

RECIPROCAL EFFECT ON EAR TIP FILLING AND DIVERSITY OF AGRONOMIC TRAITS IN F1 AND F1R MAIZE GENOTYPES BASED ON MULTIVARIATE ANALYSIS

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Abstract

The performance of maize in reciprocal crosses can be altered because the female parent supplies maternal tissues, cytoplasmic inheritance and the physiological environment for kernel development. The objective of this study was to examine agronomic variation and the association of crossing direction and ear-tip filling in direct (F1) and reciprocal (F1R) maize hybrids. The study was carried out in Randuaguang Village, Lumajang, East Java, Indonesia in March to June 2025. Twenty genotypes of 10 pairs of F1 - F1R were evaluated using randomized complete block design with three replications. Eleven agronomic traits were standardized and subjected to principal component analysis (PCA) and Ward's hierarchical clustering based on Euclidean distances. The first four principal components accounted for 72.4 % of the total variation, with PC1, PC2, PC3 and PC4 accounting for 27.8 %, 21.3 %, 12.2 % and 11.1 %, respectively. Cluster analysis separated the genotypes into four groups. Cluster 3 contained six F1R genotypes and one F1 genotype and had the longest mean unfilled ear-tip section (1.72 cm), whereas Cluster 2 comprised five F1 and three F1R genotypes and had a shorter mean value (0.52 cm). F1-G8 formed a single-genotype cluster and combined the highest ear weight (288.0 g) and kernel weight (138.0 g) with the shortest unfilled ear-tip length (0.17 cm). The results indicate that crossing direction was associated with multivariate agronomic variation, although the response differed among parental combinations. F1-G8 is therefore a promising candidate for further evaluation, while direct statistical comparisons and multi-environment testing are required to confirm reciprocal effects and performance stability

Keywords:

agronomic diversity; ear tip filling; hierarchical clustering; principal component analysis; reciprocal cross

1. Introduction

Maize (*Zea mays* L.) is a strategically important crop used for food, animal feed, and industrial raw materials; therefore, improving its productivity remains a major objective of plant breeding programs. However, productivity can be increased by developing high-yielding and stable hybrids with agronomic traits appropriate to the intended production settings. Successful hybrid generation relies not only on the individual performance of parental inbred lines but also on their ability to establish cross combinations with strong heterosis and favourable combining ability. Thus, the genetic materials obtained from the crosses should be assessed for growth, flowering, ear and grain-yield traits. Characteristics such as ear length, ear diameter, number of kernel rows per ear, number of kernels per row, kernel weight, and degree of ear filling may affect final grain yield directly or indirectly. The variation expressed in these traits indicates that superior genotypes should not be selected solely on the basis of grain yield but should also be evaluated using several interrelated agronomic traits.

One important consideration in maize hybrid development is the direction of crossing, particularly the assignment of each parental line as either the female or male parent. Crosses between the same two parental lines in which their roles as female and male parents are reversed produce direct and reciprocal hybrids, hereafter designated as F1 and F1R, respectively. Although these two hybrids theoretically carry equivalent contributions from the parental nuclear genomes, they may exhibit different phenotypes because of differences in cytoplasmic inheritance, maternal effects, nuclear–cytoplasmic interactions, and parent-of-origin effects on the expression of particular traits. Differences between F1 and F1R should therefore not be attributed exclusively to cytoplasmic effects because reciprocal effects may arise from several interrelated genetic and physiological mechanisms. Santos et al. (2017) demonstrated that the direction of crossing affected the physiological quality and seed composition of maize hybrids, while Kovačević et al. (2022) reported reciprocal effects on grain yield and several other agronomic traits. A recent diallel study also demonstrated that maternal and reciprocal effects led to variation in grain yield and its component qualities, indicating that the designation of an inbred line as a female or male parent could influence the accuracy of identifying prospective hybrid combinations (John et al., 2024).

Ear filling is a complex process, indicating the combined success of flowering, pollination, fertilisation, kernel set and accumulation of assimilates throughout kernel development. Disruption of any of these processes can result in fewer kernels developed, more unfilled ear sections, or lower kernel weight and grain yield per ear. In reciprocal crosses the female parent provides the reproductive tissues in which the kernels develop and defines the cytoplasmic background of the embryo. Differential physiological condition and genetic background of the female parent may thus lead to differential kernel development and ear-filling performance. However, impacts of cross direction are not necessarily uniform across parental combinations or agronomic variables. For example, John et al. (2024) observed that the maternal and reciprocal effects of quantitative traits in maize were different. Nagesh et al. (2024) reported no significant overall differences between groups of direct and reciprocal hybrids for the attributes assessed. Mixed results show that reciprocal effects may be specific to particular combinations of parents, attributes and perhaps test conditions. Therefore, the reciprocal effects on ear fullness and other agronomic parameters should be objectively evaluated in each breeding population but not presumed to be the same for all genetic combinations.

Reciprocal effects in plant breeding research are typically investigated using univariate methods such as analysis of variance or individual comparisons of trait means. Such approaches are important to test for changes in individual variables. They may not explain the general structure of variation when many associated agronomic traits are involved. For example, grain weight per ear may be related simultaneously to ear length, ear diameter, number of kernel rows, number of kernels per row and proportion of the ear that is entirely filled. The analysis of these features separately may ignore the precise combinations of characters that distinguish one genotype from another. Principal component analysis (PCA) can be used to reduce a set of correlated variables to a smaller number of principal components that account for most of the variation in the original dataset. A PCA biplot can be used to simultaneously show the relationships among traits and the relative positions of genotypes (Lever et al., 2017). Hierarchical clustering technique also supports PCA by categorising the genotypes based on the overall similarity of all examined features. The combination of techniques allows differences between F1 and F1R hybrids to be examined as multivariate phenotypic patterns rather than as differences in mean values of individual attributes.

PCA and hierarchical cluster analysis of F1 and F1R pairs are critical for the evaluation of whether the reversal of parental roles will lead to consistent patterns of agronomic variation or will effect only

certain cross combinations. When the F1 and F1R derived from the same parental pair are positioned close to each other in a PCA biplot and assigned to the same cluster, the direction of crossing may have only a limited effect on their overall agronomic profiles. Conversely, separation of the two hybrids in the principal component space or their placement in different clusters may indicate a multivariate reciprocal effect that should be considered when assigning parental roles. These results can be further strengthened using a multi-trait selection index to identify genotypes that are closest to a predefined ideotype based on traits with different selection directions (Olivoto & Nardino, 2021). Although reciprocal effects and agronomic variation in maize have been investigated previously, studies integrating ear-filling characteristics, PCA, hierarchical cluster analysis, and multi-trait selection indices to evaluate paired F1 and F1R genotypes remain limited. Therefore, this study aimed to evaluate the variation structure of 11 agronomic traits in 20 maize F1 and F1R genotypes, determine whether cross direction was associated with genotype clustering patterns, and identify superior genotypes by integrating PCA, hierarchical cluster analysis, and a multi-trait selection index. The results are likely to give a more complete basis for assessing cross direction and selecting potential hybrid combinations in maize breeding programs

2. Materials and Methods

This study employed observational data for 20 maize genotypes (10 pairs of direct F1 crosses and their reciprocal crosses, F1R). The genotypes were grown between March to June 2025 in Randuagung Village, Lumajang Regency, East Java Province, Indonesia. The field experiment was laid out in randomised complete block design (RCBD) with three replications. Maize was sown at spacing of 30 cm within the row and 70 cm between rows. Fertilisation consisted of a basic fertiliser, a complex NPK fertiliser and urea. The first fertiliser application was 200 kg ha⁻¹ urea and 100 kg ha⁻¹ NPK fertiliser. The second application was 100 kg ha⁻¹ urea and 300 kg ha⁻¹ NPK fertiliser, while the third application was 300 kg ha⁻¹ NPK fertiliser.

Observed Traits

Eleven agronomic traits were evaluated for each genotype: plant height, ear height, tassel length, ear length, ear husk length, ear weight, kernel weight, number of kernel rows per ear, kernel length, kernel width, and ear tip filling. Ear tip filling was defined as the length of the apical portion of the ear that was not filled with kernels.

Data Analysis

Data on agronomic traits were first normalised via z-score transformation to have a mean of zero and a standard deviation of one. Standardisation was carried out to make the features comparable across different units and scales of measurement. The standardised data matrix was then subjected to principal component analysis (PCA) to minimise data dimensionality and to determine the main patterns of variation among the genotypes. The loadings of the traits for each principal component were derived by multiplying the eigenvector coefficients by the square root of the eigenvalue of that component. Biplots were used to jointly visualise trait loadings and genotype scores for the combination of PC1–PC2 and PC3–PC4.

Hierarchical cluster analysis was performed using the Ward's minimal variance approach and Euclidean distances based on the standardised values of all the 11 agronomic traits, not only PC1 and PC2 scores. This analysis was conducted to group the genotypes according to their overall similarity across the evaluated traits. The optimum number of clusters was determined through visual examination

of the dendrogram and agronomic interpretation, while also considering the distribution of genotypes among clusters. Based on these criteria, the genotypes were classified into four clusters (k=4).

3. Results

Total Variability and Contributions of the Principal Components

Principal component analysis of 20 maize genotypes for 11 agronomic parameters revealed that the first four principal components (PC1–PC4) explained 72.4% of the overall variation in the dataset (Table 1). The biggest proportion of variation (27.8%) was explained by PC1 and thus constituted the main pattern of agronomic variation across the genotypes examined. PC2 explained a further 21.3% of the variation, with the cumulative contribution of PC1 and PC2 being 49.1%. This percentage means that the first two primary components accounted for roughly 50% of the overall variation of the 11 agronomic traits. However, the total of 49.1% also suggests that a representation of only PC1 and PC2 is not enough to adequately account for the underlying structure of genotypic variance. Therefore, the proximity or distance of genotypes in the PC1–PC2 biplot should be taken as the key trends of variation, and not as a thorough description of all agronomic variations. These results demonstrate that agronomic variation among the F1 and reciprocal F1 (F1R) maize genotypes is multidimensional and cannot be adequately explained by only one or two dimensions of variation.

Table 1. Diversity (variance) and cumulative values for the first four principal components

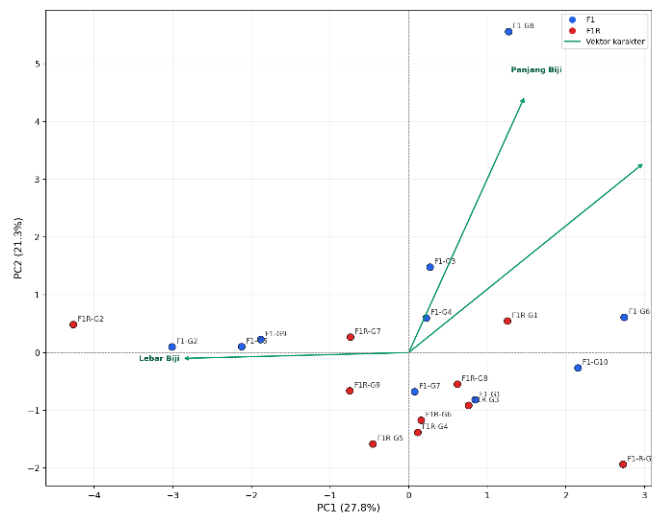
Principal Components	Variance (%)	Cumulative (%)
PC1	27,8	27,8
PC2	21,3	49,1
PC3	12,2	61,3
PC4	11,1	72,4

PC3 and PC4 explained 12.2% and 11.1% of the total variation, respectively, thereby providing an additional 23.3% of information beyond that captured by PC1 and PC2. The inclusion of PC3 increased the cumulative explained variation from 49.1% to 61.3%, whereas the inclusion of PC4 further increased it to 72.4%. The relatively similar contributions of PC3 and PC4 indicate that both components remain relevant for revealing patterns of variation not captured in the PC1–PC2 plane. Therefore, the PC3–PC4 biplot can complement the PC1–PC2 biplot when evaluating relationships among genotypes and associations among agronomic traits. The remaining 27.6% of the total variation was distributed across PC5–PC11, with each component contributing less than any of the first four principal components. The cumulative proportion of 72.4% indicates that reducing the original 11 agronomic traits to four principal components retained most of the variation contained in the dataset, although it did not capture all the observed variability. Accordingly, subsequent interpretation should integrate the PC1–PC2 and PC3–PC4 biplots and consider the loading values of individual traits to identify the characteristics that contribute most strongly to the differentiation of F1 and reciprocal F1 (F1R) genotypes.

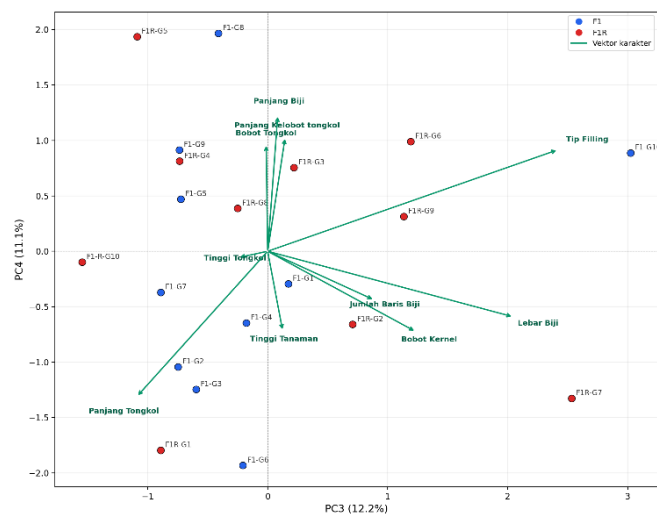
Trait Loading Patterns in the PC1–PC2 and PC3–PC4 Biplots

The PC1–PC2 biplot in Figure 1 explained 49.1% of the total variation, comprising 27.8% for PC1 and 21.3% for PC2. PC1 was primarily characterized by kernel row number, kernel weight, ear height, and plant height, whose vectors pointed in relatively similar directions, indicating positive correlations among these traits. Genotypes with positive PC1 scores were therefore expected to exhibit relatively

high values for this group of traits, whereas genotypes with negative PC1 scores showed the opposite pattern. The kernel-width vector pointed toward the negative side of PC1 and in the opposite direction from the aforementioned traits, indicating a negative association between kernel width and the combined attributes of plant size, ear position, kernel row number, and kernel weight. This pattern suggests a potential trade-off whereby genotypes with greater vegetative growth and superior ear-related components tend to produce narrower kernels. However, this relationship represents a multivariate correlation pattern within the evaluated genetic material and does not directly establish a causal relationship. Along PC2, kernel length and ear weight were directed toward the positive axis, whereas ear husk length, tassel length, and unfilled ear-tip length were directed toward the negative axis. These opposing vector directions indicate that genotypes with longer kernels and greater ear weight tend to have shorter husks and tassels and a shorter unfilled section at the ear tip.



combinations but appeared to be specific to the parental pair and the agronomic traits contributing to each principal component.



The PC3–PC4 biplot in Figure 2 explained an additional 23.3% of the total variation, comprising 12.2% for PC3 and 11.1% for PC4. Positive PC3 was primarily characterized by tip filling, measured as the unfilled ear-tip length, and kernel width, whereas ear length was oriented toward the negative side of PC3. Positive PC4 was mainly associated with kernel length, ear husk length, ear weight, and tassel length, whereas plant height and ear length tended to be positioned on the negative side of PC4. F1-G10 exhibited high positive scores for both PC3 and PC4 and was positioned relatively close to the tip-filling vector, indicating that this genotype tended to have a longer unfilled section at the ear tip. F1R-G7 also had a high positive PC3 score but was positioned on the negative side of PC4 and closer to the kernel-width vector, indicating that this genotype was characterized more strongly by relatively wide kernels than by a high tip-filling value. In contrast, F1-G8 and F1R-G5 had the highest positive PC4 scores together with negative PC3 scores, indicating stronger associations with kernel length, ear husk length, ear weight, or tassel length. F1R-G1, F1-G6, F1-G3, and F1-G2 were positioned on the negative side of PC4 and were relatively aligned with the ear-length or plant-height vectors, thereby displaying trait

patterns that differed from those of F1-G8 and F1R-G5. The separation of several F1 and F1R pairs, particularly G5, G7, G8, and G10, further indicates that responses to the direction of crossing were specific to each parental combination and were expressed through different groups of agronomic traits.

Genotype Grouping Based on Cluster Analysis

Hierarchical cluster analysis using Ward's method based on Euclidean distances calculated from the 11 agronomic traits classified the genotypes into four distinct groups (Figure 3). Cluster 1 comprised four genotypes: F1R-G2, F1-G2, F1-G5, and F1-G9. Within this cluster, F1-G5 and F1-G9 exhibited the greatest similarity because they merged at a relatively low Ward distance, after which they were joined by F1-G2 and F1R-G2 at greater distances. Cluster 2 was the largest group and comprised eight genotypes: F1-G1, F1R-G1, F1-G3, F1-G4, F1-G6, F1-G7, F1R-G8, and F1R-G10. The proximity between F1R-G1 and F1-G3 indicates that these two genotypes had relatively similar overall agronomic profiles, whereas F1-G1 and its reciprocal counterpart, F1R-G1, did not form the closest pair of branches. Cluster 3 comprised seven genotypes: F1R-G3, F1R-G4, F1R-G5, F1R-G6, F1R-G7, F1R-G9, and F1-G10. Within this cluster, F1R-G6 and F1R-G9 showed relatively high similarity, whereas F1R-G7 and F1-G10 merged at a greater Ward distance. Cluster 4 contained only F1-G8, indicating that this genotype had the most distinct agronomic profile among the 20 evaluated genotypes.

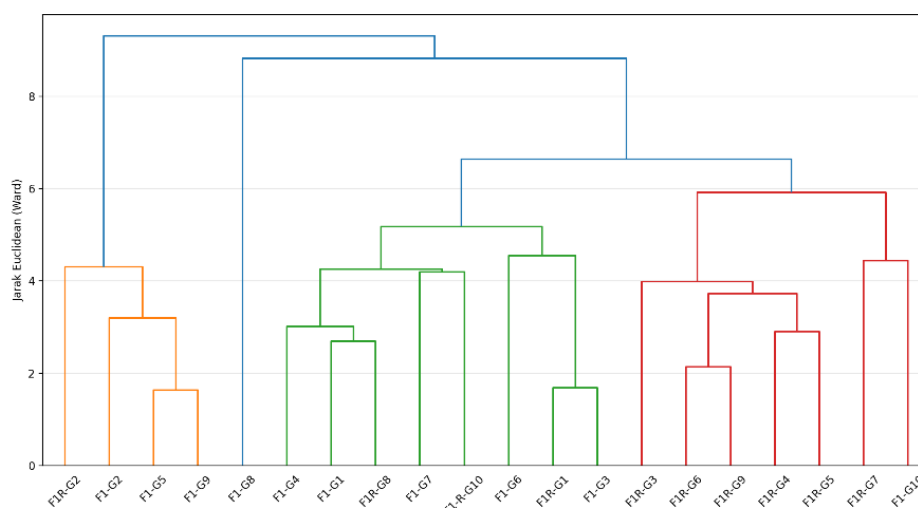


Figure 3. Dendrogram of 20 maize genotypes generated using Ward's hierarchical clustering method

Dendrogram structure also suggested that crossing direction was not a whole determinant of cluster membership, but some grouping tendencies were found between F1 and reciprocal F1 (F1R) genotypes. Cluster 2 was slightly dominated by F1 genotypes (five F1 and three F1R genotypes), but Cluster 3 was heavily dominated by F1R genotypes (six F1R and one F1 genotype). Some reciprocal pairs (F1-G2 and F1R-G2) were allocated in the same cluster, showing that the reversal of the parental roles in the G2 combination did not bring about a drastic change in its multivariate agronomic profile. Conversely, the reciprocal pairs G3, G5, G6, G7, G8, G9 and G10 were assigned to different clusters, indicating that the crossing direction was related to variations in the agronomic profiles of these combinations. The most pronounced separation was observed for the G8 pair because F1-G8 formed a singleton cluster, whereas F1R-G8 was grouped in Cluster 2 with several other genotypes. At a higher level of aggregation, Clusters 2 and 3 merged earlier than Cluster 1 and F1-G8, indicating that these two clusters retained greater overall similarity across the evaluated traits. F1-G8 merged with the remaining groups only at a high

Ward distance, further supporting its identification as an agronomic outlier. Nevertheless, this clustering pattern represents multivariate similarity and does not statistically demonstrate significant reciprocal effects; therefore, the results should be confirmed through analysis of variance and direct comparisons between each F1 and F1R pair.

4. Discussion

Reciprocal Effects on Tip Filling

The cluster analysis revealed a relatively consistent association between the direction of crossing and the degree of incomplete kernel set at the ear tip. Cluster 3, which had the highest mean unfilled ear-tip length (*tip filling*) of 1.72 cm, comprised six F1R genotypes and one F1 genotype. In contrast, Cluster 2 had a substantially lower mean *tip-filling* value of 0.52 cm and comprised five F1 and three F1R genotypes. Thus, the mean *tip-filling* value of Cluster 3 was approximately 3.3 times greater than that of Cluster 2, indicating an agronomically important difference in the completeness of kernel set. F1-G8 formed a separate cluster and exhibited the lowest *tip-filling* value of 0.17 cm, whereas its reciprocal counterpart, F1R-G8, was assigned to Cluster 2. The separation of these two genotypes suggests that reversing the female and male parental roles may be associated with changes in kernel set at the ear tip, although the magnitude and direction of these changes are likely to be specific to each parental combination. This finding is consistent with Kovačević et al. (2022) and John et al. (2024), who demonstrated that maternal effects and reciprocal differences may influence grain yield and its component traits in maize. Santos et al. (2017) also reported that reversing the parental roles can affect the physiological quality and composition of hybrid maize seed. Nevertheless, the predominance of F1R genotypes in the cluster characterized by greater unfilled ear-tip length represents evidence of a multivariate association and does not statistically demonstrate that reciprocal crosses invariably result in poorer ear filling.

In a physiological sense, partial ear-tip filling is the result of the interaction of the development of pistillate flowers, elongation of the silk, synchronisation of anthesis with silking, pollination, fertilisation, kernel establishment, and the subsequent grain filling during the reproductive phase. Generally, the ovules at the basal part of the ear develop and are pollinated earlier than those at the apical part, which develop later and are in a less favourable position to compete for photoassimilates. Yan et al. (2018) showed that plant morphology, sowing date, and plant density influence apical kernel formation, suggesting that ear-tip filling is controlled not only by genetic potential but also by plant architecture and growing environment. Kernels in the apical section of the ear have lower priority for assimilate acquisition than do kernels in the middle and basal portions of the ear. They are thus more prone to either fertilisation failure or decreased growth or kernel abortion under limited source capacity. Liu et al. (2020) showed that the number and weight of inferior kernels rose with the improvement of plant nutrient status, indicating that the ability of plant acquisition, allocation, and translocation of resources affects ear-tip filling. Furthermore, Liu et al. (2024) revealed that resistance to low-N circumstances was related to improved carbon and nitrogen metabolism and a better hormonal balance in apical kernels. More direct evidence was provided by Li et al. (2026) showing high-temperature stress decreased apical kernel weight, starch accumulation, carbon content and cell-wall invertase activity, although the negative effects could be relieved by increasing carbon supply. Overall, these results support the view that partial ear tip fill is a function of the combination of pollination success, sink strength of the apical kernels and assimilate availability, and not only of the amount of ovules originally produced. Furthermore, heat stress during pollen production might influence male fertility and effective kernel

establishment, hence environmental circumstances during flowering should be taken into account when analysing differences in tip filling among genotypes (Begcy et al., 2019).

When the direction of crossing is reversed, the inbred line previously used as the pollen donor becomes the female parent, thereby providing the ear, silks, maternal tissues, cytoplasmic genome, and physiological environment in which the kernels develop. This reversal may alter the timing of anthesis and silking, the duration of silk receptivity, the sink capacity of the ear, and the efficiency of carbon and nitrogen translocation to developing kernels. Differences in *tip filling* between F1 and F1R crosses may therefore arise from maternal effects, cytoplasmic inheritance, nuclear–cytoplasmic interactions, parent-of-origin effects in the endosperm, or differences in flowering phenology between the two crossing directions. However, the phenotypic data and cluster analysis used in the present study cannot distinguish among these underlying mechanisms. (Nagesh et al., 2024) similarly demonstrated that reversing the parental roles in maize does not necessarily produce consistent differences in hybrid grain yield, indicating that reciprocal effects should be evaluated separately for each parental combination and trait. From a practical perspective, both F1 and F1R combinations should be retained during the initial evaluation stage when complete ear filling is an important selection objective. Inbred lines producing shorter unfilled ear-tip sections when used as female parents may be prioritized, particularly when this advantage is accompanied by high ear weight, kernel weight, and kernel number. F1-G8 is a particularly promising candidate because it combined the highest ear weight with the lowest *tip-filling* value; however, its superiority over F1R-G8 should be confirmed using reciprocal contrasts or a modified diallel model. Further evaluation should include anthesis date, silking date, the anthesis–silking interval, pollen viability, ovule number, kernel-set percentage, the number or proportion of aborted kernels, and the distribution of kernel weight from the base to the tip of the ear. Multi-environment and multi-season testing is also required because apical kernel filling is sensitive to temperature, water availability, nitrogen supply, plant density, and genotype × environment interactions.

5. Conclusion

The first four principal components explained 72.4% of the total variation among the 20 maize genotypes, while cluster analysis grouped these genotypes into four distinct clusters. The dominance of the F1R genotype in the cluster with the longest unfilled ear tip length indicates a possible influence of crossing direction on the ear-filling process; however, this response is specific to each parental combination. F1-G8 exhibited the best agronomic profile, with the highest ear weight (288.0 g) and highest kernel weight (138.0 g), as well as the shortest unfilled ear tip length (0.17 cm). Therefore, F1-G8 is a potential genotype for future evaluation, and reciprocal crossing should be considered in maize hybrid selection.

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