

Genetic Variability, Heritability and Trait Pathways for Grain Yield in Bread Wheat

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ABSTRACT

Identification of highly heritable yield-associated traits is essential for accelerating genetic improvement of bread wheat (*Triticum aestivum* L.) under changing climatic conditions. Bread wheat productivity is increasingly threatened by climate variability and rising global food demand, necessitating the identification of heritable physiological and yield-related traits for sustainable genetic improvement. The present study evaluated 40 bread wheat genotypes under a randomized complete block design with three replications during the 2025-2026 growing season to dissect trait pathways governing grain yield. Significant genotypic variation ($P \leq 0.01$) was observed for all studied traits, confirming substantial genetic diversity among genotypes. Broad-sense heritability ranged from 84.49% for spikelets per spike (SPS) to 96.75% for grain yield per plant (GYP), while genetic advance as percent of mean (GAM) varied from 7.97% for relative water content (RWC) to 39.74% for GYP, indicating substantial genetic variability for major yield-associated traits. Phenotypic and genotypic correlation analyses revealed highly significant positive associations of grain yield with thousand grain weight (TGW), grains per spike (GPS), flag leaf area (FLA), and spike-related traits. Genotypic path analysis further demonstrated that GPS (0.390) and TGW (0.371) exerted the strongest positive direct effects on grain yield, whereas physiological traits mainly contributed indirectly through interconnected source-sink relationships. Similarly, phenotypic path analysis confirmed the substantial contribution of GPS and TGW toward yield formation under field conditions. Integrated graphical analyses further highlighted the coordinated interaction among physiological efficiency, grain development, and yield accumulation pathways. Overall, the findings indicate that TGW, GPS, FLA, and SPS represent reliable selection criteria for improving wheat productivity and developing high-yielding cultivars aimed at strengthening food security under variable agro-climatic environments.

Keywords: photosynthesis, heritability, correlation, path analysis, genetics.

INTRODUCTION

Bread wheat (*Triticum aestivum* L.) is one of the most important staple cereal crops grown globally, and it acts as a major source of calories, proteins, and vital nutrients for the ever-increasing world population. Increasing productivity of wheat has become a daunting challenge due to climate

variability, loss of arable lands, water scarcity, and increasing food demands (Bayisa et al., 2020; Zewdu et al., 2024). Modern wheat breeders now place an emphasis on improving grain yields by focusing on heritable traits related to grain yield and the underlying physiological mechanisms that support the trait (Bedada et al., 2022; Chen et al., 2022). Grain yield is a

complex trait governed by several interrelated systems that work together to support high grain yield, which is also very responsive to environmental conditions; therefore, it is difficult for breeders to select directly for high-yielding lines (Akbari et al., 2020; Bedada et al., 2022).

Trait associations with higher photosynthetic efficiency and plant water status improve wheat productivity. Trait associations with greater chlorophyll a, chlorophyll b, carotenoid content and relative water content enable higher photosynthetic activity, greater assimilate accumulation and improved stress endurance, enabling the grains of these plants to develop and be laid down in greater quantity at harvest (Parveen et al., 2021; Mahdavi et al., 2023; Saini et al., 2024; Balyan et al., 2025). Similar to this, flag leaf area acts as a major source of photosynthesis during grain filling and significantly associates toward final grain weight and productivity (Zewdu et al., 2024; Kumarbayeva et al., 2025). Knowledge of the relationships among yield related traits allow indirect selection for yield (Wasaya et al., 2021; Zewdu et al., 2024).

Genetic variability and heritability estimates indicate the amount of inherited variation available for selection in breeding populations (Baloch et al., 2024; Mullualem et al., 2025). High heritability coupled with substantial genetic advance usually reflects the dominant contribution of additive gene action and suggests that phenotypic selection can be highly efficient for genetic improvement (Bayisa et al., 2020; Hossain et al., 2021). Furthermore, while correlation analysis reveals how economically important traits are associated with each other, path coefficient analysis decomposes these associations into direct and indirect effects. Understanding the genetic basis and interrelationships of important plant traits can provide useful insights into plant development and support the identification of desirable characteristics for crop improvement (Baye et al., 2020; Abubakar et al., 2023).

Path coefficient analysis is an important statistical approach that provides a better understanding of complex relationships among yield-related traits by separating correlation

coefficients into direct and indirect effects. Originally introduced by Wright (Wright, 1921), this method helps identify whether a trait influences grain yield directly or contributes through its association with other characters. In wheat breeding, path analysis has been widely applied to determine the relative contribution of yield components and physiological traits, thereby assisting breeders in selecting effective traits for yield improvement (Saini et al., 2024; Zewdu et al., 2024). Recent studies have demonstrated that traits showing strong direct effects on grain yield can serve as reliable selection criteria for developing superior wheat genotypes (Saini et al., 2024; Gudeta et al., 2025).

While most previous studies have reported on agronomic and physiological traits independently, studies on complementary heritable trait pathways that modulate grain yield are limited. Accordingly, this study was undertaken to evaluate the genetic variability, heritability, phenotypic and genotypic associations, and direct-indirect contributions of physiological and yield contributing traits of diverse bread wheat genotypes. The integration of these approaches provides a comprehensive understanding of trait interactions and helps identify reliable selection criteria for future wheat improvement programs. The findings of this study will contribute to trait-based selection of high-yielding cultivars for improved food security.

MATERIAL AND METHODS

The field trial was carried out during the Rabi season of 2025-2026 at the experimental research area of the Department of Plant Breeding and Genetics (PBG), Faculty of Agriculture and Environment (FA&E), The Islamia University of Bahawalpur (IUB), Bahawalpur, Punjab, Pakistan. The experimental location lies at approximately 29°24' N latitude and 71°47' E longitude, with an elevation of nearly 117 m above sea level. The area experiences an arid to semi-arid agro-climatic environment, characterized by hot summers, cool winters, low atmospheric humidity, and irregular rainfall patterns. The soil of the experimental

field is predominantly alluvial loam, representing a suitable soil type for wheat production under the local environmental conditions. This study included the total of 40 bread wheat genotypes were evaluated in randomized complete block design (RCBD) with three replications. Genotypes were sown in rows of 3 m length while row to row and plant to plant spacing was kept 30 cm and 10 cm, respectively. Recommended agronomic and crop management practices for wheat were followed during the growing season.

Data were measured for studied attributes viz; flag leaf area (FLA), chlorophyll a (CHLA), chlorophyll b (CHLB), carotenoid content (CAR), relative water content (RWC), spike length (SL), spikelets per spike (SPS), grains per spike (GPS), thousand grain weight (TGW) and grain yield per plant (GYP). Flag leaf area was calculated by the formula given by (Müller, 1991). Chlorophyll a, chlorophyll b and carotenoid content was estimated by using method given by (Arnon, 1949) and relative water content was calculated as indicated (Barrs and Weatherley, 1962). Spike and yield traits were recorded from randomly selected representative plants from each replication as per standard protocol in case of wheat.

Analysis of variance (ANOVA) was performed to determine the genotypic variability for the traits studied (Steel and Torrie, 1981). Descriptive statistics including

mean, minimum, maximum, standard deviation, and coefficient of variation (CV%) were calculated to assess the magnitude of phenotypic variation among wheat genotypes. Broad-sense heritability (H^2), genetic advance (GA), and genetic advance as percent of mean (GAM) were estimated following the methodology described by (Johnson et al., 1955). Phenotypic and genotypic correlation coefficients were estimated according to (Al-Jibouri et al., 1958; Miller et al., 1958). Path coefficient analysis was carried out in order to partition direct and indirect effects for the traits following the original method devised by Sewall Wright in his studies on correlation and causation (Wright, 1921). All statistics and data visualizations were generated in the R Studio statistical environment (Wickham, 2016; Team, 2020).

RESULTS AND DISCUSSION

Analysis of variance revealed highly significant ($P \leq 0.01$) differences among the evaluated bread wheat genotypes for all studied traits (Table 1). The genotypic mean squares were higher than the residual mean squares of all studied traits suggesting the existence of substantial genetic variability among genotypes and considerable potential for effective phenotypic selection (Bedada et al., 2022; Geneti et al., 2022).

Table 1. Analysis of Variance (ANOVA) for Heritable Physiological and Yield-Related Traits

Source	Df	FLA	CHLA	CHLB	CAR	RWC	SL	SPS	GPS	TGW	GYP
Replication	2	2.62 ^{ns}	0.013*	0.004 ^{ns}	0.006 ^{ns}	6.441*	0.179 ^{ns}	0.102 ^{ns}	0.436 ^{ns}	1.902 ^{ns}	3.968**
Genotype	39	44.34**	0.228**	0.061**	0.011**	32.281**	2.221**	9.707**	99.472**	80.160**	89.824**
Residuals	78	1.22	0.0034	0.003	0.004	1.374	0.063	0.559	4.054	0.892	0.995

Descriptive Variability

Descriptive statistics indicated considerable variability in the evaluated bread wheat genotypes for physiological as well as yield traits (Figure 1). In this figure, the violin and boxplot distribution indicates considerable phenotypic variation, while minimum, maximum and mean values further confirm the broad variability available for selection and yield improvement. Among physiological traits, CHLA, CHLB, CAR)

and RWC showed mean values of 1.77 mg g⁻¹, 0.75 mg g⁻¹, 0.42 mg g⁻¹, and 77.91%, respectively.

Chlorophyll a ranged from 1.11 to 2.74 mg g⁻¹ with a standard deviation (SD) of 0.27 and coefficient of variation (CV) of 15.41%, whereas chlorophyll b varied between 0.41 and 1.05 mg g⁻¹ with SD of 0.13 and CV of 17.67%. Similar variability in these traits has previously been reported in wheat (Ojha et al., 2018; Alshaharni et al., 2025; Balyan et

al., 2025). Carotenoid content mean values ranged from 0.30 to 0.61 mg g⁻¹ with SD of 0.06 and CV of 14.83%, while RWC varied from 70.14 to 87.54% with SD of 3.40 and comparatively lower CV of 4.37%. The greater variation found for chlorophyll pigments and carotenoids suggests that these traits observed differences in photosynthetic

efficiency among genotypes experimented (Saini et al., 2024; Habbadi et al., 2025). The lesser variation of RWC arises from relatively stable water retention capacity. Similar observations on physiological variability in wheat was made by (Parveen et al., 2021; Wasaya et al., 2021; Saini et al., 2024).

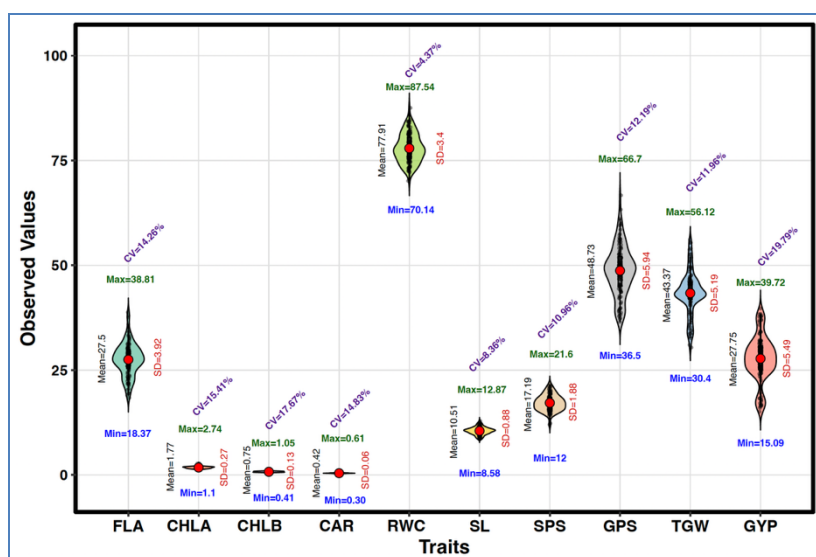


Figure 1. Distribution Patterns and Variability of Heritable Physiological and Yield-Related Traits

Among the yield contributors traits, FLA, SL, SPS, GPS, TGW and GYP showed appreciable phenotypic variation FLA ranged from 18.37 to 38.81 cm² with the averaged values of 27.50 cm², SD of 3.92, and CV of 14.26%, indicating substantial variation in photosynthetic source capacity in studied genotypes. The overall range of spike length was from 8.58 to 12.87 cm with an overall mean of 10.51 cm, SD = 0.88 cm, CV = 8.36%. The SPS ranged from 12.00 to 21.60 with corresponding mean, SD and CV of 17.19, 1.88, and 10.96%, respectively.

Grains/spike also ranged from 36.50 to 66.70 with a mean value of 48.73, 5.94, 12.19% CV. In this study, 1000-grain weight ranged from 30.40 to 56.12 g with overall mean of 43.37, SD = 5.19 and CV = 11.96, while GYP ranging from 15.09 to 39.72 g, mean = 27.75, SD = 5.49 and highest CV of 19.79%. Large variability for grain yield and its contributing traits clearly indicates a wide spectrum of genetic diversity that could be valuable for wheat improvement to increase wheat productivity and tackling food security

and similar variability for traits associated with yield has also been reported by (Bayisa et al., 2020; Geneti et al., 2022; Cui et al., 2026).

Genetic Parameters

Broad-sense heritability, GA, and GAM displayed relatively large genetic variations among evaluated bread wheat genotypes for both physiological and yield related traits (Figure 2). Among physiological attributes - CHLA revealed high heritability (95.47%) with GAM of 30.53% while CHLB exhibited heritability of 92.93% along with highest GAM value (34.12%) among physiological traits (Ali et al., 2023; Saini et al., 2024). Similarly, estimated heritability for carotenoid content (CAR) and relative water content (RWC) were 92.26% and 88.23%, with GAM values of 28.39% and 7.97%, respectively. The availability of high heritability estimates with moderate-to-high GAM values for chlorophyll pigments and carotenoids point to the preponderance of additive genetic effects and indicate that

efficacy of direct phenotypic selection to improve these physiological traits. Similar observations for chlorophyll traits in wheat

were made by (Hossain et al., 2021; Parveen et al., 2021; Balyan et al., 2025).

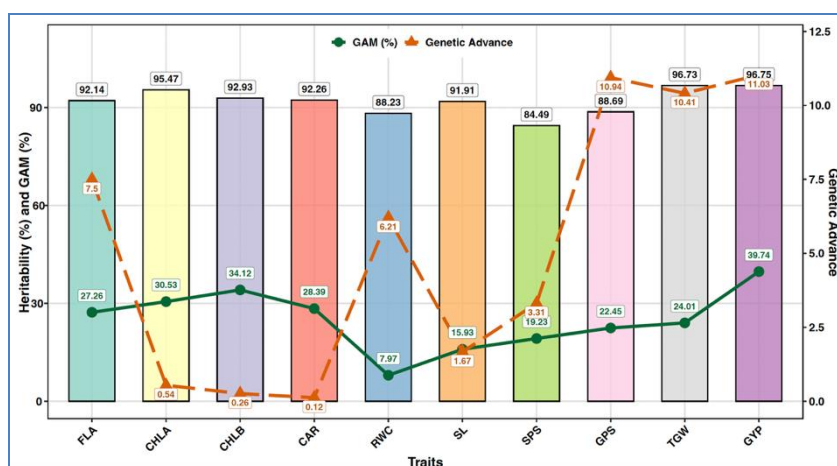


Figure 2. Integrated Visualization of Genetic Parameters

Among the yield attributing traits, flag leaf area (FLA) had a high heritability estimate of 92.14% with GAM of 27.26%. Spike length (SL), spikelets per spike (SPS), and grains per spike (GPS) also showed high heritability estimates of 91.91%, 84.49%, and 88.69%, respectively, corresponding GAM values were 15.93%, 19.23%, and 22.45%, respectively. Thousand grain weight (TGW) and grain yield per plant (GYP) showed also showed high heritability estimates of 96.73% and 96.75%, respectively, with GAM of 24.01% and 39.74%. The existence of both high heritability and high GAM for TGW and GYP designates that both attributes having additive types of genes action and would be amenable to selection (Hossain et al., 2021; Zewdu et al., 2024; Cui et al., 2026). The extremely high GAM for grain yield further suggests that there is exploitable genetic variability for improving wheat productivity and food security. The same relationship between high heritability, genetic advance and effective selection response was also obtained by (Akbari et al., 2020; Bayisa et al., 2020) in bread wheat.

Genotypic Correlation

Genotypic correlation studies revealed comparatively strong associations between the physiological traits and yield parameters than those indicated by the respective

phenotypic correlations, suggesting that most trait relationships were more strongly influenced by genotypic than phenotypic effects (Figure 3). Among physiological traits, CHLA traits were strongly positively associated with FLA (0.85**), CHLB (0.71**) and CAR (0.66**). Likewise, FLA was positively correlated with CHLB (0.72**) and CAR (0.77**), indicating good genetic co-ordination among photosynthetic traits. RWC was found to be positively correlated with CHLA (0.58**), TGW (0.59**) and GYP (0.56**), indicating that an improvement in plant water status contributes genetically towards the more assimilates being produced in leaf tissue and thus to a greater grain filling of the spikelets. Similar genotypic correlations among physiological traits have been reported in bread wheat by (Barman et al., 2020; Baye et al., 2020; Saini et al., 2024; Balyan et al., 2025).

Among yield traits, SL was strongly and positively correlated to SPS (0.72**), GPS (0.75**) and TGW (0.78**). SPS had strong positive association with GPS (0.78**) and also TGW (0.78**), indicating strong genetic coordination among the main yield components. Grain yield per plant had highly significant positive association with all observed indices, the strongest being with TGW (0.91**); GPS (0.89**), SPS (0.80**),

SL (0.79**) and FLA (0.82**). The stronger genotypic correlations of TGW and GPS with GYP than the corresponding phenotypic correlations imply that these traits are under strong genetic control and would be good selection targets for breeders aiming to

improve yield in bread wheat. Similar conclusions regarding the significance of spike-related traits for yield improvement have been reported by (Upadhyay, 2020; Geneti et al., 2022; Saini et al., 2024).

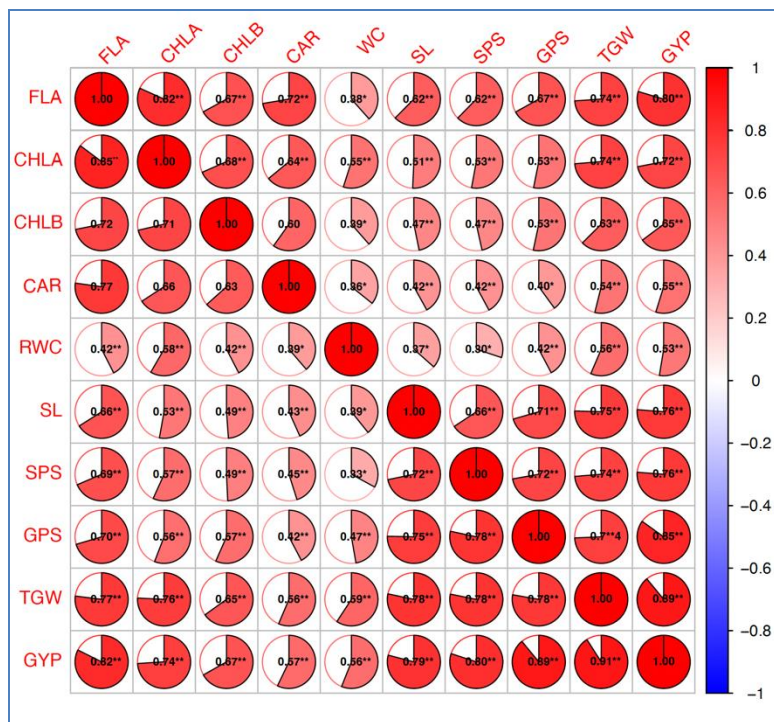


Figure 3. Integrated Phenotypic (upper triangle) and Genotypic (lower triangle) Correlation Matrix among Physiological and Yield-Related Traits

Phenotypic Correlation

The phenotypic correlation analysis revealed in Figure 3 that there were generally positive and significant correlations. Among physiological traits, CHLA had strong positive correlations with FLA (0.82**) as well as CHLB (0.68**) and CAR (0.64*), demonstrating some level of co-regulation of photosynthetic pigments. CHLB also correlated positively with CAR (0.60**) and RWC ($r = 0.39^*$) and improved pigment accumulation and enhanced the status of water in plant parts (Ojha et al., 2018; Saini et al., 2024). Among the yield contributing traits, SL showed significant positive correlation with SPS (0.66**), GPS (0.71**) and TGW (0.75**), thus better spike architecture resulted in better sink activity and consequent increase in grain number.

Likewise, SPS showed significant positive association with GPS ($r = 0.72^{**}$), and TGW

($r = 0.74^{**}$). The GYP trait exhibited very highly significant positive correlation with all the studied indices, especially with TGW (0.89**), GPS (0.85**), and FLA (0.80**), SPS (0.76**) and SL (0.76**). These close associations point to the action of spike productivity, grain development and photosynthetic source capacity as the most effective means whereby improvement of grain yield is likely to take place in bread wheat (Baye et al., 2020; Geneti et al., 2022). The strong positive association between FLA and GYP suggests that assimilates produced via the mediation of the flag leaf are important for the filling of the grains. The strong positive associations between TGW, GPS and GYP suggest that these traits may therefore be good indirect selection criteria for improving yield in wheat breeding programmes.

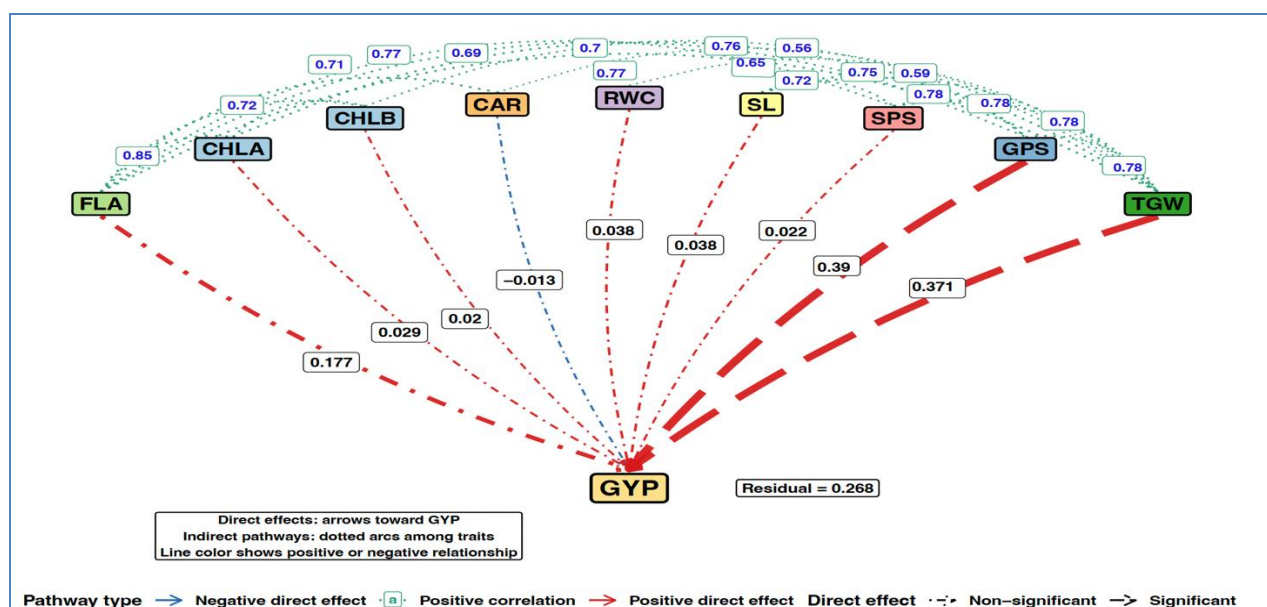
Genotypic Path Coefficient Analysis

The genotypic path coefficient analysis (Figure 4) indicated that physiological traits and yield components contribute directly and indirectly to grain yield formation of bread wheat genotypes (Figure 4). Positive direct effect is indicated by red arrows while blue arrows denote negative direct effects and dotted green pathways indicate positive indirect association of traits. Evaluating the physiological traits, RWC had the highest positive direct effect (0.038), followed by CHLA (0.029) and CHLB (0.020) while carotenoid content (CAR) had a very small (slightly negative) direct effect (-0.013). Despite its negative direct contribution, CAR had a positive total correlation with grain yield ($r = 0.571$) through the indirect effects of GPS (0.165) and TGW (0.209) (Mahdavi et al., 2023; Saini et al. 2024).

Flag leaf area (FLA) although having moderate direct effect (0.177), had strong positive contribution through GPS (0.275) and TGW (0.286), producing high overall correlation with grain yield ($r = 0.824$). Thus, flag leaf area is helpful in improving yield primarily through increased assimilation production and grain filling. Similar physiological contribution towards wheat

productivity has been shown (Barman et al., 2020; Upadhyay, 2020; Gudeta et al., 2025). Among these yield component traits, GPS showed the highest positive direct effect (0.390) on grain yield, followed by TGW (0.371), indicating that these are the most potent yield determining components in the evaluated genotypes (Alshaharni et al., 2025; Sarfraz et al., 2025).

The traits like SPS and SL showed relatively low direct effect with values of 0.022 and 0.038, respectively, but their appreciable contribution is via the more direct pathway of these traits leading to greater GPS and TGW. For example, SPS showed strong indirect effects shown via GPS (0.306) and TGW (0.290) and SL contributed indirectly through GPS (0.294) and TGW (0.291). Consequently, GPS and TGW showed the highest total correlations with grain yield with correlation coefficient of 0.890 and 0.909 respectively. The preponderance of direct effects for GPS and TGW indicates their important direct contribution to grain yield; thus, a more reliable selection approach of improving grain yield in bread wheat can be done through these traits as earlier observed by (Baye et al., 2020; Mullualem et al., 2025).



Solid and dashed arrows represent significant and non-significant direct effects, respectively, whereas dotted arcs indicate indirect inter-trait associations.

Figure 4. Genotypic Path Coefficient Diagram Illustrating Direct and Indirect Effects of Physiological and Yield-Related Traits

Table 2. Genotypic Path Coefficient Matrix Showing Direct (Diagonal) and Indirect (Off-Diagonal) Effects of Physiological and Yield-Related Traits on Grain Yield

Trait	FLA	CHLA	CHLB	CAR	RWC	SL	SPS	GPS	TGW	Cor-GYP
FLA	0.177	0.025	0.015	-0.01	0.016	0.025	0.015	0.275	0.286	0.824
CHLA	0.151	0.029	0.014	-0.009	0.022	0.02	0.013	0.218	0.282	0.74
CHLB	0.127	0.021	0.02	-0.008	0.016	0.019	0.011	0.221	0.242	0.668
CAR	0.136	0.019	0.013	-0.013	0.015	0.017	0.01	0.165	0.209	0.571
RWC	0.075	0.017	0.009	-0.005	0.038	0.015	0.007	0.184	0.22	0.561
SL	0.117	0.015	0.01	-0.006	0.015	0.038	0.016	0.294	0.291	0.791
SPS	0.121	0.016	0.01	-0.006	0.013	0.028	0.022	0.306	0.29	0.8
GPS	0.125	0.016	0.011	-0.006	0.018	0.029	0.017	0.39	0.289	0.89
TGW	0.136	0.022	0.013	-0.007	0.023	0.03	0.017	0.304	0.371	0.909

Phenotypic Path Coefficient Analysis

The phenotypic path analysis exhibited substantial direct and indirect contribution of physiological and yield contributing traits towards grain yield in bread wheat genotypes (Figure 5). Among physiological traits, RWC had the higher positive direct effect (0.058), followed by CHLB (0.051) and CHLA (0.020) while carotenoid content CAR (-0.021). As a result of its negative direct contribution, CAR still maintained a positive overall correlation with grain yield ($r = 0.548$) due to indirect effects via grains per spike (0.122) and thousand grain weight (0.186). Flag leaf area FLA also exhibited high positive direct effect (0.183) and strong indirect contribution through GPS (0.205) and TGW (0.255) and as a result contributed largely to the high positive correlation with grain yield $r = 0.796$.

Such physiological relationships were found to influence wheat productivity by (Barman et al., 2020; Mahdavi et al., 2023). Among the yield related traits, GPS exhibited

the highest positive direct effect (0.306) on grain yield and TGW (0.344). The SPS and SL had comparatively lower direct effects of 0.084 and 0.072 respectively, but had a great impact through indirect pathways in GPS and TGW (SPS via GPS = 0.221; TGW = 0.254) and SL had an influence via GPS (0.216) and TGW (0.260). Consequently, this might account for TGW and GPS having the highest total correlations with grain yield, with correlation coefficients of 0.891 and 0.849 respectively.

The predominance of positive direct effects for GPS and TGW indicated that grain number and grain weight are the main phenotypic components of grain yield, in the suite of wheat genotypes investigated here (Zhang et al., 2026). Similar accounts underscoring the significance of grain number and grain weight in improvement of yield of wheat have recently been provided by (Upadhyay, 2020; Jaisi et al., 2021; Gudeta et al., 2025).

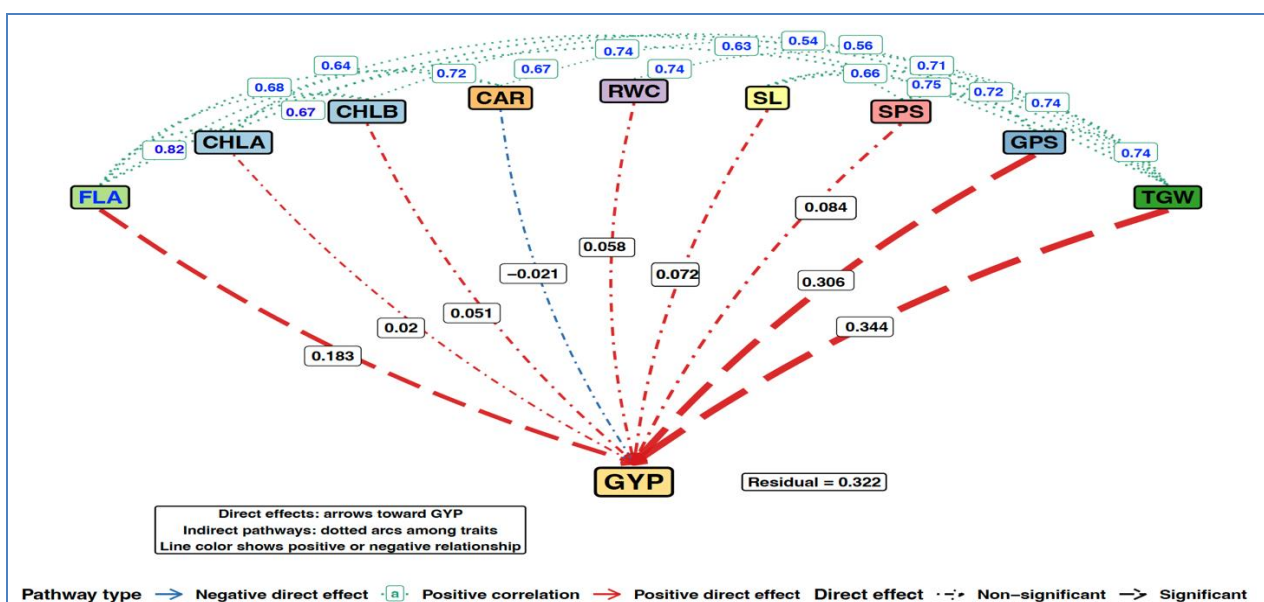


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Trait	FLA	CHLA	CHLB	CAR	RWC	SL	SPS	GPS	TGW	Cor-GYP
FLA	0.183	0.016	0.034	-0.016	0.022	0.045	0.053	0.205	0.255	0.796
CHLA	0.149	0.02	0.035	-0.014	0.032	0.036	0.045	0.163	0.254	0.719
CHLB	0.122	0.014	0.051	-0.013	0.022	0.034	0.039	0.163	0.215	0.648
CAR	0.132	0.013	0.03	-0.021	0.021	0.03	0.036	0.122	0.186	0.548
RWC	0.07	0.011	0.02	-0.008	0.058	0.026	0.025	0.129	0.194	0.526
SL	0.114	0.01	0.024	-0.009	0.021	0.072	0.055	0.216	0.26	0.763
SPS	0.114	0.011	0.024	-0.009	0.017	0.047	0.084	0.221	0.254	0.763
GPS	0.122	0.011	0.027	-0.009	0.024	0.051	0.061	0.306	0.256	0.849
TGW	0.135	0.015	0.032	-0.012	0.033	0.054	0.062	0.227	0.344	0.891

CONCLUSIONS

The present study elucidated the heritable physiological and yield-related pathways governing grain yield in bread wheat genotypes and identified key traits for effective selection in breeding programs. Significant genetic variability across evaluated traits confirmed the presence of considerable breeding resources for wheat improvement. High broad-sense heritability along with substantial genetic advance for grain yield per plant (96.75%; 39.74%), thousand grain weight (96.73%; 24.01%), and grains per spike (88.69%; 22.45%) indicated the predominance of additive gene action and the effectiveness of direct phenotypic selection for these economically important traits. Strong positive phenotypic and genotypic correlations among flag leaf

area, spike-related traits, grain weight, and grain yield further revealed the coordinated contribution of source and sink components to productivity. Path coefficient analyses confirmed that grains per spike and thousand grain weight exerted the strongest direct effects on grain yield, while physiological traits including chlorophyll pigments and relative water content contributed mainly through indirect effects by enhancing assimilate production and translocation. The consistently stronger genotypic than phenotypic associations indicated a stronger genetic contribution to the observed associations among major yield-determining traits a stronger genetic contribution to the observed associations among major yield-determining traits. Overall, thousand grain weight, grains per spike, flag leaf area, and spikelets per spike emerged as reliable

selection criteria for developing high-yielding bread wheat cultivars. These results provide an important framework for trait-based breeding to improve wheat productivity and for enhancing long-term food security in changing environments.

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