects through panicle length (0.0008), number of productive tillers (0.0001), panicle weight (0.0012), and per day productivity (0.0078). This pattern concurs with findings from Golam *et al.* (2015)^[16] and Rajendra Prasad *et al.* (2017)^[34] regarding the influence of flowering time and yield components.

Plant height showed a slight negative direct effect (-0.0095) on yield alongside negative indirect effects through plant height (-0.0306), spikelet fertility (-0.0029), panicle weight (-0.0020), and per day productivity (-0.0047). On the contrary, it had positive indirect effects through days to 50% flowering (0.0347), panicle length (0.0021), number of productive tillers (0.0021), and test weight (0.0015), reflecting multifaceted influences on yield. Similar trends were reported by Kiranmayee *et al.* (2018)^[19], Satturu *et al.* (2023), Pandey *et al.* (2012)^[30], and Ratna *et al.* (2015)^[38].

Panicle length contributed a small positive direct effect (0.0043) to grain yield, with negative indirect effects via days to heading (-0.0266), plant height (-0.0047), and spikelet fertility (-0.0028), but substantial positive indirect effects through days to 50% flowering (0.0313), productive tillers (0.0003), test weight (0.0021), panicle weight (0.0002), and per day productivity (0.2059). This underscores the importance of panicle length, especially through its impact on productivity pathways, supporting observations by Ravi *et al.* (2014)^[39] and Srijan *et al.* (2016)^[45].

Number of productive tillers had a small negative direct effect (-0.0069) but exerted positive indirect effects through days to heading (0.0036), plant height (0.0029), total grains per panicle (0.0003), panicle weight (0.0046), and per day productivity (0.0449). This indicates that selection focused on indirectly enhancing these related traits may improve

overall yield. These results align with Rahman *et al.* (2014), Ratna *et al.* (2015)^[38], and Rajendra Prasad *et al.* (2017)^[34]. Total grains per panicle showed a slight negative direct effect (-0.0010) but positive indirect effects via days to 50% flowering (0.0277), spikelet fertility (0.0077), and per day productivity (0.1122). This suggests its substantial contribution to yield is mainly mediated through these pathways, consistent with findings by Patel *et al.* (2014) and Ganapati *et al.* (2014)^[31, 15].

Spikelet fertility exhibited a positive direct effect (0.0205) alongside minor negative indirect effects on yield. Its strong positive indirect effect through per day productivity (0.1496) highlights its importance, particularly via its role in grain filling and seed set.

Test weight had a positive direct effect (0.0070) on single plant yield, with considerable positive indirect effects through per day productivity (0.3621), days to heading (0.0233), and panicle length (0.0013). The overall contribution of test weight underscores its importance as a selection criterion, reinforcing observations of Rajamadhan *et al.* (2011)^[33] and Ratna *et al.* (2015)^[38].

Panicle weight exhibited a negative direct effect (-0.0075) but exerted positive indirect effects through days to heading (0.0238), number of productive tillers (0.0042), spikelet fertility (0.0002), and per day productivity (0.0497), indicating that indirect enhancement of associated traits could improve this component's contribution to yield.

Most notably, per day productivity had the strongest positive direct effect on grain yield (0.9939), dominating both the direct and indirect influences. Its central role as a driver of productivity highlights it as a prime target in breeding programs.

Conclusion

The comprehensive correlation analysis conducted in this study underscores the fundamental role of trait interrelationships in guiding effective selection strategies for rice breeding programs. By systematically examining associations among 11 key agronomic and yield-related traits across 129 diverse rice genotypes, significant positive correlations emerged between single plant yield and critical components such as panicle length ($r = 0.1422$), number of productive tillers ($r = 0.1418$), test weight ($r = 0.2588$), and per day productivity ($r = 0.9999$). These robust linkages highlight the potential of these traits as reliable indicators for yield enhancement, enabling breeders to focus selection efforts on genotypes exhibiting superior performance in these attributes (Bhadru *et al.*, 2012; Srijan *et al.*, 2016)^[8, 45].

Furthermore, phenological traits like days to 50% flowering demonstrated strong positive associations with morphological characteristics including plant height ($r = 0.1789$), panicle length ($r = 0.127$), and total grains per panicle ($r = 0.1397$), alongside panicle weight. This interconnectedness reveals how developmental timing influences reproductive architecture and grain filling efficiency, contributing to overall productivity. Such patterns align closely with observations from prior

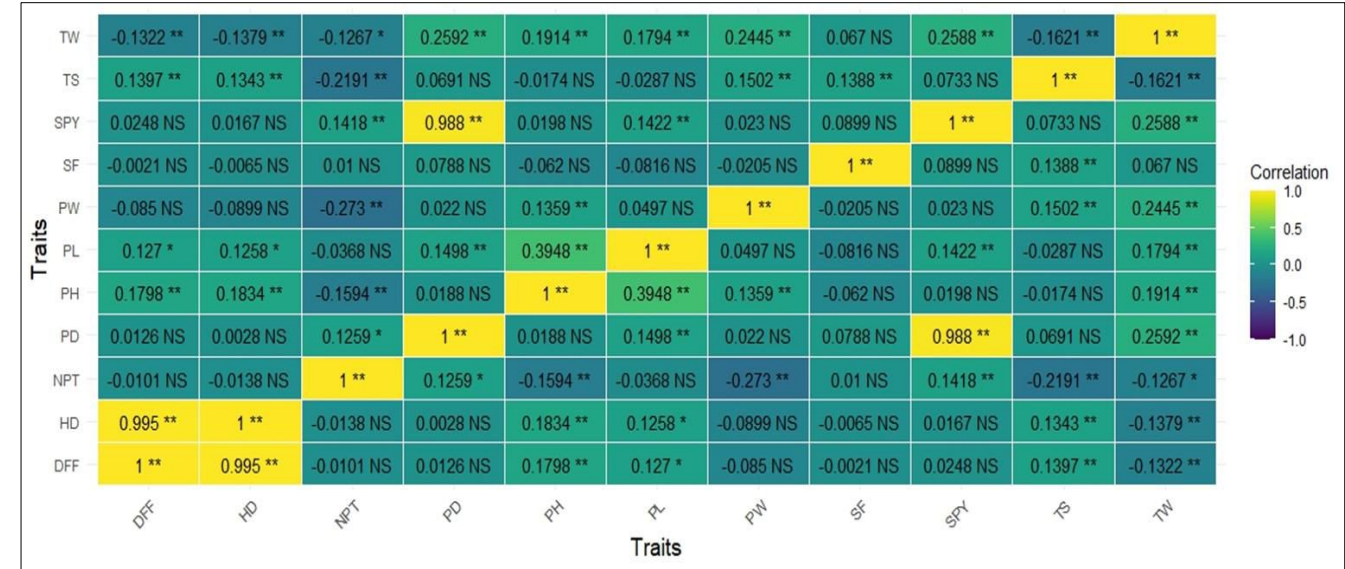
investigations across varied rice germplasm, confirming the stability of these relationships under different genetic and environmental contexts (Ravinder Babu *et al.*, 2012; Eswara Reddy *et al.*, 2013)^[40, 12]. This consistency validates the integration of multi-trait correlation frameworks into breeding pipelines, particularly for developing ideotypes that balance yield potential with optimal plant architecture, maturity duration, and biomass partitioning.

The synergistic clustering observed among panicle length, test weight, and productive tillers not only their individual correlations with yield but also mutual associations presents a valuable trait constellation for exploitative breeding. Selection targeting this complex could amplify genetic gains through pleiotropic and linkage effects, indirectly optimizing plant stature and resource allocation for higher harvest index (Nandan *et al.*, 2010; Mishra *et al.*, 2014)^[27, 24]. These interdependencies offer a strategic blueprint for ideotype design, where simultaneous improvement of correlated traits maximizes yield stability and adaptability.

Path coefficient analysis provided deeper mechanistic insights, partitioning correlations into direct and indirect effects to reveal causal hierarchies influencing single plant yield. Per day productivity exerted the most dominant positive direct effect (0.9939), positioning it as the primary yield driver and a paramount selection criterion in restorer line development. Complementary positive direct contributions came from days to 50% flowering (0.1755) and spikelet fertility (0.0205), which enhance reproductive efficiency and seed set. In contrast, traits like days to heading (-0.1530), plant height (-0.0095), and panicle weight (-0.0075) displayed negative direct effects, yet achieved net positive contributions through potent indirect pathways predominantly via per day productivity, days to 50% flowering, and test weight (Dewey & Lu, 1959; Ravi *et al.*, 2014)^[39].

For instance, panicle length's modest direct effect (0.0043) was substantially amplified by indirect influences through per day productivity (0.2059) and days to 50% flowering (0.0313), underscoring its role as a secondary but valuable mediator. Similarly, test weight and spikelet fertility bolstered yield indirectly, emphasizing the multifaceted nature of yield determination where no single trait operates in isolation (Rajendra Prasad *et al.*, 2017; Kiranmayee *et al.*, 2018)^[34, 19]. These findings illuminate the complexity of gene-trait interactions, advocating for holistic selection indices over univariate approaches.

In summary, this investigation affirms the efficacy of combined correlation and path analyses for dissecting yield architecture in promising restorer lines, identifying per day productivity, test weight, and productive tillers as cornerstone targets for hybrid rice improvement. The revealed trait networks provide actionable intelligence for breeders, facilitating the development of high-yielding hybrids with balanced agronomics. Future research should validate these associations across multi-location trials and incorporate genomic tools like GWAS to uncover underlying QTLs, accelerating marker-assisted selection for sustainable rice productivity (Sharma *et al.*, 2021)^[43].



Significance at 5% level (P <= 0.05); **Significance at 1% level ** P <= 0.01. d.f- Degrees of freedom, HD-Days to Heading, DFF-days to 50 percent Flowering, PH- Plant Height (cm), PL-Panicle Length(cm), NT- Number of Tillers, NPT- Number of productive Tillers, TS- Total grains per panicle, SF-Spikelet Fertility (%), TW-Thousand grain weight (g), SPY- Single Plant Yield (g), PDP-Per Day Productivity.

Fig 1: Correlation analysis of the 129 genotypes studied during Kharif, 2024 and Rabi,2024-2025

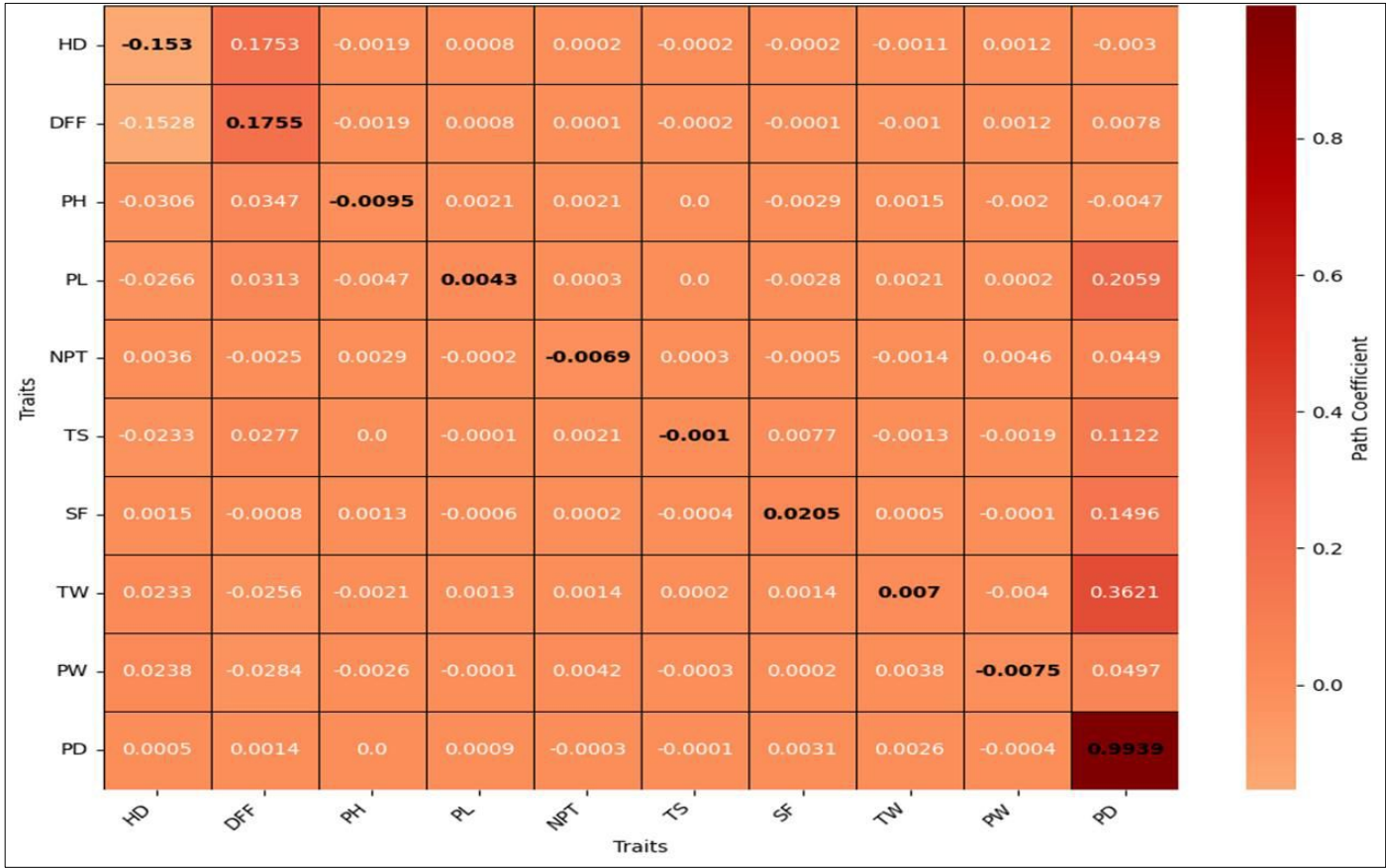


Fig 2: Path coefficient analysis of the 129 genotypes studied during Kharif, 2024 and Rabi,2024-2025

Table 1: Direct and Indirect Effects of Yield-Related Traits on Single Plant Yield (Path Coefficient Analysis)

Trait	Direct Effect	Major Indirect Pathways	Total Effect Interpretation
Per day productivity	+0.9939	Minor indirect negative effects through tillers, grains, weight	Dominant positive impact
Days to 50% flowering	+0.1755	Indirect via panicle length, productive tillers, productivity	Positive overall
Spikelet fertility	+0.0205	Indirect via fertility and productivity	Positive contribution
Test weight	+0.0070	Indirect via productivity, heading, panicle length	Positive influence

Panicle length	+0.0043	Strong indirect via productivity and flowering	Moderate positive effect
Days to heading	-0.1530	Mixed indirect positive via flowering but negative via others	Overall negative direct effect
Plant height	-0.0095	Indirect via flowering and tillers positively	Weak negative direct effect
Number of productive tillers	-0.0069	Indirect via productivity and panicle weight	Minor negative direct effect
Total grains per panicle	-0.0010	Indirect via fertility and productivity	Slightly negative direct effect
Panicle weight	-0.0075	Positive indirect through heading, tillers	Small negative direct effect

Figure 1: Heatmap showing phenotypic correlations among 11 yield-related traits in 129 rice genotypes evaluated during Kharif 2024 and Rabi 2024-2025. Positive correlations are indicated in red shades and negative correlations in blue. Values are correlation coefficients with significance levels indicated.

Figure 2: Path diagram illustrating direct (solid arrows) and indirect (dashed arrows) effects of yield-related traits on single plant yield. Arrow thickness corresponds to the magnitude of effects derived from path coefficient analysis, highlighting the dominant role of per day productivity and the complex indirect interactions among other traits.

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