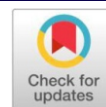


Original Research Article

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Identification of superior maize double haploid lines for compact plant architecture through multivariate and path analyses



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ABSTRACT

Maize (*Zea mays* L.) productivity under high-density planting is strongly influenced by plant architecture, physiological efficiency, and yield components. However, improving yield under dense planting conditions remains challenging due to complex interactions among architectural, physiological and reproductive traits as well as multicollinearity that complicates simultaneous trait selection. The present study evaluated 70 maize double haploid (DH) lines to identify superior genotypes with compact plant architecture suitable for high-density cultivation. The DH lines were assessed during Kharif 2023 and Rabi 2024 using an Augmented Block Design II, recording 21 morphological, physiological, phenological, and yield-related traits. Analysis of variance revealed highly significant genetic variation among DH lines for most traits, indicating substantial exploitable variability. Path analysis identified plant height and photosynthetic rate as major contributors to grain yield through strong positive direct effects, while ear diameter and ear length emerged as key yield components. Principal component analysis extracted seven principal components explaining 73.67% of the total variability highlighting considerable multivariate diversity among the DH lines. Hierarchical cluster analysis grouped the DH lines into three distinct clusters, confirming genetic divergence and enabling effective classification of genotypes based on trait performance. By integrating multivariate and causal analytical approaches, this study provides a systematic framework for dissecting complex trait interactions and identifying genotypes with optimal plant stature, efficient canopy architecture, and superior yield attributes. The findings contribute to the development of high-density tolerant maize ideotypes and offer valuable genetic resources for accelerating modern maize breeding programs.

Keywords: Planting density, Plant architecture, Variability, Double haploids, Multivariate, Cluster analysis, Yield attributes.

Introduction

Maize (*Zea mays* L.) stands as one of the most vital cereal crops globally, serving as a primary source of food, animal feed, and industrial raw materials (1). With the continuous expansion of the global population and the increasing demand for agricultural products, there is a persistent need to enhance maize productivity. High-density planting is a crucial strategy for maximizing yield per unit area; however, it often presents challenges such as increased lodging, inefficient light interception, and reduced photosynthetic efficiency, which can ultimately limit yield potential (1, 2).

To overcome these limitations, breeding for an optimized plant ideotype, particularly one with compact plant architecture, has become a paramount objective in modern maize breeding programs. Compact plant architecture is characterized by traits such as reduced plant height and ear height, more erect leaf angles, and a reduced number of tassel branches (1, 3). This architecture allows for more efficient light capture, improved ventilation within the canopy, enhanced lodging resistance, and better partitioning of assimilates under high-density planting conditions, consequently leading to higher population yields (1,2). Dwarf mutants, for instance, exhibit short, compact plants with desirable traits for lodging resistance (4).

The development and utilisation of double haploid lines have revolutionized maize breeding by significantly accelerating the breeding cycle and enhancing the efficiency of selection processes (5, 6, 7). DH technology offers several advantages, including the rapid achievement of homozygosity, leading to maximum genetic variance between lines from the first generation and increased efficiency in marker-assisted selection (6,7).

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Furthermore, DH lines derived from diverse genetic backgrounds, such as landraces or earlier cycles of recurrent selection, can unlock and broaden the genetic diversity available for breeders, enabling the identification of genotypes with desirable plant architecture traits suited for high plant density (8, 9).

Understanding the complex genetic basis of compact plant architecture requires sophisticated statistical approaches. Principal Component Analysis is an invaluable multivariate technique for reducing the dimensionality of complex phenotypic data by transforming multiple correlated traits into a smaller set of independent principal components (10). PCA has been effectively used in maize to evaluate performance components, identify key contributing traits to overall variation, and dissect genetic networks controlling complex traits like plant architecture (10, 11, 12, 13). Analysis of Variance, another fundamental statistical tool, is crucial for identifying significant genetic variations among different genotypes and treatments, as well as for assessing genetic control over various agronomic and morphological traits (14, 15).

To further refine selection and identify superior genotypes that exhibit both high mean performance and stability across multiple desirable traits, the Multi-Trait Stability Index offers a robust approach. MTSI is a novel technique in plant breeding that addresses the challenges of incorporating multiple trait data without issues of multicollinearity, allowing for the simultaneous selection of genotypes based on a comprehensive set of criteria (16, 17). The experimental setup will employ Advanced Breeding Designs to ensure the efficient and precise evaluation of the genetic material, providing a structured framework for data collection and analysis, particularly in quantitative trait loci mapping studies (18, 19, 20).

This study aims to analyze double haploid lines of maize for compact plant architecture. By integrating Principal Component Analysis, Analysis of Variance, Advanced Breeding Designs, and the Multi-Trait Stability Index, we seek to identify superior genotypes and unravel the genetic factors contributing to an improved plant ideotype for high-density planting in maize. The findings from this research are expected to contribute valuable insights for developing maize varieties with enhanced yield potential and adaptability to modern agricultural practices.

Material and Methods

Experimental material

The experimental material consisted of 70 double haploid (DH) lines of maize (*Zea mays* L.) derived from diverse parental sources of Department of Millets, Tamil Nadu Agricultural University, Coimbatore. The DH lines were developed through in vivo haploid induction followed by chromosome doubling to achieve complete homozygosity at the Double Haploid Production facility, Kunigal, Karnataka. These lines were obtained through collaborative programs involving the International Maize and Wheat Improvement Centre (CIMMYT), India and ICAR-Indian Institute of Maize Research (IIMR), Ludhiana. The lines represented diverse genetic backgrounds suitable for evaluating genetic variability and performance under field conditions. All 70 DH lines were grown and evaluated during the *Kharif* 2023 and *Rabi* 2024 seasons at the Department of Millets, Tamil Nadu Agricultural University (TNAU), Coimbatore.

Experimental design

The experiment was laid out in an Augmented Block Design II consisting of five blocks each accommodating 70 double haploid (DH) lines along with five check varieties (UMI 1220, UMI 1230, UMI 1205, UMI 1200 and UMI 1254). The check varieties were replicated once in each block, while the DH lines were unreplicated, following the standard structure of the ABD II. Each entry was planted in a single row of 4 m length, with a row-to-row spacing of 60 cm and plant-to-plant spacing of 25 cm maintaining an optimum plant density for uniform growth and development. All recommended agronomic and crop management practices were followed uniformly throughout the growing period to ensure proper crop establishment and reliable data collection.

Trait measurement

Observations were recorded on 21 traits encompassing morphological, physiological, and yield-related characters following standard maize descriptors. The compact plant architectural traits included plant height (cm), ear height (cm), leaf angle (°), leaf length (cm), leaf width (cm), internode number and internode length (cm). Phenological parameters such as days to 50% tasseling (DTT) and days to 50% silking (DTS) were recorded to study flowering behaviour. Yield-contributing traits comprised cob length (cm), cob diameter (cm), kernel row number (KRN), number of grains per row (GPKR), hundred seed weight (g) and grain yield. Physiological traits related to canopy photosynthetic efficiency were also measured, including photosynthetically active radiation (PAR; $\mu\text{mol m}^{-2} \text{s}^{-1}$) photosynthetic rate (P; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$) transpiration rate (E; $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$) stomatal conductance (C; $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$) intercellular CO_2 concentration (CO_2 ; $\mu\text{mol mol}^{-1}$) and SPAD chlorophyll index. Data were collected on a plot basis or from representative plants within each plot, depending on the nature of the trait. Traits such as plant height, ear height, leaf characteristics, flowering traits, yield components and grain yield were recorded at appropriate crop growth stages.

Data analysis and Software

All statistical analyses were performed using R software (version 4.3.0).

Results

Analysis of Variance

Analysis of variance (ANOVA) performed under Augmented Block Design II revealed highly significant differences among the maize double haploid (DH) lines for the majority of morphological, physiological and yield-related traits. Treatment mean squares were highly significant ($p \leq 0.01$) for key traits including days to 50% tasseling (DTT), days to 50% silking (DTS), plant height (PH), leaf angle (LA), leaf length (LL), leaf width (LW), ear height (EH), internode length (IL), photosynthetically active radiation (PAR), photosynthetic rate (P), transpiration rate (E), stomatal conductance (C), intercellular CO_2 concentration, ear length (EL), ear diameter (ED), grains per kernel row (GPKR), hundred-seed weight (HSW) and grain yield (GY). Block effects reflecting field heterogeneity within the augmented design were non-significant for most traits, indicating uniform experimental conditions and effective crop management. However, significant block effects were observed for plant height, leaf angle, leaf length, ear height and internode number.

Both the check entries and DH test lines as well as their comparative effect (Test vs. Check) exhibited highly significant variation for most traits evaluated. Moderate residual variances were observed for plant height (8.78), leaf angle (7.69), leaf length (4.05), ear height (4.17), and grain yield (8110.86), whereas traits such as leaf width (0.32), ear diameter (0.10), and ear length (0.63) showed very low experimental error.

Path analysis

Path analysis revealed that grain yield (GY) in maize was primarily influenced by a few key architectural, physiological, and yield component traits Figure 1. Among all predictors, plant height exhibited the strongest positive direct effect on grain yield ($\beta = 0.416$, $p = 0.002$), indicating that plants with an optimum stature contributed directly to higher yield. Similarly, photosynthetic rate had a significant and positive direct influence on grain yield ($\beta = 0.368$, $p < 0.001$), emphasizing the importance of carbon assimilation efficiency in determining final productivity (Table 1). Among yield components, ear diameter ($\beta = 0.254$, $p = 0.001$) and ear length ($\beta = 0.205$, $p = 0.003$) showed significant positive direct effects on grain yield, suggesting that improvement in ear size directly enhances kernel number and grain filling. In contrast, kernel rows per ear exerted a significant negative direct effect on grain yield ($\beta = -0.262$, $p = 0.001$), implying that an excessive number of kernel rows may impose sink limitations or lead to inefficient assimilate distribution under the studied genetic background. Other traits, including 100-seed weight, grains per kernel row, SPAD chlorophyll index and ear height, exhibited non-significant direct effects on grain yield indicating that their contribution to yield is largely indirect rather than through direct pathways (Table 2). The analysis further revealed strong interrelationships among plant architectural traits and yield components Figure 2. Plant height showed a highly significant positive direct effect on ear diameter ($\beta = 0.601$, $p < 0.001$), indicating that taller plants tended to develop thicker ears. At the same time, plant height had a significant negative effect on kernel rows per ear ($\beta = -0.564$, $p < 0.001$), suggesting a trade-off between vertical growth and kernel row formation. Conversely, ear height exhibited a significant negative direct effect on ear diameter ($\beta = -0.583$, $p < 0.001$) and a positive direct effect on kernel rows per ear ($\beta = 0.529$, $p = 0.001$). These opposing effects highlight the complex role of ear placement in shaping ear architecture and yield components.

Indirect effects analysis demonstrated that several architectural traits influenced grain yield predominantly through their effects on yield components. Plant height exerted substantial positive indirect effects on grain yield via ear diameter (0.153) and kernel rows per ear (0.148). These results indicate that the contribution of plant height to yield is not only direct but also mediated through its influence on ear structural traits. Ear height showed negative indirect effects on grain yield through both ear diameter (-0.148) and kernel rows per ear (-0.139), suggesting that higher ear placement may adversely affect ear development and ultimately reduce grain yield. Leaf angle influenced grain yield exclusively through indirect pathways. Leaf angle showed a positive indirect effect via ear diameter (0.046) and a small negative indirect effect via kernel rows per ear (-0.020) (Table 3). These findings indicate that erect leaf orientation contributes to yield primarily by improving ear development rather than through a direct effect on grain yield. Similarly, SPAD chlorophyll index exhibited a positive indirect effect on grain yield through kernel rows per ear (0.097), reinforcing the role of leaf physiological status in modulating yield components.

Principle component analysis

Principal component analysis (PCA) was performed to summarize the multidimensional variation among the 70 maize double haploid (DH) lines and to identify the major components contributing to total variability Figure 4. The results revealed that seven principal components (PCs) with eigenvalues greater than unity were extracted, collectively explaining 73.67% of the total variation among the DH lines (Table 4). The first principal component (PC1) had an eigenvalue of 4.20 and accounted for 19.98% of the total variance. The second principal component (PC2) explained 14.61% of the total variation with an eigenvalue of 3.07, bringing the cumulative variance explained by the first two components to 34.59%. The third principal component (PC3) contributed 11.31% of the total variance (eigenvalue = 2.37), while the fourth principal component (PC4) explained 9.08% of the variation (eigenvalue = 1.91). The fifth (PC5), sixth (PC6) and seventh (PC7) principal components contributed 7.55%, 5.91%, and 5.23% of the total variance, respectively. Inclusion of these components increased the cumulative variance explained to 73.67%.

The principal component scores revealed wide dispersion of the 70 maize DH lines and check genotypes across the extracted components, indicating substantial multivariate diversity (Table 4). Several genotypes exhibited extreme positive or negative scores in one or more components reflecting their distinct trait combinations. Among the DH lines DH-94, DH-32, DH-62, DH-43, DH-84, DH-115 and DH-48 recorded high positive scores in major components, highlighting their strong contribution to overall variability (Fig 5). In contrast, genotypes such as DH-75, DH-20, DH-3, DH-2 and DH-46 showed large negative scores, indicating divergent phenotypic performance.

Cluster analysis

Hierarchical cluster analysis using Ward's minimum variance method (Ward.D2) based on Euclidean distance grouped the 70 maize double haploid (DH) lines into three distinct clusters, as illustrated in the dendrogram (Figure 6) and summarized in Table 5. The dendrogram showed clear separation among the clusters at higher linkage distances, indicating substantial genetic divergence among the DH lines. Cluster I comprised 17 DH lines representing a group of genotypes with relatively similar trait combinations. Cluster II consisted of 19 DH lines forming a moderately divergent cluster. Cluster III, the largest cluster, included 34 DH lines, indicating a broad group of genotypes sharing common agro-morphological and physiological characteristics (Table 5). The clustering pattern reflected considerable diversity among the DH lines with genotypes within each cluster showing greater similarity to one another than to those in other clusters. The distinct separation of clusters further corroborated the results of principal component analysis, confirming the presence of substantial genetic variability for plant architecture, physiological and yield-related traits.

Discussion

This study employed a comprehensive approach, integrating Analysis of Variance, Path Analysis, Principal Component Analysis and Cluster Analysis to dissect the genetic variability and interrelationships of morphological, physiological and yield-related traits in 70 maize double haploid lines. The ultimate goal was to identify superior genotypes with compact plant architecture suitable for high-density planting systems, a critical objective for enhancing maize productivity (1,2).

The Analysis of Variance conducted under an Augmented Block Design II provided robust evidence of highly significant genetic differences among the DH lines for nearly all evaluated traits. This high level of variability is paramount for effective selection in breeding programs, confirming that the DH population is a rich resource for identifying lines with desirable attributes for compact plant architecture and improved yield (6, 9). The non-significant block effects for most traits underscore the effectiveness of the experimental design in controlling field heterogeneity, thereby increasing the reliability of the observed genetic differences. The moderate to very low residual variances for various traits, especially for leaf width, ear diameter and ear length, further validate the precision of the experimental measurements and the inherent genetic control over these traits (15). The significant variation observed between the check entries and the DH test lines as well as their comparative effect indicates the potential for selecting DH lines that outperform existing varieties or possess novel trait combinations valuable for breeding.

Path Analysis offered crucial insights into the direct and indirect causal relationships influencing grain yield, allowing for a more targeted breeding strategy. The strong positive direct effects of plant height and photosynthetic rate on grain yield highlight their importance as primary drivers of productivity. While compact plant architecture generally aims for reduced plant height to prevent lodging and improve light penetration under high density (1, 2), this finding suggests an "optimum stature" rather than absolute reduction is beneficial for yield, likely balancing structural integrity with photosynthetic capacity. The significant positive direct effects of ear diameter and ear length on grain yield underscore the importance of ear size as a major yield component influencing kernel number and grain filling (21). Conversely, the significant negative direct effect of kernel rows per ear on grain yield suggests a potential trade-off or sink limitation in the studied genetic background where an excessive number of rows might not translate to higher yield. Such trade-offs are common in complex biological systems and are crucial considerations for multi-trait selection (16). The observed strong interrelationships such as plant height positively affecting ear diameter but negatively impacting kernel rows per ear, and ear height showing inverse effects on ear diameter and kernel rows, reveal the intricate balance required to optimize plant and ear architecture (Fig 1). Furthermore, the analysis of indirect effects demonstrated that several architectural traits, including plant height, ear height, and leaf angle, influence grain yield through their impact on yield components (Fig 2). For instance, plant height substantial positive indirect effects on grain yield via ear diameter and kernel rows per ear suggest its multi-faceted contribution beyond direct effects, aligning with the concept of an ideal plant ideotype (4).

The Principal Component Analysis effectively summarized the multidimensional variation, with the first seven principal components cumulatively explaining a substantial 73.67% of the total variability among the DH lines (Fig 3). This high proportion indicates considerable genetic diversity within the population, making it a valuable resource for identifying genotypes with unique combinations of desirable traits (10, 12). The wide dispersion of the DH lines and check genotypes across the principal components further confirms the presence of significant multivariate diversity, which is essential for successful breeding programs (13).

Identifying specific lines like DH-94, DH-32, and DH-62 with high positive scores in major components, or DH-75, DH-20 with large negative scores, provides clear targets for selection (Fig 5). These lines represent genetic extremes that could be utilized as parents for developing new varieties or for further genetic studies to unravel the underlying genetic mechanisms of compact architecture (8).

Hierarchical Cluster Analysis corroborated the PCA findings by grouping the 70 DH lines into three distinct clusters (Fig 6). This clustering pattern based on Ward's minimum variance method, reflects significant genetic divergence and the presence of genetically distinct groups within the population. Such groupings are invaluable for breeders, as they allow for the selection of diverse parents for hybridization to maximize heterosis or for identifying groups of lines with similar desirable traits for specific breeding objectives (18). For instance, one cluster might contain lines optimized for reduced plant height and erect leaf angles, while another might be characterized by superior ear development and yield components. The identification of such distinct clusters simplifies the selection process and facilitates the development of improved maize varieties tailored for high-density planting conditions (22).

Table 1: Standardized direct effects of component traits on grain yield (GY) in maize

Predictor	Std. direct effect	P-value	Effect
Plant height (PH)	0.416	0.002	Positive
Photosynthesis (P)	0.368	<0.001	Positive
Ear diameter (ED)	0.254	0.001	Positive
Ear length (EL)	0.205	0.003	Positive
Kernel rows (KR)	-0.262	0.001	Negative
100-seed weight (HSW)	0.102	0.134	NS
GPKR	-0.102	0.156	NS
SPAD	0.037	0.626	NS
Ear height (EH)	0.020	0.883	NS

Table 2: Standardized direct effects among yield-related traits

Path	Std. effect	P-value
PH → ED	0.601	<0.001
EH → ED	-0.583	<0.001
PH → KR	-0.564	<0.001
EH → KR	0.529	0.001
PH → GPKR	0.397	0.025
P → GPKR	-0.243	0.024

Table 3: Key indirect effects of plant architecture traits on grain yield in maize

Indirect path	Calculation	Indirect effect
PH → ED → GY	0.601×0.254	0.153
PH → KR → GY	-0.564×-0.262	0.148
EH → ED → GY	-0.583×0.254	-0.148
EH → KR → GY	0.529×-0.262	-0.139
LA → ED → GY	0.182×0.254	0.046
LA → KR → GY	0.076×-0.262	-0.020
SPAD → KR → GY	-0.372×-0.262	0.097

Table 4: Eigenvalues and percentage contribution of principal components explaining variability among maize traits

PC	Eigenvalue	Percentage of Variance	Cumulative Percentage of Variance
PC1	4.195375	19.97798	19.97798
PC2	3.06821	14.61052	34.5885
PC3	2.374941	11.30924	45.89774
PC4	1.907147	9.081653	54.9794
PC5	1.584709	7.546231	62.52563
PC6	1.242128	5.914896	68.44052
PC7	1.097485	5.226117	73.66664

Table 5: Grouping of seventy double haploid lines into three cluster based on agro-morphological traits

Cluster I	Cluster II	Cluster III
DH-50, DH-3, DH-81, DH-32, DH-66, DH-94, DH-43, DH-20, DH-110, DH-75, DH-84, DH-21, DH-56, DH-68, DH-13, DH-33, DH-103	DH-58, DH-112, DH-31, DH-29, DH-27, DH-34, DH-72, DH-18, DH-2, DH-115, DH-19, DH-55, DH-41, DH-49, DH-25, DH-48, DH-79, DH-44, DH-17, DH-85	DH-6, DH-47, DH-91, DH-116, DH-23, DH-39, DH-22, DH-102, DH-80, DH-100, DH-73, DH-99, DH-45, DH-63, DH-67, DH-38, DH-59, DH-90, DH-69, DH-53, DH-62, DH-52, DH-28, DH-37, DH-40, DH-46, DH-109, DH-35, DH-108, DH-26, DH-71, DH-93, DH-42

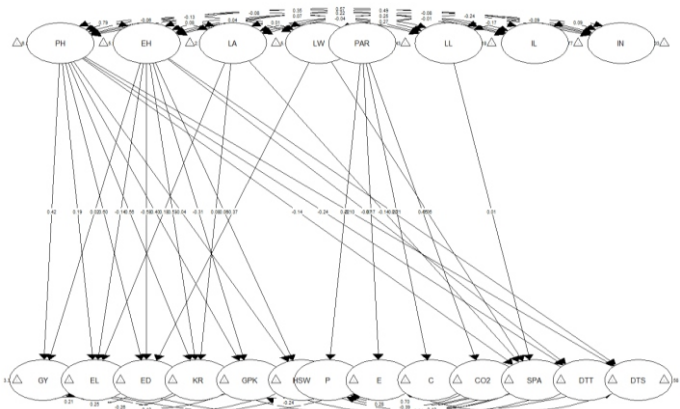


Figure 1. Path analysis of plant architecture traits influencing yield in maize

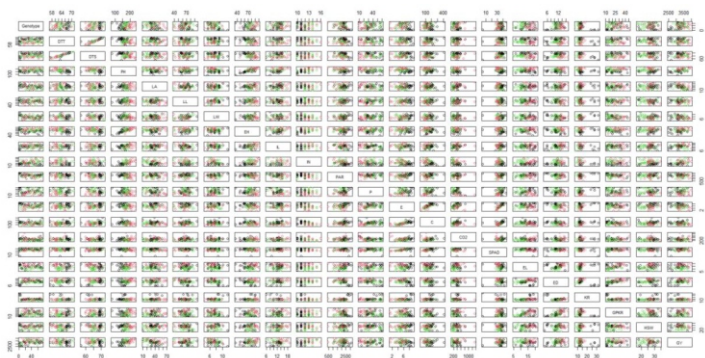


Figure 2. Pairwise scatter plot matrix illustrating interrelationships among studied traits in maize double haploid lines

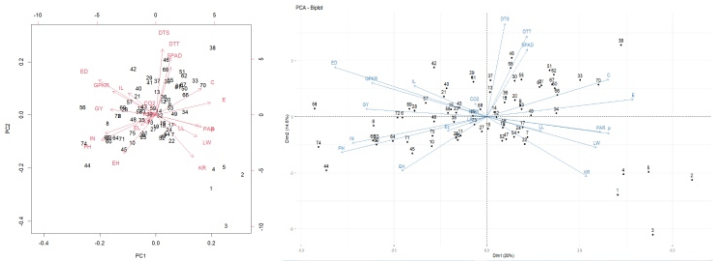


Figure 3. PCA biplot of maize DH lines based on agro-morphological and physiological traits

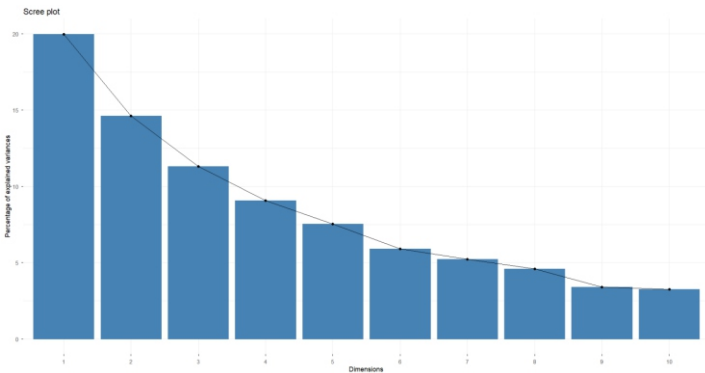


Figure 4. Scree plot showing the percentage of variance explained by the first ten principal components.

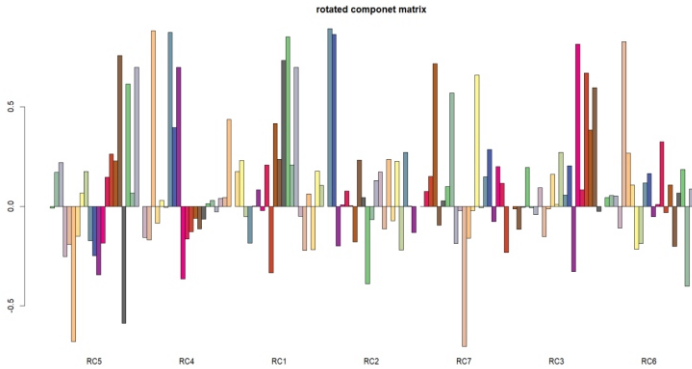


Figure 5. Rotated component matrix showing factor loadings of traits across principal components

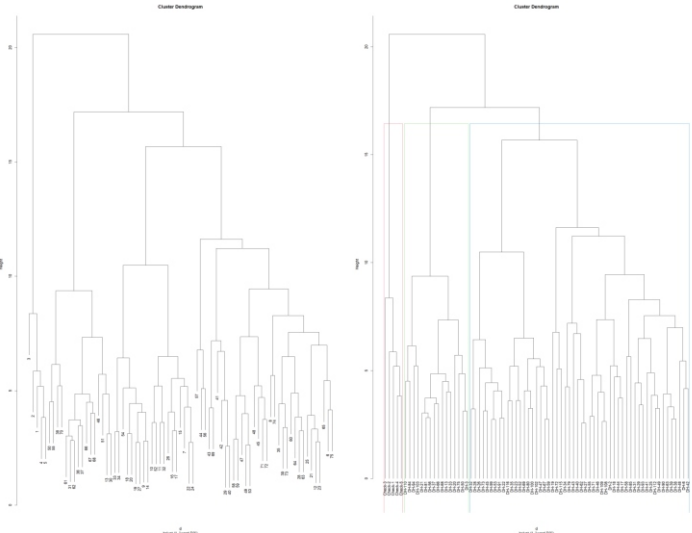


Figure 6. Dendrogram showing hierarchical clustering of 70 maize DH lines using Ward's minimum variance method based on Euclidean distance

Conclusion

The present investigation demonstrated substantial genetic variability among maize double haploid lines for compact plant architecture, physiological traits and grain yield under high-density planting conditions. The significant differences revealed through analysis of variance confirm the effectiveness of double haploid technology in generating diverse and homozygous breeding material suitable for precise selection. Path analysis highlighted plant height and photosynthetic rate as critical determinants of grain yield emphasizing the importance of achieving an optimum plant stature rather than extreme dwarfism for maximizing productivity. Ear diameter and ear length were identified as key yield components with strong direct effects on grain yield, while several architectural traits contributed indirectly through their influence on ear development. Principal component analysis effectively summarized the complex trait relationships revealing substantial multivariate diversity and enabling the identification of DH lines with unique and desirable trait combinations. The clustering of DH lines into three distinct groups further confirmed the genetic divergence within the population and provided a practical framework for selecting diverse parents and superior genotypes for breeding programs.

The study concludes that selecting genotypes with optimal plant height, efficient canopy structure, enhanced photosynthetic capacity and superior ear traits can significantly improve grain yield under high-density planting. The identified DH lines offer valuable genetic resources for developing maize varieties adapted to modern intensive agricultural systems and can serve as potential parents for future hybrid development and genetic mapping studies targeting compact plant architecture.

Future Scope

Although the present study successfully identified superior DH lines for compact plant architecture and yield under high-density planting, further research is required to validate their performance across diverse agro-climatic conditions and multi-location trials. Future investigations may incorporate genomic tools such as marker-assisted selection and genome-wide association studies to dissect the underlying genetic architecture of compact plant type and yield-related traits. Integrating physiological modeling and high-throughput phenotyping approaches could enhance the precision of ideotype breeding. The identified DH lines may also be utilized in hybrid development programs and quantitative trait loci (QTL) mapping to accelerate the development of climate-resilient, high-density tolerant maize hybrids.

Data Availability Statement

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

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Conflict of Interest

The authors declare that they have no conflict of interest.

References

- Jafari, F., Wang, B., Wang, H., & Zou, J. (2024). Breeding maize of ideal plant architecture for high-density planting tolerance through modulating shade avoidance response and beyond. *Journal of Integrative Plant Biology*, 66(5), 849-864.
- Sheng, H., Zhang, H., Deng, H., Zhang, Z., Qiu, F., & Yang, F. (2025). Maize COMPACT PLANT 3 regulates plant architecture and facilitates high-density planting. *The Plant Cell*, 37(2), koaf029.
- Sarkar, A., Sandhu, S., Pal, L., Kushwah, A., & Kumar, M. (2022). Productivity-based assessment of tolerance to high plant density stress in tropical maize (Zea mays L.) inbred lines and their single cross hybrids. *Indian Journal of Genetics and Plant Breeding*, 82(02), 153-160.
- Khunsa Khakwani, K. K., Muhammad Rafique, M. R., Malhi, A. R., Muhammad Altaf, M. A., Saira Saleem, S. S., & Muhammad Arshad, M. A. (2018). Maize ideotype breeding for changing environmental conditions.
- Pires, R. M. O., Ribeiro, B. G., Bustamante, F. O., Von Pinho, E. V. R., Santos, H. O., & Von Pinho, R. G. (2019). Identification of double-haploid maize plants one generation after the chromosomes doubling. *Journal of Agricultural Science*, 111(11), 1-41.
- Sserumaga, J. P., Oikeh, S. O., Mugo, S., Asea, G., Otim, M., Beyene, Y., ... & Kikafunda, J. (2016). Genotype by environment interactions and agronomic performance of doubled haploids testcross maize (Zea mays L.) hybrids. *Euphytica*, 207(2), 353-365.
- Beyene, Y., Mugo, S., Oikeh, S. O., Juma, C., Olsen, M., & Prasanna, B. M. (2017). Hybrids performance of doubled haploid lines derived from 10 tropical bi-parental maize populations evaluated in contrasting environments in Kenya. *African Journal of Biotechnology*, 16(8), 371-379.
- Ledesma, A., Santana, A. S., Sales Ribeiro, F. A., Aguilar, F. S., Edwards, J., Frei, U., & Lübberstedt, T. (2023). Genome-wide association analysis of plant architecture traits using doubled haploid lines derived from different cycles of the Iowa Stiff Stalk Synthetic maize population. *Frontiers in Plant Science*, 14, 1294507.
- Strigens, A., Schipprack, W., Reif, J. C., & Melchinger, A. E. (2013). Unlocking the genetic diversity of maize landraces with doubled haploids opens new avenues for breeding. *PloS one*, 8(2), e57234.
- Liu, H., Long, S. X., Pinson, S. R., Tang, Z., Guerinot, M. L., Salt, D. E., ... & Huang, X. Y. (2021). Univariate and multivariate QTL analyses reveal covariance among mineral elements in the rice ionome. *Frontiers in genetics*, 12, 638555.
- Miao, X., Zhu, W., Jin, Q., Song, Z., & Li, L. (2023). ZmHox32 is related to photosynthesis and likely functions in plant architecture of maize. *Frontiers in Plant Science*, 14, 1119678.
- Mounika, K., Ahamed, M. L., & Umar, S. N. (2018). Principal component and cluster analysis in inbred lines of maize (Zea mays L.). *Int. J. Curr. Microbiol. App. Sci*, 7(06), 3221-3229.
- Shrestha, J. (2016). Cluster analysis of maize inbred lines.
- Azrai, M., Aqil, M., Efendi, R., Zainuddin, B., Syam'un, E., Anshori, M. F., ... & Syam, A. (2025). Canopy architectural and physiological traits for optimizing maize yield under high planting density. *Frontiers in Sustainable Food Systems*, 9, 1469305.
- Ordas, B., Malvar, R. A., & Hill, W. G. (2008). Genetic variation and quantitative trait loci associated with developmental stability and the environmental correlation between traits in maize. *Genetics research*, 90(5), 385-395.
- Olivoto, T., Nardino, M., Meira, D., Meier, C., Follmann, D. N., de Souza, V. Q., ... & Baretta, D. (2021). Multi-trait selection for mean performance and stability in maize. *Agronomy Journal*, 113(5), 3968-3974.
- Singamsetti, A., Zaidi, P. H., Seetharam, K., Vinayan, M. T., Olivoto, T., Mahato, A., ... & Shikha, K. (2023). Genetic gains in tropical maize hybrids across moisture regimes with multi-trait-based index selection. *Frontiers in Plant Science*, 14, 1147424.
- Civan, P., Rincen, R., Danguy-Des-Deserts, A., Elsen, J. M., & Bouchet, S. (2021). Population genomics along with quantitative genetics provides a more efficient valorization of crop plant genetic diversity in breeding and pre-breeding programs. In *Population Genomics: Crop Plants* (pp. 225-288). Cham: Springer International Publishing.
- Dell'Acqua, M., Gatti, D. M., Pea, G., Cattonaro, F., Coppens, F., Magris, G., ... & Pè, M. E. (2015). Genetic properties of the MAGIC maize population: a new platform for high definition QTL mapping in Zea mays. *Genome biology*, 16(1), 167.
- Federer, W. T., & Crossa, J. (2012). I. 4 screening experimental designs for quantitative trait loci, association mapping, genotype-by environment interaction, and other investigations. *Frontiers in Physiology*, 3, 156.
- Zhou, Z., Zhang, C., Zhou, Y., Hao, Z., Wang, Z., Zeng, X., ... & Li, X. (2016). Genetic dissection of maize plant architecture with an ultra-high density bin map based on recombinant inbred lines. *Bmc Genomics*, 17(1), 178.
- Kuang, T., Hu, C., Shaw, R. K., Zhang, Y., Fan, J., Bi, Y., ... & Fan, X. (2023). A potential candidate gene associated with the angles of the ear leaf and the second leaf above the ear leaf in maize. *BMC Plant Biology*, 23(1), 540.