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Number of grains per square meter as a key predictor of yield potential in winter wheat

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Abstract. *In effort to establish an approach to evaluate yield components to their importance for grain yield formation 118 winter wheat varieties ware used over three growing seasons (2013-2015) at DZI-General Toshevo, Bulgaria. Traits included in this study are grain yield (GY), Number of Grains per Square Meter (NGM), Thousand Grain Weight (TGW), Number of Productive Tillers (NPT), Number of Grains per Spike (NGS), and Plant Height (PH). The goal is to establish whether NGM can serve as a predictive tool in wheat breeding programs for enhancing yield. Significant G × E interactions were observed for all traits examined, with NGM displaying the highest interaction, indicating its potential as a marker for assessing genotypic variation across different environments. Linear mixed model was used to explore the predictive power of NGM on GY. Results showed that NGM had the highest conditional R^2 (0.942), suggesting that it explains a substantial portion of the variance in GY when considering both fixed effects (NGM) and random effects (Genotype, Environment, and their interaction G × E). When excluding the variation of Genotype, Environment and G x E interaction from predictive potential of the yield components NGM had the highest predictive capacity with marginal $R^2 = 0.393$. This is a sizeable portion of yield variability, supporting its use as a valuable tool in wheat breeding for yield improvement.*

Keywords: winter wheat, yield, yield components, yield prediction, linear mixed model

Introduction

The Number of Grains per Square Meter (NGM) is a fundamental metric for evaluating the yield potential of wheat, directly reflecting the quantity of grains that can be harvested from a given area (Slafer et al., 2022). NGM's significance extends across several critical areas: *i) Yield Prediction.* NGM sets the upper limit for grain yield, essentially defining the maximum number of grains that can be produced. This is because, regardless of grain filling efficiency, the yield cannot exceed the number of grains initially set (Fischer et al., 2024). The article by Fischer (2024) highlights that targeting the duration of the critical period for grain formation can increase NGM, thereby influencing yield potential. This understanding is vital for predicting yield outcomes in different climatic scenarios; *ii) Genetic and Environmental Interaction.* NGM is not only a product of genetic makeup but also highly responsive to environmental conditions. Slafer et al. (2022) outline how physiological drivers affect the response of grains per square meter to both genetic and environmental factors. Grains per spike, influenced by genetics, interact with environmental conditions like temperature, light and water availability during the flowering stage (Kim et al., 2024). This complex interaction necessitates a

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nuanced approach in wheat breeding to select varieties that maintain or increase NGM across various environments; *iii) Crop Management.* Effective crop management strategies can be tailored based on NGM, focusing on optimizing grain numbers through controlled plant density, spike number, and grains per spike (Fischer et al., 2024). Fischer and Maurer (1978) and Calderini et al. (2020) discuss how manipulating these factors can lead to higher yields. For instance, adjusting planting density or managing water and nutrient supply to enhance grain set during critical developmental stages can significantly impact NGM, offering a practical pathway to increase yield; *iv) Climate Adaptation*. With the backdrop of climate change, optimizing NGM becomes even more critical. Variability in environmental conditions, like heat waves or drought, as discussed by Kim et al. (2024), can drastically affect grain number. Therefore, breeding for traits that ensure stability or even enhancement of NGM under adverse conditions is essential (Slafer et al., 2023; Murchie et al., 2023). Research by Ferrante et al. (2017) and Fischer et al. (2024) underscores the need for genotypes that can adapt to changing climates by maintaining or increasing NGM, which could lead to significant yield improvements. *v) Breeding efficiency.* Breeding progress in wheat has historically concentrated on improving grain yield (GY) by selecting traits that enhance yield stability across various environmental conditions. Among these traits, the Number of Grains per Square Meter (NGM) plays a crucial role, directly influencing GY. It is recognized as a key yield component and a powerful predictor of final yield potential. Despite the extensive body of research on yield components, the specific focus on NGM, particularly its stability and its role across diverse environments, remains an area of ongoing interest in wheat breeding.

Recent studies have underscored the importance of NGM in contributing to yield stability, with breeding progress showing significant gains in GY through improvements in source- and sink-related traits, including NGM, under varying environmental conditions (Wang et al., 2025). However, as highlighted by the most recent research, the continued study of NGM's role remains crucial, particularly given its relationship with environmental factors. The breeding progress in wheat has indeed led to advancements, but does NGM receive the same focused attention as other traits like biomass or harvest index? There is a growing consensus that evaluating NGM across multiple environments is vital for enhancing breeding strategies, though this aspect of breeding has not always been fully optimized for all conditions.

The variety set under study represents an opportunity to assess this important yield component across diverse environments to better understand its predictive capacity. These trials aim to determine whether there is enough variation in NGM among the genotypes to be of use in breeding programs that focus on improving GY stability and resilience. This dataset allows for an in-depth analysis of how NGM behaves across environments and whether there is noticeable progress in the genetic improvement of this trait.

In countries where wheat breeding efforts are well-established, such as those of CIMMYT or international programs, there is substantial literature indicating that NGM has proven its effectiveness as a yield-related trait. For example, in the CIMMYT breeding program, traits such as biomass, harvest index, and NGM have been key to yield improvements, especially under stress conditions like drought and heat (Mondal et al., 2020). These findings underline the relevance of NGM in strategic wheat breeding and its potential for enhancing resilience to environmental variability.

In conclusion, the current study's focus on 118 wheat genotypes provides an exciting opportunity to refine our understanding of NGM's role in yield potential. Although significant progress has been made in selecting for traits that affect GY, the specific study of NGM across contrasting environments remains a valuable area of research, especially for breeding programs aiming to increase GY and ensure more sustainable wheat production. The collected data will help assess whether the trait's effectiveness aligns with the global literature and inform breeding practices moving forward.

Material and methods

Plant Material and traits

A total of 118 common winter wheat (*Triticum aestivum* L.) accessions, selected from diverse geographical origins but adapted to conditions similar to those in Bulgaria, were evaluated. The varieties primarily came from Central and Eastern Europe, with specific contributions from Russia and Ukraine (23), Western Europe (13), and North America (9). Data collection occurred over three growing seasons (2012-2015) to assess the impact of environmental variability on wheat performance. The following traits were measured across all replications: Number of Productive Tillers (NPT), Stem Height (SH), Number of Grains per Spike (NGS), Number of Grains per m² (NGM), 1000 Kernel Weight (TKW) and Grain Yield (GY).

Experimental Design

The study adopted a randomized block design with three replications. Each genotype was planted in plots measuring 7.5 m² at the Agricultural Institute, General Toshevo research Institute located in South Dobrudja, north-eastern Bulgaria, known for its temperate continental climate influenced by the Black Sea, with an average annual temperature of about 11°C and fertile soil conducive to wheat cultivation.

Statistical analyses

Descriptive statistics (including mean, variation coefficient, and standard deviation) were computed for each trait to evaluate the distribution and variability of the data. This analysis involved AMMI by GEA-R analysis of variation to determine significant G x E interactions (Pacheco et al., 2015), offering insights into the stability and adaptability of the wheat accessions across the varied climatic conditions over the span of the investigation. Linear Mixed Model fitted by REML was performed using R software (Bates et al., 2015) to evaluate the effect of predictors: NGM, TGW, NGS, NPT and PH on grain yield. Variance components in the mixed models were estimated using Restricted Maximum Likelihood (REML), a method originally proposed by Bartlett (1937) and later refined by Corbeil and Searle (1976) and Harville (1977). REML is preferred over standard Maximum Likelihood (ML) for unbiased estimation of variance components, particularly in unbalanced data structures. The models incorporated random effects for environments and genotypes to account for the genotype-by-environment interaction.

Climatic growing conditions.

During the winter (Nov–Feb), temperatures between -0.4°C and 3.7°C supported vernalization and minimized winterkill. In spring, warmer temperatures in 2014 accelerated plant growth, while summer heat (22.4°C in 2015) led to heat stress, reducing grain weight (TGW). Rainfall was highly variable. In 2013, well-distributed rainfall promoted healthy growth and grain filling, contributing to higher yields. In contrast, 2014 saw excess moisture in early growth (April–May), causing lodging and disease, resulting in the lowest yield (5.50 t/ha). The drier conditions in 2015 reduced tillering and increased drought stress during grain filling, limiting yield potential. In summary, temperature and precipitation fluctuations between years significantly impacted yield components, emphasizing the need to manage these climatic factors for stable wheat productivity.

Results

The data were arranged in year-by-year configuration (Table 1) to better capture the dynamic processes between the traits of interest and gauge their effect on yield. Close values of Mean and Median indicate balanced distribution with minimal skewness. The coefficients of variation (CV) suggested greater variability in 2014 for most traits, particularly in GY (18.8%) and NGS (22.0%), highlighting increased data dispersion in that season. The greatest variability (CV = 19.5% on average) was observed on the number of grains per spike (NGS) highlighting that this trait is more sensitive to environmental factors, regarding the sensitivity of grain number to environmental conditions. With the lowest CV= 10.2% for plant height (PH) and average variability between all variables was CV= 13.97.

Understanding the variability in agronomic traits under different environmental conditions is crucial for genotype selection and agronomic management. In this study we examined plant height (PH), number of productive tillers (NPT), thousand-grain weight (TGW), number of grains per spike (NGS), number of grains per square meter (NGM), and grain yield (GY). The analysis of yield traits across three growing seasons revealed significant variations, as confirmed by Duncan's Multiple Range Test (DMRT). Overall, the statistical assessment confirmed distinct performance trends for each agronomic trait, underscoring the importance of evaluating individual trait responses across growing seasons.

Table 1. Descriptive statistics of investigated traits by growing season.

Trait	Year	Mean	Median	Min	Max	SD	CV	Duncan test
PH	2013	95.6	95	70	120	9.78	10.2	95.6 b
	2014	104.0	102	82	130	9.54	9.21	104.0 c
	2015	89.4	88	70	118	10.0	11.2	89.4 a
NPT	2013	691	684	428	1036	111	16.0	691 c
	2014	649	640	390	965	117	18.0	649 b
	2015	477	470	265	810	88.6	18.6	477 a
TGW	2013	47.1	47.1	34.3	60.4	4.51	9.57	47.1 c
	2014	32.7	32.6	20.5	53.5	5.07	15.5	32.7 a
	2015	44.2	44.1	34.0	55.5	3.96	8.95	44.2 b
NGS	2013	29.5	29.3	16.9	46.9	4.84	16.4	29.5 b
	2014	26.7	26.2	13.2	45.5	5.89	22.0	26.7 a
	2015	35.2	34.1	13.4	59.4	7.05	20.0	35.2 c
NGM	2013	19732	19394	11572	30790	3101	15.7	19732 c
	2014	16883	16748	10317	25433	2660	15.8	16883 b
	2015	16398	16374	7959	24121	2567	15.7	16398 a
GY	2013	9.07	9	5.59	13.8	1.46	16.1	9.07 c
	2014	5.50	5.62	2.49	8.13	1.03	18.8	5.50 a
	2015	7.21	7.22	2.71	9.6	0.986	13.7	7.21 b

In order to better assess the source of variability, AMMI analysis of variation was preformed (Figure 1). All the main effects and interaction were highly significant ($p = 0.001$). The source of variation of each component was observed to be uniquely influenced by the factors or the interaction of them. To better gauge the variability, Sum of Square was calculated in percentage of attributed variability.

Most notably, the highest effect of the genotype was observed in plant height (PH) with 62.76% of the entire variability of the trait. Another yield component which has prevailing effect of genotype in variability, even though the slightest over environment, is NGS with 39.65% of variability attributed to genotype.

The rest of the measured yield components including Grain yield has the strongest influence of environment over their expression with the only exception of NGM and PH.

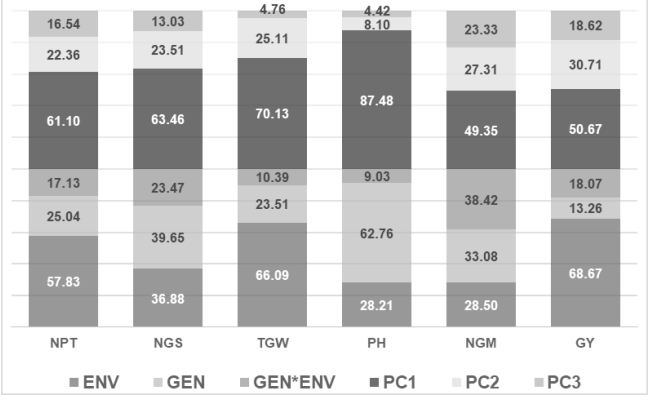

Figure1. Combined AMMI and ANOVA for traits by GEA-R statistics

Table 2. Pearson correlation between agronomic traits by growing season

Trait	Year	PH	NPT	TGW	NGS	NGM
NPT	2013	0.148		-0.271	-0.529	0.455
	2014	0.006		-0.038	-0.687	0.176
	2015	0.114		-0.271	-0.641	0.360
TGW	2013	0.019	-0.271		0.070	-0.214
	2014	-0.074	-0.038		-0.117	-0.191
	2015	0.069	-0.271		-0.165	-0.479
NGS	2013	-0.246	-0.529	0.070		0.483
	2014	-0.227	-0.687	-0.117		0.561
	2015	0.077	-0.641	-0.165		0.457
NGM	2013	-0.108	0.455	-0.214	0.483	
	2014	-0.329	0.176	-0.191	0.561	
	2015	0.239	0.360	-0.479	0.457	
GY	2013	-0.076	0.290	0.336	0.470	0.833
	2014	-0.324	0.114	0.601	0.354	0.658
	2015	0.322	0.252	0.078	0.405	0.830

NGM has its variability widely distributed across factors with the highest amount of almost 40% attributed to G x E interaction. PC1 explained the majority of the variation in most traits, especially PH (87.48%), TGW (70.13%), and NPT (61.10%), suggesting that these traits are largely captured by the first principal component. NGM was more evenly spread across PC1 (49.35%), PC2 (27.31%), and PC3 (23.33%), reflecting its complex interaction between genotype and environment. Grain yield (GY) had its variability distributed across PC1 (50.67%), PC2 (30.71%) and PC3 (18.62%), showing that multiple factors contribute to its performance.

Many agronomic traits do not have a straightforward or linear relationship with yield, and these relationships can vary by environment or genotype. While variation analysis shows which factors influence traits, correlation analysis (Table 2) helps to explore the nature of these relationships. This information could be used to make more informed decisions about which traits to prioritize under varying environmental conditions. The correlation between NPT and NGS is negative, suggesting a trade-off, where more tillers result in fewer grains per spike. However, NPT shows a positive relationship with NGM, indicating that more tillers lead to more grains per unit area. NGS and NGM are positively correlated, meaning that more grains per spike generally contribute to a higher number of grains per square meter, both of which are linked to increased grain yield. Non-linear response of NGM emerges as a consistent and strong predictor of grain yield (GY) across all three seasons. Number of productive tillers (NPT) and number of grains per spike (NGS) show complex relationships with TGW and GY, with trade-offs between certain traits. These correlations are valuable in forming breeding decisions focused on improving both yield and other agronomic traits. NGM consistently emerges as a reliable predictor of GY across seasons. However, NPT, NGS, and TGW exhibit more variable relationships, suggesting the need for careful consideration of these traits in breeding programs. Understanding these complex correlations can guide breeding decisions to optimize both grain yield and other important agronomic trait.

A Linear Mixed Model (LMM) fitted by REML (Restricted Maximum Likelihood) was used to analyse the relationship between grain yield (GY) and key predictors, including all the traits studied. The model considers fixed effects for each of the traits as predictors and random effects for environment (Env) and genotype (Var) to account for genotype-by-environment (G × E) interactions. The analysis was performed using the "lme4" package in R (Bates et al., 2015).

To assess model fit and predictive performance, the Akaike Information Criterion (AIC) was used. AIC serves as a comparative measure of model goodness-of-fit, balancing model accuracy and complexity. It is important to note that AIC values are only meaningful in comparison to other models fitted to the same dataset, rather than as absolute indicators of quality. Table 3 presents the AIC values, Conditional R^2, and Marginal R^2 for models using different predictors.

Table 3. Model Fit Statistics for Different Predictors of GY

Predictor	AIC - Scaled	AIC - Unscaled	Conditional R2	Marginal R2
NGM	405.93	1755.91	0,942	0,393
TGW	1853.93	3192,82	0,663	0,182
NGS	1799.85	3138.53	0,782	0,064
PH	1949.82	3289.49	0,783	0,009
NPT	1835.58	3180.28	0,799	0,064

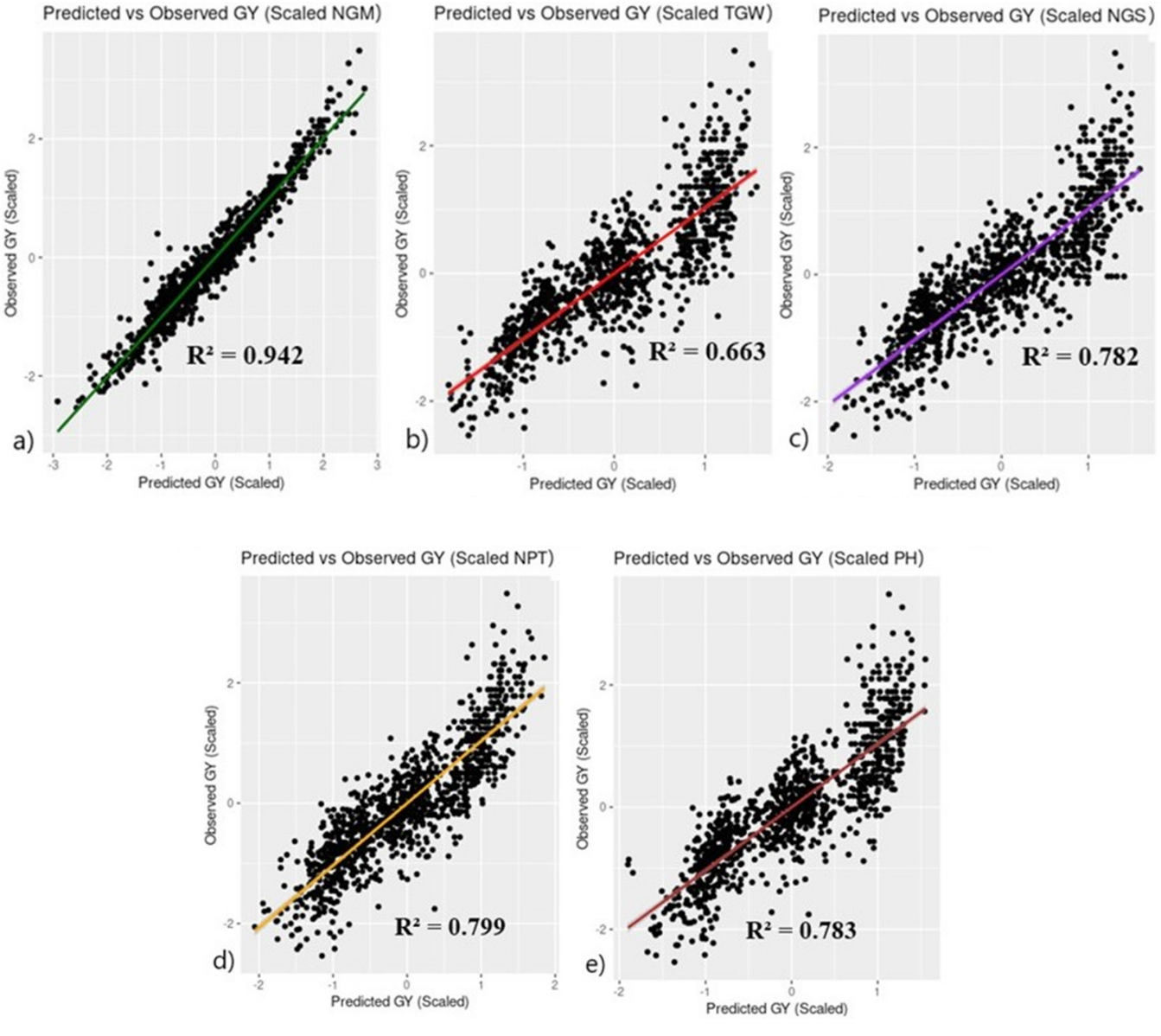

Figure 2. Linear Mixed Model fitted by REML for studied yield components.

The parameter Conditional R^2 represents the proportion of total variation explained by the model, including both fixed and random effects. The Marginal R^2, quantifies the proportion of variation explained only by the fixed effects, excluding the influence of random factors (environment and genotype).

Among the predictors, NGM exhibited the highest explanatory power, with a Conditional R^2 of 0.942 (Figure 2a), indicating that 94.2% of the total variability in GY was captured when considering both fixed and random effects. The Marginal R^2 of 0.393 suggests that 39.3% of the variation in GY is attributed to NGM alone, independent of environmental and genotypic variability.

In contrast, TGW, NGS, NPT, and PH showed lower predictive power for GY, particularly in terms of Marginal R^2. Among these, PH had the weakest association with GY, with a Marginal R^2 of only 0.009, indicating that plant height alone was not a particularly good determinant of grain yield in this study. However, the relatively high Conditional R^2 for PH (Figure 2e) suggests that its role in yield variability may be more environment- and genotype-dependent.

These results reinforce the importance of NGM as a key determinant of grain yield while highlighting the role of environmental and genetic factors in influencing trait performance.

Discussion

The results indicate that there are distinct patterns of variability across years, with significant genotype-by-environment (G × E) interactions influencing the expression of these traits, consistent with findings by Tsenov et al. (2022) and Dyulgerova and Dyulgerov (2024). *i) Trait Variability*. The descriptive statistics show that most traits were normally distributed, with close values for the mean and median, reflecting consistent data patterns. However, TGW and NGS exhibited broader ranges, with some extreme values indicating the presence of outliers, potentially due to genotype-environment interactions.

Results from analysis of variation revealed that the main effects of environment and genotype were significant for all traits, with G × E interactions playing a notable role in the variation of several traits, particularly NGM. These findings are supported by previous research by Calderini et al. (2020) and Bicego et al. (2024), which emphasize the role of genotype and environment in shaping yield component variability. Notably, the genotype explained the largest proportion of variability in plant height (62.76%) and NGS (39.65%), while the environment was the most significant factor for other traits, including TGW and NPT. This is consistent with the results of Tsenov et al. (2022), who found that environmental factors predominantly influence TGW and NPT.

NGM shows potential as a key trait for yield prediction, with a balanced contribution from genotype, environment, and G × E interaction. Its relatively high genetic control (33.08%) makes it a better breeding target than GY itself, which is largely environment-dependent (68.67%).

PH and NGS are genetically controlled traits that could be used for indirect selection, particularly PH, which had the highest genetic control (62.76%). TGW is highly environment-dependent (66.09%), meaning selection based on this trait alone may be unreliable unless stable environments can be identified. GY is heavily influenced by the environment, making direct selection difficult. Instead, selecting for NGM could provide a more stable pathway to improving yield across environments. The G × E interaction for NGM (38.42%) suggests that selecting for high NGM genotypes should involve multi-environment trials to ensure stability across diverse conditions. *ii) Mixed Models - Predictive Power.* Linear Mixed Models (LMM) with Restricted Maximum Likelihood (REML) estimation are widely used in agronomic research to account for both fixed and random effects, improving predictive accuracy for complex traits like yield (Bates et al., 2015). The REML approach, developed by Bartlett (1937) and later expanded by Corbeil and Searle (1976) and Harville (1977), was critical in estimating variance components in our models. Its ability to account for random effects without bias in unbalanced data makes it well-suited for agronomic studies involving genotype × environment interactions. In this study, model fit improved substantially

when variables were scaled, as indicated by large AIC scaled – unscaled difference (Table 3) for all traits. The high Conditional R^2 for NGM suggests that both genetic and environmental influences on grain number per square meter are critical for yield prediction, aligning with Fischer et al. (2024). The lower Marginal R^2 reinforces the importance of including random effects to capture variation beyond the fixed predictors. These findings confirm the strength of LMM in identifying key yield components, supporting its application in wheat breeding and agronomic modeling.

This indicates that, while NGM is a strong predictor, a significant amount of variability in GY is explained by random effects (genotype and environment). Other traits such as TGW and NGS showed lower Marginal R^2 values, implying that they contribute less to explaining the variability in GY when considered independently of the random effects. This is in line with findings of Xie and Sparkes (2021) and Kim et al. (2024), who reported that trade-offs between grain number and weight complicate the direct prediction of GY. *iii) Implications for Breeding.* The results highlight that NGM is a promising candidate for use in predicting grain yield. The high proportion of explained variability for NGM indicates that, despite its non-linear response to genotype-environment interactions, it is a reliable predictor of GY across different environments. Furthermore, the strong correlation (0.65-0.83) between NGM and GY, particularly across the three growing seasons, suggests that selection for high NGM could be a key strategy for improving grain yield in wheat breeding programs. This conclusion is supported by Jaisi et al. (2021), Murchie et al. (2023) and Slafer et al. (2023), who highlighted the role of source-sink relationships in driving yield potential.

On the other hand, traits such as NPT and NGS, while statistically significant, showed lower predictive power in isolation. TGW, in particular, had lower Marginal R^2 value than NGM, indicating that its predictive capacity for GY is lower. The performance of these traits may be attributed to environmental influences, which can obscure their genetic potential, as suggested by Love et al. (2023) and Beral et al. (2020).

The relationship between grain number per square meter (NGM) and thousand-grain weight (TGW) plays a crucial role in wheat yield improvement. However, this relationship is often constrained by a trade-off, which is strongly influenced by genotype × environment (G × E) interactions (Quintero et al., 2018). Our findings reinforce this complexity, as NGM consistently emerged as the most influential predictor of yield, while TGW exhibited a weaker but still significant contribution. This highlights the importance of selecting genotypes that optimize both traits under varying environmental conditions.

Despite the decrease in yield progress of new cultivars, grain number remains as the main component that best explains variation in grain yield (Valvo et al., 2018). The genetic progress in wheat breeding has historically focused on increasing NGM while maintaining TGW at stable levels (Valvo et al., 2018). This trend is evident in our study, where variation in NGM explained a significant portion of yield differences across environments. The high contribution of G × E interaction to NGM (38.42%) further supports the need for breeding strategies that enhance yield stability across diverse growing conditions. These insights emphasize the importance of LMM-based predictive modelling in identifying key selection traits, ultimately guiding breeding programs toward more resilient and high-yielding wheat varieties.

iv. Future Directions. Future research could explore the non-linear relationships between these traits and yield, as well as the underlying genetic mechanisms that contribute to the observed G × E interactions. Additionally, incorporating more environmental factors and expanding the dataset across more years and diverse locations would provide a more comprehensive understanding of the stability and predictive power of yield components. Studies such as Mirosavljević et al. (2018) and Gubatov et al. (2021) suggest that integrating genetic parameters and multi-environment trials could further refine our understanding of yield determinants.

Conclusion

In conclusion, this study highlights NGM as a crucial factor influencing grain yield and a robust trait for wheat breeding programs. Its strong association with yield, genetic and environmental responsiveness, and predictive performance make it an essential target for selection. The results indicate that genotypes with high NGM should be prioritized early in breeding due to its efficiency in increasing grain yield, while considering its variability and adaptability across different environments. The compelling evidence of NGM as a powerful yield indicator is reinforced by its consistently strong correlation with GY and balanced distribution of variation across genotype and environment. Incorporating NGM-focused strategies into breeding programs can enhance selection accuracy and yield potential. Additionally, further research on its expression and inheritance under contrasting conditions would help to effectively and robustly increase wheat yield across diverse environments.

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