PLANT SCIENCE TODAY
ISSN 2348-1900 (online)
Vol x(x): xx–xx
https://doi.org/10.14719/pst.6659

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RESEARCH ARTICLE

Genetic variability and yield trait associations in F2 populations of traditional rice (*Oryza sativa* L.) varieties

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ARTICLE HISTORY

Received: 11 December 2024
Accepted: 15 January 2025

Available online
Version 1.0 : 03 April 2025

Check for updates

Additional information

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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Prapakaran M, Pushpam R, John Joel A, Manonmani S, Uma D, Sritharan N, Suresh R. Genetic variability and yield trait associations in F2 populations of traditional rice (*Oryza sativa* L.) varieties. Plant Science Today (Early Access). https://doi.org/10.14719/pst.6659

Abstract

Analyzing genetic variability and trait correlations is essential for designing effective breeding programs and improving crop characteristics. This study aimed to estimate variability parameters, heritability, genetic advance, skewness, kurtosis, associations, and path coefficients for 13 traits in the F_2 population derived from the crosses CO 54 × IC 378202 and CO 54 × IC 467496. The cross CO 54 × IC 378202 cross exhibited notable panicle weight with high Genotypic Coefficients of Variation (GCV) (35.94) and Phenotypic Coefficients of Variation (PCV) (36.40), elevated Heritability (H^2) (97.48), significant Genetic Advance as a Percentage of Mean (GAM) (73.10), and positive skewness (0.52). Similarly, the CO 54 × IC 467496 cross demonstrated exceptional total tillers per plant, characterized by high Genotypic Coefficients of Variation (33.63) and Phenotypic Coefficients of Variation (35.25), substantial Heritability (90.99), notable Genetic Advance as a Percentage of Mean (66.08), and pronounced positive skewness (0.67). In the CO 54 × IC 378202 cross, panicle weight, displayed significant positive correlations (0.641) and direct positive effects (0.2370) on grain yield per plant. Similarly, the CO 54 × IC 467496 cross grains per panicle exhibited strong positive correlations (0.383) and direct effects (0.5360) on grain yield. These findings underscore the significance of panicle weight and grain number per panicle, key determinants of grain yield, as prime targets for selection in rice breeding programs. The observed predominance of additive gene action for these traits suggests their amenability to improvement through pure line selection. By prioritizing these traits, breeders can develop high-yielding rice cultivars, thereby enhancing agricultural productivity and contributing to global food security endeavors.

Keywords

correlation; F2 population; genetic advance; heritability; rice; variability

Introduction

Rice is a crucial source of sustenance for nearly 70% of the global population and serves as the primary livelihood for approximately 120 to 150 million people in rural areas (1). The increasing global demand for rice is closely associated with the rising population, particularly in Asia, where rice is a fundamental dietary staple for over half of the world's population. Currently, global rice production stands at about 759.6 million tonnes, with India contributing significantly at around 172.58 million tonnes. An individual in India consumes about 103 kg of rice annually. However, projections indicate that the population in India could reach 1.824 billion by 2050, which poses a notable threat to current rice production levels. To meet this growing demand, it is estimated that rice yields must increase from the current output of 37 million hectares to approximately 137 million tonnes by 2050, necessitating a yield enhancement of nearly 50% over the next three decades to ensure food security (1). This challenge highlights the indispensable role of rice breeders in securing future food supplies, especially given the stagnation observed in both rice production and productivity trends (2). There is an urgent need for rice varieties that demonstrate higher productivity and possess favorable agronomic traits to overcome yield barriers. The foundation for advancing these yield improvements lies in genetic diversity and the implementation of effective selection strategies, as emphasized by (3). Addressing these challenges will be essential for maintaining food security and supporting the livelihoods of millions dependent on rice cultivation.

Genetic diversity is paramount for crop adaptation to climate change and yield enhancement under abiotic stress. Traditional rice varieties, or landraces, exhibit significantly greater genetic diversity than modern cultivars. Landraces constitute a treasure trove of adaptable genes, providing a rich source of traits for breeding climate-resilient cultivars. High genetic variability equips crops to withstand environmental challenges like drought, salinity, and temperature extremes. By leveraging stress tolerance traits, breeders can cultivate climate-resilient crops. Moreover, variability in yield-related traits facilitates the development of high-yielding varieties that maintain productivity under stress, ensuring food security amidst global climate challenges. Genetic variation presents significant opportunities for integrating favorable alleles aimed at achieving desired improvements in rice cultivation (4). The (GCV) is a crucial metric that quantifies the extent of genetic variability within a population, reflecting the heritable component of this variability. Heritability serves as a key indicator of trait inheritance from parents to offspring, providing insights into the potential for traits to be passed down through generations (5). Genetic advance is another important parameter that indicates the expected improvement in traits following selection within a population (6). When expressed as a percentage of the mean, genetic advancement offers a clearer perspective on the potential gains achievable through selective breeding. Kurtosis and skewness are statistical measures that enhance our understanding of genetic effects and the distribution of genes associated with specific traits (7). Association analysis plays a vital role in identifying traits that exhibit positive or negative correlations with yield, which can inform breeding strategies aimed at optimizing plant stature. Furthermore, correlation and path analysis provide deeper insights into the relationships between various traits, aiding in the formulation of effective breeding techniques to develop superior rice varieties. Collectively, these genetic parameters are essential for advancing rice breeding programs and improving overall crop productivity.

Traditional rice varieties, or landraces, exhibit a high degree of genetic heterogeneity compared to modern cultivars. While these landraces are a valuable source of genes that confer adaptability, they often yield poorly. Consequently, there is a pressing need for varietal improvement in these traditional strains. To establish a sustainable breeding program, it is essential to have precise knowledge of genetic divergence concerning yield components, as successful varietal enhancement primarily relies on selecting parents with substantial genetic divergence during hybridization. The effective utilization of F_2 segregating populations has facilitated specific trait improvements by fixing desirable trait combinations. The current study aims to estimate the variability, heritability, and genetic advance as a percentage of the mean for grain yield and its components in the F_2 segregating generation derived from two selected crosses. Additionally, it seeks to analyze the frequency distribution patterns based on skewness and kurtosis. Understanding these genetic parameters is indispensable for enhancing breeding strategies and improving rice yield traits.

Materials and Methods

The study was carried out in a non-replicated design at the time of the *Kharif* season of 2024 at the research farm of the Tamil Nadu Rice Research Station, located in Aduthurai, Thanjavur. The experimental material comprised the F_2 generation of two cross combinations: CO 54 × IC 378202 and CO 54 × IC 467496, developed using traditional rice varieties. The F_2 generation is the preferred choice for genetic studies due to its inherent diversity and segregating nature, arising from the self-pollination of the F_1 hybrid. This generation exhibits a broad spectrum of genetic variability, a consequence of independent assortment and recombination of alleles inherited from the parental lines. The F_2 population comprises a mosaic of homozygous and heterozygous genotypes, providing an ideal platform for investigating the inheritance patterns of traits. Unlike the F_1 generation, the F_2 generation facilitates the expression of recessive traits, enabling the study of their phenotypic influence. The variability inherent within the F_2 generation is particularly advantageous for studying complex traits governed by multiple genes, such as yield, and stress tolerance. This high degree of variability within the F_2 generation serves as a foundation for the selection of superior genotypes possessing desirable traits for subsequent breeding programs. Genetically pure seeds of CO 54, IC 378202, and IC 467496 were obtained, and the parental seeds were cultivated to facilitate crossing between these varieties. The resulting hybrid seeds were used to establish the F_1 generation. Individual plants from the F_1 generation were harvested and advanced to produce the F_2 generation. The F_2 seeds of the two cross combinations were sown in a nursery alongside the parental lines. After 25 days, the seedlings were transplanted into the main field, with one seedling planted per hill. A total of 400 segregating plants were grown in the F_2 generation, maintaining a spacing of 20 × 20 cm, while adhering to appropriate agronomic practices.

Observations were recorded from 300 randomly selected plants in the F_2 population. Selecting 300 plants from the F_2 population ensures a balance between maximizing sample size and maintaining practical feasibility. This selection captures 75% of the population, representing genetic diversity while minimizing the exclusion of rare phenotypes. It provides sufficient statistical power to detect significant trait variations and ensures accurate estimates of heritability and genetic advancement. Although analyzing all 400 plants might enhance precision, resource constraints make 300 a manageable yet reliable choice, reducing standard errors and improving result validity. For each parent, a total of 20 plants were grown, and data were gathered from 10 randomly chosen plants. 13 traits were evaluated in the individual F_2 plants, including days to 50% flowering (DFF), days to maturity (DM), plant height (cm) (PH), total tillers per plant (TTP), effective tillers per plant (ETP), flag leaf length (cm) (FL), flag leaf breadth (cm) (FB), panicle length (cm) (PL), panicle weight (g) (PW), grains per panicle (GPP), spikelet fertility (%) (SF), test weight (g) (TW), and grain yield per plant (g) (GYP).

Statistical analysis

The genotypic coefficient of variation (GCV) and phenotypic coefficient of variation (PCV) were enumerated following the method recommended by (8). The variations were categorized into three ranges: low (< 10%), moderate (10–20%), and high (> 20%), as described by (9). Since segregants were not evaluated in replicated trials, environmental variance was estimated using data from parents grown in replicated trials. Broad-sense heritability was enumerated using the formula proposed by (10) and classified into high (> 60%), moderate (30–60%), and low (0–30%) categories. Skewness (third-order statistics) and kurtosis (fourth-order statistics) were estimated following the approach outlined by (11) to examine the distribution patterns of 13 quantitative traits in the F_2 population. Genetic advance as a percentage of the mean (GAM) was calculated using the method delineated by (12), with classifications of low (< 10%), moderate (10–20%), and high (> 20%).

The association between yield and its integrant traits, together with relationships among other traits, was analyzed using the formula provided by (13). Path analysis was performed using the procedure outlined by (14). Statistical analyses were generated using TNAUSTAT software, while the association plots were generated using R software version 1.4.1717. SPSS 16.0 software was employed to create histograms illustrating the frequency distribution of the studied traits. The selection of SPSS and TNAUSTAT for correlation and path analyses is justified by their distinctive strengths, ease of use, and efficacy in managing agricultural data. SPSS offers a user-friendly interface, comprehensive statistical methodologies, and customizable graphical outputs, rendering it an excellent choice for researchers. TNAUSTAT, tailored for agricultural research, boasts optimized algorithms for plant breeding and crop improvement, yielding detailed outputs aligned with breeding research requirements.

Results and Discussion

The potential of a cross in plant breeding is assessed not only by its average performance but also by the degree of variability it exhibits. Understanding both the nature and extent of genotypic and phenotypic variability in crop species is crucial for developing effective breeding programs (3). Attention should be given to the magnitude of genotypic and phenotypic coefficients of variability, particularly in early segregating generations (9). Furthermore, another study proposed that crosses that achieve early homozygosity are optimal for subsequent breeding efforts (15). The means, ranges, and variability estimates including the (GCV), (PCV), heritability (broad sense), and (GAM) are presented in (Tables 1 and 2) for each cross separately. The variability observed across all the studied traits was considerable. Analysis of the segregating populations indicated that the PCV was consistently slightly higher than the GCV across all traits examined in both crosses, highlighting the influence of environmental factors on trait expression (Tables 1 and 2). Traits such as TTP, ETP, GPP, FL, PW, GYP, and TW exhibited high GCV alongside high PCV in both crosses, corroborating findings by other studies (2,16).

Table 1. Genetic variability parameters of different biometrical traits in F_2 generation of CO 54 × IC 378202

	Mean	Max	Min	PCV	GCV	h^2	GAM	Skewness	Kurtosis
DFF	103.22	136.00	80.00	11.42	11.40	99.55	23.43	0.23	-0.70*
DM	132.00	165.00	108.00	9.73	9.67	98.96	19.83	0.24	-0.77*
PH	124.80	186.00	54.00	20.65	20.32	96.84	41.20	-0.01	-0.43
TTP	17.95	42.00	7.00	35.70	34.44	93.06	68.44	0.72*	0.28
ETP	15.97	34.00	6.00	34.04	32.46	90.93	63.76	0.68*	0.00
FL	32.38	59.00	14.00	27.67	25.12	82.42	46.98	0.34*	-0.23
FB	1.09	1.70	0.60	17.95	13.98	60.65	22.42	-0.17	-0.11
PL	24.33	32.00	15.00	15.63	14.35	84.34	27.15	-0.29*	-0.61*
PW	2.49	4.93	1.01	36.40	35.94	97.48	73.10	0.52*	-0.40
GPP	91.12	176.00	34.00	31.05	26.62	73.48	47.01	0.53*	0.00
SF	81.45	98.65	43.75	12.25	11.97	95.54	24.10	-1.10*	1.38*
GYP	29.29	45.34	10.72	28.51	27.97	96.26	56.53	-0.47*	-0.58*
TW	25.81	35.87	11.00	24.94	24.54	96.84	49.74	-0.44*	-0.63*

*****Significant at 5 % and ****** Significant at 1 %level.

Table 2. Genetic variability parameters of different biometrical traits in F_2 generation of CO 54 × IC 467496

	Mean	Max	Min	PCV	GCV	h^2	GAM	Skewness	Kurtosis
DFF	106.85	133.00	84.00	8.79	8.78	99.73	18.06	0.20	-0.62*
DM	136.90	165.00	111.00	7.77	7.72	98.75	15.81	0.06	-0.62*
PH	134.71	192.00	77.50	17.82	17.62	97.74	35.87	-0.09	-0.53
TTP	15.95	39.00	5.00	35.25	33.63	90.99	66.08	0.67*	0.76*
ETP	14.30	31.00	5.00	31.15	29.01	86.70	55.64	0.61*	0.52
FL	43.79	77.40	12.50	29.23	28.33	93.93	56.55	0.20	-0.79*
FB	1.05	1.50	0.60	16.09	12.33	58.68	19.45	0.07	-0.43
PL	24.57	33.00	16.00	13.98	12.79	83.60	24.08	-0.25	-0.57*
PW	2.53	5.09	1.03	32.44	32.09	97.83	65.39	0.57*	0.11
GPP	110.25	205.00	38.00	28.38	25.24	79.09	46.23	0.19	-0.21
SF	85.95	98.37	44.17	11.17	10.81	93.73	21.57	-1.76*	3.62*
GYP	27.64	39.75	11.20	26.31	25.07	90.79	49.21	-0.46*	-0.59*
TW	22.54	33.81	11.26	21.87	21.01	92.29	41.59	0.24	-0.37

*Significant at 5 % and ** Significant at 1 % level. **DFF** = days to 50% flowering, **DM** = days to maturity, **PH** = plant height (cm), **TTP** = total tillers per plant, **ETP** = effective tillers per plant, **FL**= flag leaf length (cm), **FB** = flag leaf breadth (cm), **PL** = panicle length (cm), **PW** = panicle weight (g), **GPP** = grains per panicle, **SF**= spikelet fertility (%), **TW**= test weight (g), **GYP** = grain yield per plant (g).

Traits like effective tillers and panicle weight exhibit high heritability and GAM due to their strong genetic regulation and minimal environmental impact, making them ideal for selection in breeding programs. Effective tillers, governed by additive gene effects, significantly impact grain yield by increasing panicle numbers and optimizing resource use. Similarly, panicle weight, a key yield component reflecting grain capacity, integrates grain number and size, with high GAM indicating substantial improvement potential. Enhancing these traits ensures greater productivity, better harvest indices, and superior grain quality, supporting yield stability under diverse conditions

In the cross-combination CO 54 × IC 378202, low (GCV) and (PCV) were observed for DM. Conversely, moderate GCV and PCV were noted for traits such as DFF, PH, FB, PL, and SF indicating moderate variability in these characteristics. For the cross CO 54 × IC 467496, low values of both (GCV) and (PCV) were observed for traits like DFF and DM. In contrast, traits such as PH, FB, PL, and SF exhibited moderate GCV and PCV, indicating a moderate level of variability in these traits. These findings align with the observations reported (17,18). In the cross-combination CO 54 × IC 378202, all traits under investigation exhibited high heritability. Similarly, CO 54 × IC 467496 showed high heritability for all traits, except FB (Tables 1 and 2). These findings align with the observations reported by several researchers (16,19). Additionally, a high range of heritability coupled with a higher (GAM) was recorded for all traits, except DM in CO 54 × IC 378202, and DFF, DM, and FB in CO 54 × IC 467496 suggest the presence of cumulative gene effects, indicating that targeted selection strategies could effectively enhance the advancement of these traits. This aligns with the observations of other studies (16). A moderate level of (GAM) with high heritability was observed for DM in the cross of CO 54 x IC 378202. Additionally, this was also noted for DFF, DM, besides FB in the cross of CO 54 x IC 467496, which aligns with the findings of (19). High heritability accompanied by a low GAM indicates the predominance of non-additive genetic effects. This suggests that selecting for such traits may not achieve substantial genetic improvement.

The genetic architecture of complex, heritable traits like spikelet fertility and test weight is characterized by polygenic control, involving multiple loci with subtle, additive effects, epistatic interactions, and pleiotropic influences. Genomic interplay, environmental factors, and spontaneous mutations collectively govern phenotypic variation, Traits exhibiting high heritability are characterized by robust genetic control, consistent quantitative trait loci (QTL) effects, and minimal environmental influence, rendering them amenable to significant improvement through selective breeding programs The frequency distribution patterns of 13 quantitative traits, analyzed through skewness and kurtosis as illustrated in (Fig. 1 and 2), revealed a pronounced positively skewed leptokurtic distribution for the (TTP) in the cross CO 54 x IC 378202, as well as for TTP, ETP, PW in the cross CO 54 x IC 467496. Conversely, a significantly negatively skewed leptokurtic distribution was observed for SF traits in both CO 54 x IC 378202 and CO 54 x IC 467496, corroborating the findings (20,21).

The trait of SF seems to be regulated by a limited number of segregating genes, with most demonstrating a diminishing effect and exhibiting dominance-based complementary gene interactions. This is supported by the leptokurtic and significantly negatively skewed distribution observed in the populations of CO 54 x IC 378202 and CO 54 x IC 467496. Significant negative skewness and a platykurtic distribution were observed for PL, GYP, and TW in the cross CO 54 x IC 378202 and for GYP in CO 54 x IC 467496. This suggests the potential presence of dominance and dominance-based duplicate epistasis, indicating that multiple genes govern these traits. The occurrence of transgressive segregants, resulting from the accumulation of favorable alleles across various studied traits,

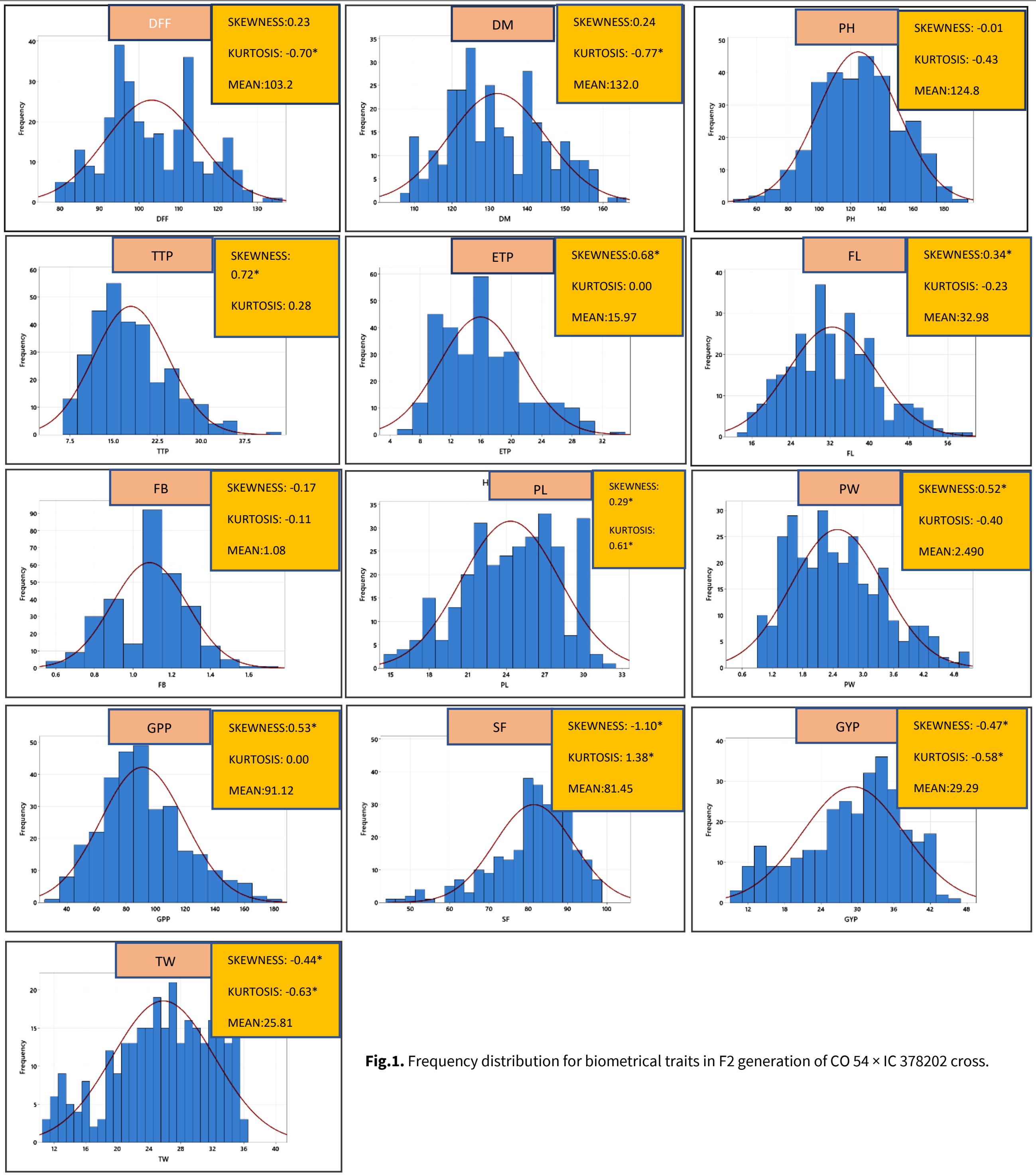


Fig.1. Frequency distribution for biometrical traits in F2 generation of CO 54 × IC 378202 cross.

provides an opportunity for selecting individuals at both extremes of the phenotypic spectrum.

Given the complexity of yield as a quantitative trait, improving yield should involve indirect selection of associated traits, which can be effectively achieved through association studies. These analyses were conducted to explore the relationships among various traits and their contributions to yield. Since focusing on a single trait may directly or indirectly affect the performance of other traits especially in the case of the complex trait of yield direct selection is often less effective. The findings from the correlation analysis are summarized in (Tables 3 and 4) In this study, association analysis revealed that GYP exhibited a significant positive correlation with several traits, including PL, PW, PH, TTP, ETP, FL, FB, GPP, and TW in the cross CO 54 x IC 378202 (Fig. 3).

Similarly, in the cross CO 54 x IC 467496, GYP also showed a significant positive correlation with PL, PW, PH, TTP, ETP, FL, SF, GPP, and, TW (Fig. 4). Similar findings were reported by several studies regarding PL and the GPP (18,20), while (22) observed comparable results for ETP. In the F_2 population resulting from the cross CO 54 x IC 378202, DFF demonstrated a highly significant positive correlation with several traits, including PH, FL, FB, DM, PL, PW, GPP, GYP, and TW. Additionally, it showed a highly significant negative correlation with both TTP, ETP, and SF (Fig. 3). In the cross CO 54 x IC 467496, DFF also exhibited a highly significant positive correlation with PH, FL, DM, PL,

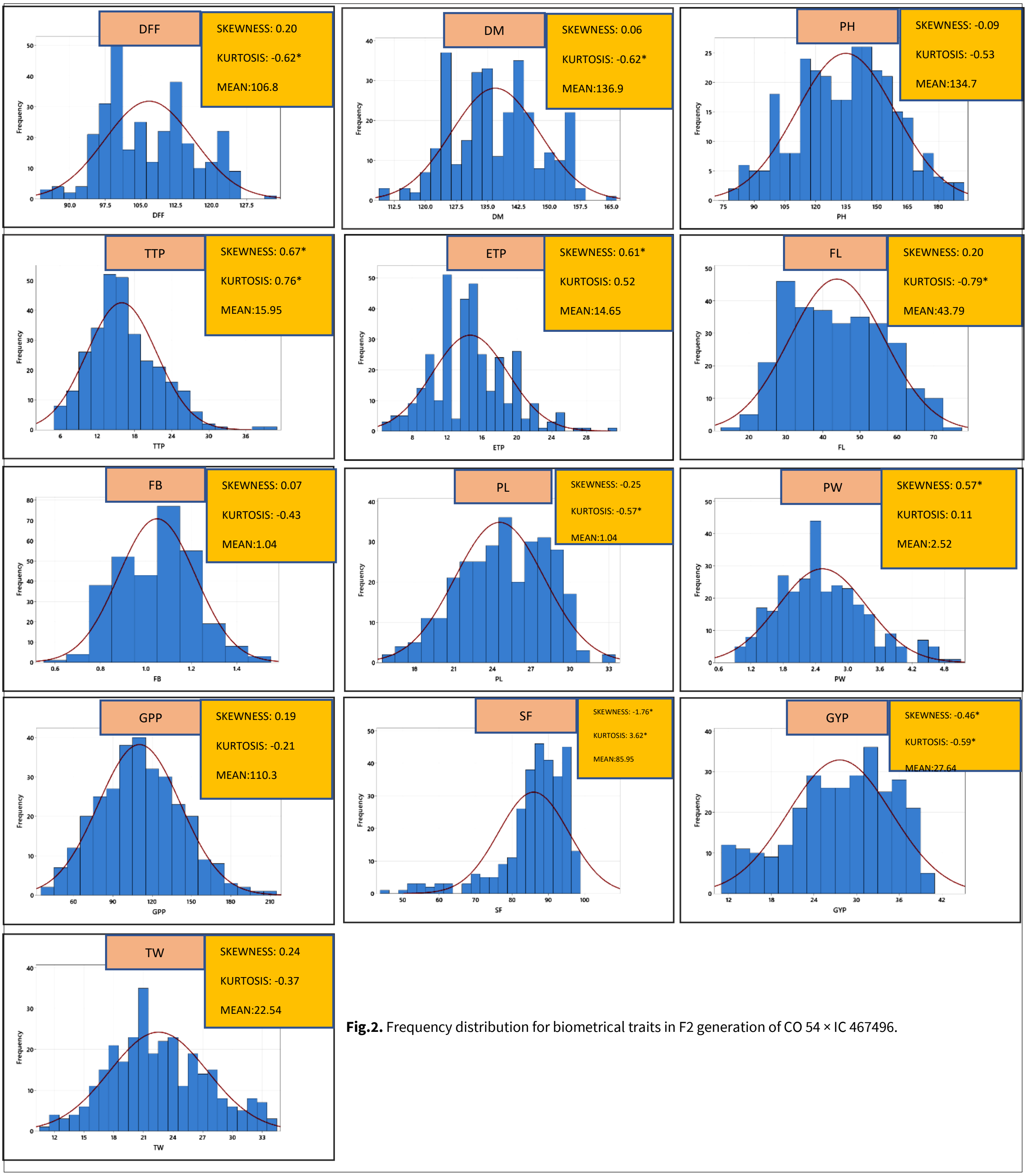


Fig.2. Frequency distribution for biometrical traits in F2 generation of CO 54 × IC 467496.

PW, GPP, and TW, along with significant negative correlations with TTP and ETP (Fig. 4). In the F_2 population derived from the CO 54 × IC 378202 cross, DM exhibited a highly significant positive correlation with various traits, including PH, FL, FB, DFF, PL, PW, GPP, GYP, and TW. Conversely, it showed a highly significant negative correlation between TTP and ETP (Fig. 3). Similarly, in the CO 54 × IC 467496 cross, DM demonstrated a highly significant positive correlation with PH, FL, DFF, PL, PW, PW, and TW, while also displaying significant negative correlations with TTP and ETP (Fig. 4).

In the F_2 population derived from the CO 54 × IC 378202 cross, PH exhibited a highly significant positive correlation with several traits, including FL, FB, DFF, DM, PL, PW, GPP, GYP, and TW (Fig. 3). Similarly, in the CO 54 × IC 467496 cross, PH showed a highly significant positive correlation with DM, FL, DFF, PL, PW, GPP, GYP, and TW. Similar findings were reported by (23) and (24) regarding DM; (17) for DM; and (25) for DM, PH, and GYP (Fig. 4).

Path coefficient analysis (PCA) was conducted using GYP as the dependent variable, alongside 12 independent traits, to differentiate between the direct and indirect effects of these traits on yield. While correlation analysis can provide insights into relationships among traits, it may

Table 3. Correlation analysis in F_2 segregating populations of CO 54 × IC 378202

	DFF	DM	PH	TTP	ETP	FL	FB	PL	PW	GPP	SF	GYP	TW
DFF	1.000**	0.995**	0.560**	-0.141*	-0.139*	0.506**	0.377**	0.500**	0.486**	0.293**	-0.011	0.233**	0.347**
DM	0.995**	1.000**	0.568**	-0.132*	-0.132*	0.511**	0.385**	0.498**	0.492**	0.298**	-0.011	0.240**	0.350**
PH	0.560**	0.568**	1.000**	-0.095	-0.081	0.607**	0.464**	0.701**	0.634**	0.427**	0.024	0.456**	0.425**
TTP	-0.141*	-0.132*	-0.095	1.000**	0.983**	-0.075	0.009	-0.038	-0.101	-0.004	-0.092	0.302**	-0.136*
ETP	-0.139*	-0.132*	-0.081	0.983**	1.000**	-0.067	0.019	-0.038	-0.09	0.014	-0.079	0.315**	-0.140*
FL	0.506**	0.511**	0.607**	-0.075	-0.067	1.000**	0.554**	0.684**	0.529**	0.358**	-0.009	0.408**	0.404**
FB	0.377**	0.385**	0.464**	0.009	0.019	0.554**	1.000**	0.475**	0.540**	0.319**	0.015	0.465**	0.428**
PL	0.500**	0.498**	0.701**	-0.038	-0.038	0.684**	0.475**	1.000**	0.622**	0.387**	-0.024	0.500**	0.501**
PW	0.486**	0.492**	0.634**	-0.101	-0.09	0.529**	0.540**	0.622**	1.000**	0.666**	0.176**	0.641**	0.616**
GPP	0.293**	0.298**	0.427**	-0.004	0.014	0.358**	0.319**	0.387**	0.666**	1.000**	0.440**	0.452**	0.005
SF	-0.011	-0.011	0.024	-0.092	-0.079	-0.009	0.015	-0.024	0.176**	0.440**	1.000**	0.051	-0.141*
GYP	0.233**	0.240**	0.456**	0.302**	0.315**	0.408**	0.465**	0.500**	0.641**	0.452**	0.051	1.000**	0.483**
TW	0.347**	0.350**	0.425**	-0.136*	-0.140*	0.404**	0.428**	0.501**	0.616**	0.005	-0.141*	0.483**	1.000**

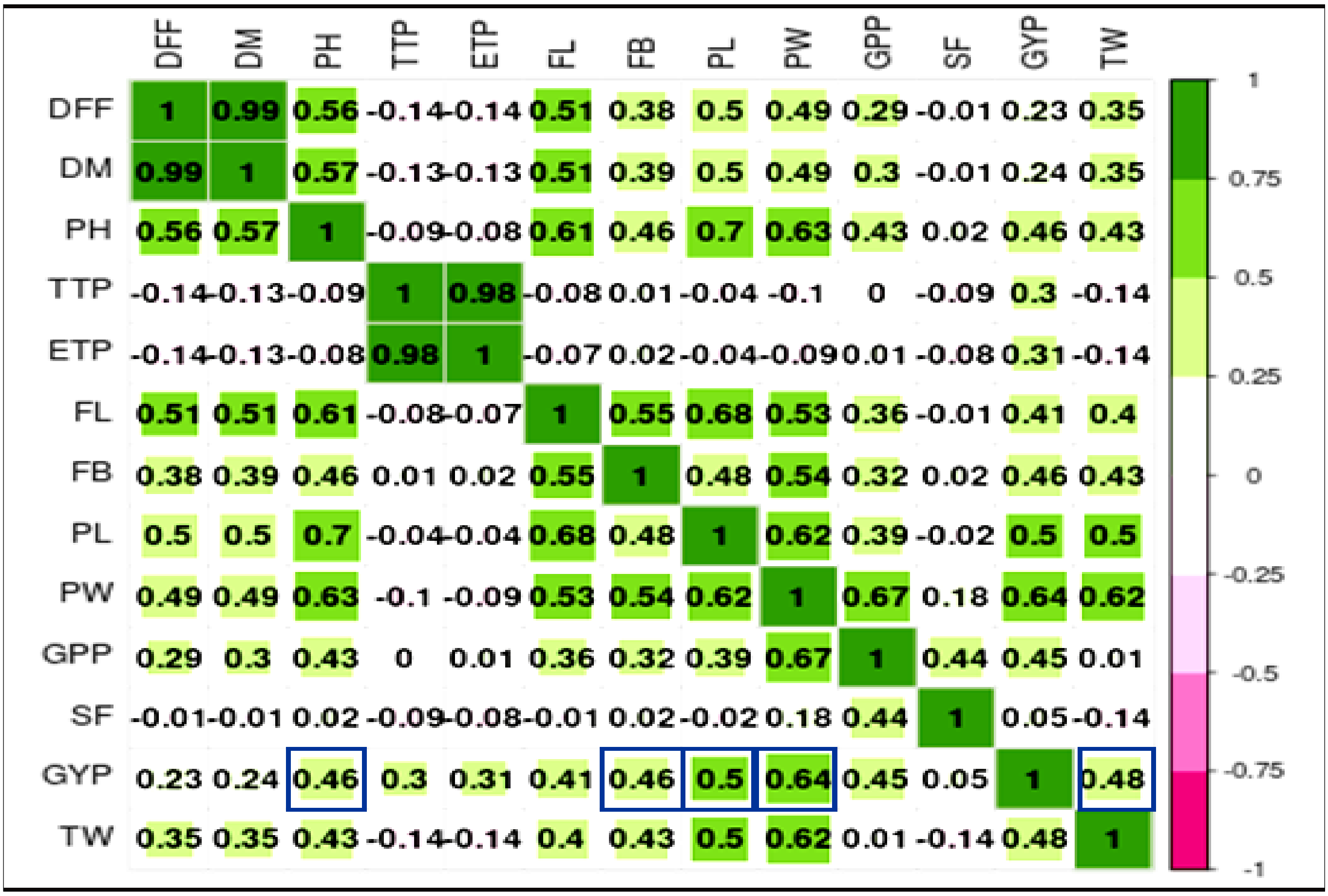
*****=significant at 5 %, ****** = significant at 1 % and NS = non-significant.

Table 4. Correlation analysis in F_2 segregating populations of CO 54 × IC 467496

	DFF	DM	PH	TTP	ETP	FL	FB	PL	PW	GPP	SF	GYP	TW
DFF	1.000**	0.992**	0.397**	-0.190**	-0.186**	0.371**	0.09	0.202**	0.269**	0.156**	0.03	0.053	0.226**
DM	0.992**	1.000**	0.395**	-0.195**	-0.190**	0.373**	0.1	0.206**	0.269**	0.155**	0.027	0.052	0.221**
PH	0.397**	0.395**	1.000**	0.053	0.068	0.541**	0.069	0.490**	0.435**	0.316**	0.047	0.274**	0.280**
TTP	-0.190**	-0.195**	0.053	1.000**	0.983**	0.057	0.148*	0.083	0.042	0.06	-0.04	0.336**	-0.021
ETP	-0.186**	-0.190**	0.068	0.983**	1.000**	0.067	0.153**	0.098	0.048	0.076	-0.019	0.344**	-0.029
FL	0.371**	0.373**	0.541**	0.057	0.067	1.000**	0.113*	0.589**	0.253**	0.128*	-0.083	0.169**	0.207**
FB	0.09	0.1	0.069	0.148*	0.153**	0.113*	1.000**	0.137*	0.192**	0.083	-0.048	0.086	0.086
PL	0.202**	0.206**	0.490**	0.083	0.098	0.589**	0.137*	1.000**	0.379**	0.273**	-0.063	0.256**	0.239**
PW	0.269**	0.269**	0.435**	0.042	0.048	0.253**	0.192**	0.379**	1.000**	0.727**	0.283**	0.406**	0.496**
GPP	0.156**	0.155**	0.316**	0.06	0.076	0.128*	0.083	0.273**	0.727**	1.000**	0.526**	0.383**	-0.102
SF	0.03	0.027	0.047	-0.04	-0.019	-0.083	-0.048	-0.063	0.283**	0.526**	1.000**	0.171**	-0.169**
GYP	0.053	0.052	0.274**	0.336**	0.344**	0.169**	0.086	0.256**	0.406**	0.383**	0.171**	1.000**	0.240**
TW	0.226**	0.221**	0.280**	-0.021	-0.029	0.207**	0.086	0.239**	0.496**	-0.102	-0.169**	0.240**	1.000**

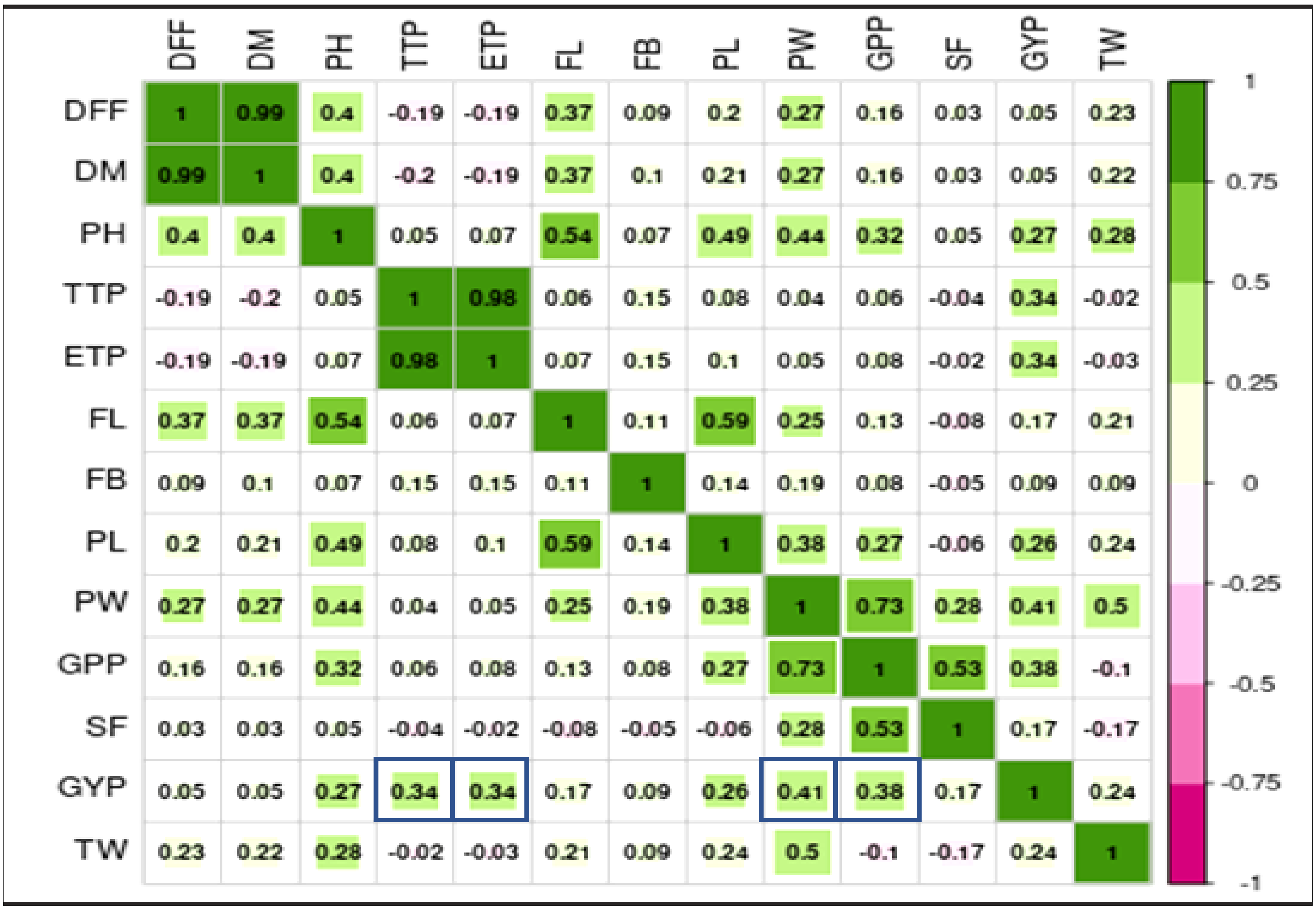
not accurately reflect the relative importance of those contributing to yield. Therefore, path analysis was employed to clarify the direct and indirect influence of various traits on GYP (Table 5 & 6). The results from the phenotypic path coefficient analysis indicated that ETP, TW, GPP, and PW exhibited the highest positive direct effects on GYP (Fig. 5). Additionally, significant direct effects were also noted for traits such as FB, PL (26), and TTP (4). Conversely, negative direct effects on grain yield per plant were observed for DFF, DM, and SF (27) in the cross CO 54 × IC 378202 (Fig. 5). These findings emphasize the utility of path analysis in understanding the complex relationships between yield and its contributing traits. The phenotypic path coefficient analysis for the CO 54 × IC 467496 cross revealed that traits such as GPP, TW, ETP (22), TTP (17), and DM exerted the strongest positive direct effects on GYP (Fig. 6). Furthermore, notable positive direct effects were observed for PH, PL, and SF. In contrast, traits like DFF, FB, and PW demonstrated negative direct effects on GYP (Fig. 6). These results highlight the importance of path analysis in unraveling the intricate relationships between yield and its associated traits. Our study revealed significant direct effects between ETP(28), GPP(29,30), TW(31), and GYP, while DFF(32) exhibited a detrimental effect. These findings underscore the efficacy of path analysis in elucidating the intricate relationships between yield and its constituent traits. Consistent with previous research ETP, GPP, and TW emerged as pivotal drivers of grain yield, highlighting the importance of preserving genetic diversity to bolster resilience in breeding programs (28,33,34).

Although traits such as DFF, DM, and SF exhibited negative direct effects on GYP in the CO 54 × IC 378202 cross, they demonstrated positive indirect effects on GYP through ETP and TTP (Fig. 5). Similarly, in the CO 54 × IC 467496 cross, while DFF showed a negative direct effect on GYP, it also contributed positively to grain yield indirectly via ETP and TTP (Fig. 6). In the CO 54 × IC 378202 cross, traits including ETP, PW, GPP, and TW exhibited highly significant and positive correlations alongside positive direct effects on GYP (Fig. 3 & 5). Similarly, in the CO 54 × IC 467496 cross, TTP, ETP, TW, and GPP showed strong significant positive correlations coupled with positive direct effects on GYP (Fig. 4 & 6). This suggests that the direct



	DFF	DM	PH	TTP	ETP	FL	FB	PL	PW	GPP	SF	GYP	TW
DFF	1	0.99	0.56	-0.14	-0.14	0.51	0.38	0.5	0.49	0.29	-0.01	0.23	0.35
DM	0.99	1	0.57	-0.13	-0.13	0.51	0.39	0.5	0.49	0.3	-0.01	0.24	0.35
PH	0.56	0.57	1	-0.09	-0.08	0.61	0.46	0.7	0.63	0.43	0.02	0.46	0.43
TTP	-0.14	-0.13	-0.09	1	0.98	-0.08	0.01	-0.04	-0.1	0	-0.09	0.3	-0.14
ETP	-0.14	-0.13	-0.08	0.98	1	-0.07	0.02	-0.04	-0.09	0.01	-0.08	0.31	-0.14
FL	0.51	0.51	0.61	-0.08	-0.07	1	0.55	0.68	0.53	0.36	-0.01	0.41	0.4
FB	0.38	0.39	0.46	0.01	0.02	0.55	1	0.48	0.54	0.32	0.02	0.46	0.43
PL	0.5	0.5	0.7	-0.04	-0.04	0.68	0.48	1	0.62	0.39	-0.02	0.5	0.5
PW	0.49	0.49	0.63	-0.1	-0.09	0.53	0.54	0.62	1	0.67	0.18	0.64	0.62
GPP	0.29	0.3	0.43	0	0.01	0.36	0.32	0.39	0.67	1	0.44	0.45	0.01
SF	-0.01	-0.01	0.02	-0.09	-0.08	-0.01	0.02	-0.02	0.18	0.44	1	0.05	-0.14
GYP	0.23	0.24	0.46	0.3	0.31	0.41	0.46	0.5	0.64	0.45	0.05	1	0.48
TW	0.35	0.35	0.43	-0.14	-0.14	0.4	0.43	0.5	0.62	0.01	-0.14	0.48	1

Fig. 3. Heat map depicting phenotypic correlation among the biometrical traits in F_2 generation of CO 54 × IC 378202 cross. Trait ▭ showing notable significant positive correlation with GYP.



	DFF	DM	PH	TTP	ETP	FL	FB	PL	PW	GPP	SF	GYP	TW
DFF	1	0.99	0.4	-0.19	-0.19	0.37	0.09	0.2	0.27	0.16	0.03	0.05	0.23
DM	0.99	1	0.4	-0.2	-0.19	0.37	0.1	0.21	0.27	0.16	0.03	0.05	0.22
PH	0.4	0.4	1	0.05	0.07	0.54	0.07	0.49	0.44	0.32	0.05	0.27	0.28
TTP	-0.19	-0.2	0.05	1	0.98	0.06	0.15	0.08	0.04	0.06	-0.04	0.34	-0.02
ETP	-0.19	-0.19	0.07	0.98	1	0.07	0.15	0.1	0.05	0.08	-0.02	0.34	-0.03
FL	0.37	0.37	0.54	0.06	0.07	1	0.11	0.59	0.25	0.13	-0.08	0.17	0.21
FB	0.09	0.1	0.07	0.15	0.15	0.11	1	0.14	0.19	0.08	-0.05	0.09	0.09
PL	0.2	0.21	0.49	0.08	0.1	0.59	0.14	1	0.38	0.27	-0.06	0.26	0.24
PW	0.27	0.27	0.44	0.04	0.05	0.25	0.19	0.38	1	0.73	0.28	0.41	0.5
GPP	0.16	0.16	0.32	0.06	0.08	0.13	0.08	0.27	0.73	1	0.53	0.38	-0.1
SF	0.03	0.03	0.05	-0.04	-0.02	-0.08	-0.05	-0.06	0.28	0.53	1	0.17	-0.17
GYP	0.05	0.05	0.27	0.34	0.34	0.17	0.09	0.26	0.41	0.38	0.17	1	0.24
TW	0.23	0.22	0.28	-0.02	-0.03	0.21	0.09	0.24	0.5	-0.1	-0.17	0.24	1

Fig. 4. Heat map depicting phenotypic correlation among the biometrical traits in F_2 generation of CO 54 × IC 467496 cross. Trait ▭ showing notable significant positive correlation with GYP.

Table 5. Direct and indirect effects of different biometrical traits as partitioned by path analysis for the cross CO 54 × IC 378202

	DFF	DM	PH	TTP	ETP	FL	FB	PL	PW	GPP	SF	TW
DFF	-0.0150	-0.0150	-0.0090	0.0020	0.0020	-0.0080	-0.0060	-0.0080	-0.0070	-0.0040	0.0000	-0.0050
DM	-0.1150	-0.1160	-0.0660	0.0150	0.0150	-0.0590	-0.0450	-0.0580	-0.0570	-0.0350	0.0010	-0.0410
PH	0.0360	0.0370	0.0650	-0.0060	-0.0050	0.0390	0.0300	0.0450	0.0410	0.0280	0.0020	0.0270
TTP	-0.0040	-0.0030	-0.0020	0.0260	0.0260	-0.0020	0.0000	-0.0010	-0.0030	0.0000	-0.0020	-0.0040
ETP	-0.0470	-0.0450	-0.0270	0.3340	0.3390	-0.0230	0.0060	-0.0130	-0.0310	0.0050	-0.0270	-0.0480
FL	0.0070	0.0070	0.0080	-0.0010	-0.0010	0.0130	0.0070	0.0090	0.0070	0.0050	0.0000	0.0050
FB	0.0340	0.0350	0.0420	0.0010	0.0020	0.0500	0.0910	0.0430	0.0490	0.0290	0.0010	0.0390
PL	0.0400	0.0390	0.0550	-0.0030	-0.0030	0.0540	0.0380	0.0790	0.0490	0.0310	-0.0020	0.0400
PW	0.1150	0.1160	0.1500	-0.0240	-0.0210	0.1250	0.1280	0.1470	0.2370	0.1580	0.0420	0.1460
GPP	0.0730	0.0740	0.1060	-0.0010	0.0030	0.0890	0.0790	0.0960	0.1650	0.2480	0.1090	0.0010
SF	0.0000	0.0000	-0.0010	0.0030	0.0020	0.0000	0.0000	0.0010	-0.0050	-0.0120	-0.0280	0.0040
TW	0.1100	0.1110	0.1350	-0.0430	-0.0450	0.1290	0.1360	0.1590	0.1960	0.0020	-0.0450	0.3180

Table 6. Direct and indirect effects of different biometrical traits as partitioned by path analysis for the cross CO 54 × IC 467496

	DFF	DM	PH	TTP	ETP	FL	FB	PL	PW	GPP	SF	TW
DFF	-0.1770	-0.1760	-0.0700	0.0340	0.0330	-0.0660	-0.0160	-0.0360	-0.0480	-0.0280	-0.0050	-0.0400
DM	0.1410	0.1420	0.0560	-0.0280	-0.0270	0.0530	0.0140	0.0290	0.0380	0.0220	0.0040	0.0310
PH	0.0240	0.0240	0.0600	0.0030	0.0040	0.0320	0.0040	0.0290	0.0260	0.0190	0.0030	0.0170
TTP	-0.0230	-0.0240	0.0060	0.1220	0.1200	0.0070	0.0180	0.0100	0.0050	0.0070	-0.0050	-0.0030
ETP	-0.0360	-0.0360	0.0130	0.1890	0.1920	0.0130	0.0290	0.0190	0.0090	0.0150	-0.0040	-0.0060
FL	0.0050	0.0050	0.0080	0.0010	0.0010	0.0140	0.0020	0.0080	0.0040	0.0020	-0.0010	0.0030
FB	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	-0.0010	0.0000	0.0000	0.0000	0.0000	0.0000
PL	0.0100	0.0100	0.0240	0.0040	0.0050	0.0290	0.0070	0.0500	0.0190	0.0140	-0.0030	0.0120
PW	-0.0680	-0.0680	-0.1110	-0.0110	-0.0120	-0.0640	-0.0490	-0.0960	-0.2540	-0.1850	-0.0720	-0.1260
GPP	0.0840	0.0830	0.1690	0.0320	0.0410	0.0690	0.0440	0.1460	0.3900	0.5360	0.2820	-0.0540
SF	0.0010	0.0010	0.0020	-0.0020	-0.0010	-0.0040	-0.0020	-0.0030	0.0120	0.0220	0.0420	-0.0070
TW	0.0930	0.0910	0.1160	-0.0090	-0.0120	0.0860	0.0360	0.0990	0.2050	-0.0420	-0.0700	0.4130

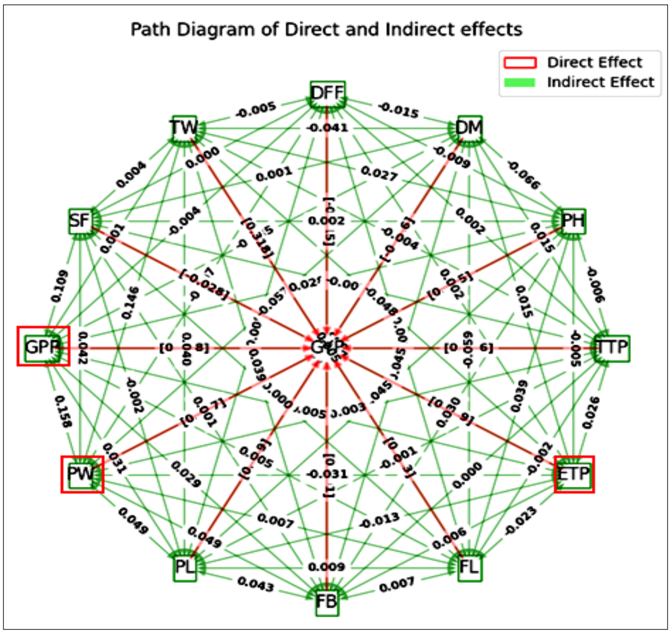


Fig. 5. Path analysis diagram for the cross CO 54 × IC 378202.

🟥 Trait showing notable significant positive direct effect with GYP.

🟦 Traits showing notable significant negative direct effect with GYP

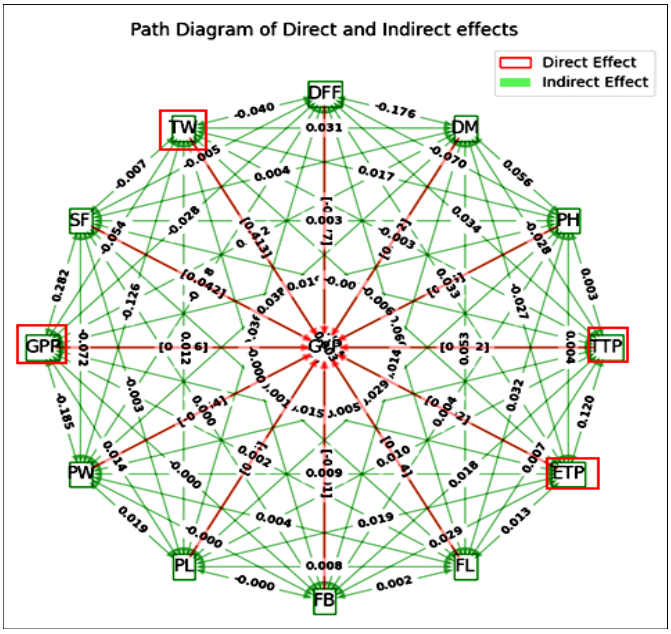


Fig. 6. Path analysis diagram for the cross CO 54 × IC 467496.

🟥 Trait showing notable significant positive direct effect with GYP.

🟦 Traits showing notable significant negative direct effect with GYP effects of these traits on GYP constituted a significant portion of the total correlation observed between them. Thus, direct selection based on these traits would be effective and beneficial. A similar pattern of relationships, characterized by positive direct effects and positive correlations of most of these traits with grain yield per plant, has been documented in previous studies (35).

Conclusion

The CO 54 × IC 378202 cross exhibited high GCV, PCV, H^2, positive skewness, and GAM for TTP, ETP, FL, PW, and GPP, highlighting additive gene effects and strong selection potential. Similarly, the CO 54 × IC 467496 cross showed high GCV, PCV, H^2, positive skewness, and GAM for TTP, ETP, and PW. Key traits like ETP, GPP, and PW in CO 54 × IC 378202, and TTP and ETP in CO 54 × IC 467496, showed high heritability, genetic advance, and strong correlations and direct effects with GYP, making them suitable for F2 selection. To enhance the variability, inter-mating and biparental mating within and between these populations are recommended. The observed predominance of additive gene action for these traits suggests their amenability to improvement through pure line selection. By prioritizing these traits, breeders can develop high-yielding rice cultivars, thereby enhancing agricultural productivity and contributing to global food security endeavors.

Acknowledgements

We thank the Department of Rice, Centre for Plant Breeding and Genetics, Tamil Nadu Agricultural University, Coimbatore for providing financial and field assistance for conducting this research.

Authors' contributions

PM performed the field experiments, measurements, and data analysis and drafted the manuscript, and PR supervised and worked on the manuscript. All authors were involved in planning and providing critical feedback on the manuscript.

Compliance with ethical standards

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

Ethical issues: None

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