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Selection of popcorn genotypes resistant to *Spodoptera frugiperda* and identification of resistance-related key traits

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ABSTRACT. The *Spodoptera frugiperda,* is one of the most deleterious pests of popcorn and the identification of resistant genotypes is determinant in breeding programs. The objective of this study was to select popcorn genotypes resistant to *S. frugiperda* and the key traits related to the identification of resistance. The popcorn varieties UEM J1, Composto Márcia, Arachida, Composto Gaúcho, and Zapalote Chico (resistant check) were evaluated in a completely randomized design with 100 replications. The experimental unit consisted of one Petri dish, containing plant material and a caterpillar The following traits were evaluated: larval stage duration (LSt), food intake weight(IW), final larva weight (FW), mean larva weight (MW), feces (F), assimilated (A) and metabolized food weight (M), relative consumption rate (RCR), relative metabolic rate (RMR), relative growth rate (RGR), conversion efficiency of ingested food (CEI), apparent digestibility (AD), conversion efficiency of digested food (CED), and leaf area consumed (LAC). The diagnosis of multicollinearity, analysis of canonical variables, genetic divergence, hierarchical clustering, factor analysis and canonical correspondence analysis were carried out to perform multivariate analysis. After the multicollinearity test, the traits FW, IW, RCR, AD, and LAC were maintained for further analysis. The traits IW, FW and AD were determinant in the resistance by antixenosis expressed by the varieties Zapalote Chico and Arachida, for the varieties Composto Gaúcho and Composto Márcia the determining characteristics were RCR and LAC and for the variety UEM J1 the variable LAC showed greater importance. Variety Arachida was considered resistant to *S. frugiperda* by antixenosis and can be used in the future as a source of favorable alleles to breed resistant popcorn hybrids. The traits relative consumption rate, apparent digestibility and leaf area consumed were considered key traits in the identification of resistance against *S. frugiperda* in popcorn genotypes.

Keywords: fall armyworm; genetic resistance; *Zea mays*.

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Introduction

The fall armyworm, *Spodoptera frugiperda*, is considered one of the most deleterious pests of maize in all maize-producing regions (Juárez et al., 2012, He et al., 2021). In the tropics, it causes significant economic damage because it feeds on maize from the seedling to the reproductive stage (Overton et al., 2021). In popcorn, which has been less the focus of breeding efforts than field corn, the damage tends to be more severe, since no resistant or tolerant genotypes are available on the market. Considering the increasing nationwide and worldwide demand for and importance of popcorn (Hebei Cici Co., Ltd., 2018; Caranhato et al., 2022; Stipp et al., 2024), the possibility of control by the development of resistant genotypes must be investigated and improved, since the number of insecticide applications has increased considerably over the years (Omoto et al., 2016), resulting in excessive costs and increased environmental risks.

In view of the concern to reduce or even eliminate insecticide applications and only a few of studies involving *S. frugiperda* resistance in popcorn, breeding programs ought to intensify studies to the selection of resistant and tolerant popcorn genotypes, as well as to elucidate key traits related to the identification of resistance (Oliveira et al., 2018; Paiva et al., 2016).

Although some traits related to identification of *S. frugiperda* resistance, e.g., larval stage duration, final and mean larva weight, consumption rates and leaf area consumed have been studied in maize breeding programs (Oliveira et al., 2018), they have not yet been conclusively proven and used as key traits. A likely reason may be that the trials were analyzed based on a univariate and inconclusive approach. The use of multivariate techniques is required, which can be an adequate and more efficient tool in the analysis of resistance-related data in popcorn (Aaliya et al., 2016; Veturi et al., 2012).

Resistance is the set of physical, chemical and morphological traits that will negatively affect the insect's oviposition and feeding behavior, while tolerance is the set of traits that will cause plants to withstand the attack of insects without substantial reductions in productivity in comparison with other susceptible genotypes (Aaliya et al., 2016; Veturi et al.,2012).

In this study, the hypothesis was proposed that resistance to *S. frugiperda* can be found in popcorn germplasm from tropical regions and that multivariate analysis can discriminate the main traits related to the identification of resistance. The objective of this study was to select popcorn genotypes resistant to *S. frugiperda* and the key traits related to the identification of resistance.

Material and methods

The trial was carried out in Maringá, Paraná State, Brazil, to evaluate five popcorn varieties (Table 1) for resistance to fall armyworm (*Spodoptera frugiperda*), as well as the key traits related to the identification of this resistance.

Table 1. Description of the varieties selected for study.

Code	Variety	Origin	Grain type	Genetic base
1	UEM J1	LIV	Popcorn	Open-pollinated variety
2	Zapalote Chico	CIMMYT	Field corn	Open-pollinated variety
3	Composto Márcia	MABH	Popcorn	Open-pollinated variety
4	Arachida	LIV	Popcorn	Open-pollinated variety
5	Composto Gaúcho	MABH	Popcorn	Open-pollinated variety

LIV: local landrace varieties, MABH: mixture of American and Brazilian hybrids.

The popcorn genotypes used in the trial consisted of plants of the varieties UEM J1, Composto Márcia, Arachida, Composto Gaúcho, and Zapalote Chico. The first four evaluated varieties were developed by the Specialty Corn Breeding program of the State University of Maringá. The variety used as check, Zapalote Chico, was introduced from Central América and has resistance against fall armyworm on the basis of antixenosis (alimentary avoidance) and antibiosis (lower insect survival after feeding on host tissue) (Cabrera-Toledo, Carballo-Carballo, Mejía-Contreras, García-De los Santos, & Vaquera-Huerta, 2019).

The plants were grown in a greenhouse with automatic irrigation. Crop management was carried out in accordance with the recommendations for corn culture (Oliveira et al., 2018). The seeds were separated and three sown in each pot, which contained soil and substrate (3:1). After sowing, the pots were irrigated daily and side-dressed with urea (45% N). The other cultural treatments were applied as required for full crop development, without using any other chemical product, so as not to affect larva growth.

The corn leaves used to feed the caterpillar were collected when the plants were in the eight-leaf (V8) stage, so that all varieties were evaluated when the plants were in the same developmental stage (Oliveira et al., 2018; Paiva et al., 2016; Sanches et al., 2019).

The insects required to initiate the trial were hatched from *S. frugiperda* eggs donated by Embrapa Soybean, in Londrina, Paraná State, Brazil, and from eggs collected in corn fields on the Experimental Farm of Iguatemi – Maringá, Paraná State, Brazil. The larvae hatched from these eggs were fed an artificial diet and three generations were reared to be used in our trial.

The laboratory trial was carried out in a completely randomized design, with five treatments and 100 replications in an air-conditioned chamber at 25 ± 1°C, air humidity of 70 ± 10%, and a 12h photoperiod. Each experimental unit consisted of a sterile acrylic Petri dish (diameter 9.0 cm, height 1.5 cm), lined with filter paper moistened with distilled water to maintain the leaf turgor, containing only one larva per dish, to avoid insect cannibalism. Each treatment consisted of three Petri dishes with moist filter paper and plant material, to calculate the water loss.

After hatching of the fourth larva generation raised on artificial diet, they were distributed in separate Petri dishes. The filter paper was changed, plant material was supplied to feed the larvae and the biological parameters were evaluated daily. Plant material of the same variety was continuously supplied until the end of the larval stage.

The traits were evaluated as proposed by Waldbauer (1968) with changes made by Scriber and Slansky Jr. (1981) as follows:

Larval stage duration: LSt
Food intake weight: IW
Final larva weight: FW
Mean larva weight: MW
Time period (days): T
Feces: F
Assimilated food: $A = IW - F$
Metabolized food: $M = A - FW$
Relative consumption rate: $RCR = IW/(MW * T)$
Relative metabolic rate: $RMR = M (MW * T)$
Relative growth rate: $RGR = FW/ (MW * T)$
Conversion efficiency of ingested food: $CEI = (FW/IW) * 100$
Apparent digestibility: $AD = ((A-F)/A) * 100$
Conversion efficiency of digested food: $CED = FW/A * 100$
Leaf area consumed: $LAC = IW/SDm$, where SDm: Mean surface density.

Food consumption and use were evaluated daily throughout the larval stage, by weighing the fresh food weight, leftover food weight, feces weight and larva weight. The values were measured for each larva and the mean for each repetition was calculated according to the number of live larvae on the day of the evaluation. The final data were obtained from the mean of the 100 replications per treatment.

The larva weight was measured directly by individual weighing during the whole larval stage. The daily weighing of the larvae was only initiated the 5^d after egg hatch. Food intake weight (IW) was calculated indirectly, by subtracting of the statistically corrected leftover food (Lc) weight from the weight of the supplied food (SF) on the day before.

The excreta were collected and weighed individually for each larva during the entire larval stage to obtain the total weight of feces produced (F). The leaf area consumed (LAC) was calculated indirectly from the relationship between food intake (IW) and mean surface density (SDm).

The assumptions of normality of residuals and homogeneity of variances were evaluated by the Shapiro-Wilk and Levene tests, respectively. The data were processed statistically by multivariate analysis of variance (MANOVA), using the statistical software Genes (Cruz, 2016) integrated with R software (R Core Team, 2018).

The Variance Inflation Factor (VIF) and the Condition Index (CI) were used as criteria to assess the degree of multicollinearity between the predictive traits. Variance inflation factors of >10 are generally considered evidence of substantial multicollinearity and normally the reason for the removal of certain predictors. In addition, multicollinearity is considered weak when the CI is less than 100 (Montgomery, Peck, & Vining, 2001).

Genetic divergence between the genotypes was evaluated by UPGMA (Unweighted Pair-Group Method using Arithmetic Averages), based on Mahalanobis distance. The groups were established according to the methodology proposed by Mojena (1977). Then, canonical variable analysis was carried out with clustering by the Tocher method, factor analysis and later canonical correspondence analysis (Friendly & Sigal, 2017).

Factor analysis was performed considering all evaluated traits (Johnson & Wichern, 2002). The factorial loads were extracted by the principal component method, and the factors established by varimax rotation. In this study, factor loads above 0.90 as well as the highest values for the community were considered (Keith & Reynolds, 2018). Canonical correspondence analysis was performed as described by Greenacre (1984).

The analyses were performed using the statistical software Genes (Cruz, 2016) and SAS (SAS Institute, 2015) at 1% probability.

Results and discussion

Normality ($p > 0.01$) and homogeneity of variances ($p > 0.01$) were reported for all evaluated traits. The MANOVA test showed significant differences between the mean vectors of the genotypes for all evaluated traits ($p < 0.01$), indicating the existence of genetic variability.

Multicollinearity among traits was assessed by the criteria VIF and CI. Traits with VIF and CI values greater than 10 and 100, respectively, are generally considered evidence of substantial multicollinearity among variables and makes the removal of these predictors necessary (Prunier, Colyn, Legendre, Nimon, & Flamand, 2015). The traits LSt, MW, F, A, M, RMR, RGR, CEI, and CED had high VIF and CI values and were therefore eliminated. On the other hand, the traits FW, IW, RCR, AD, and LAC had VIF and CI had values below 10 and 100, respectively, and were therefore maintained for subsequent analyses (Table 2).

Table 2. Diagnosis of multicollinearity for traits related to *Spodoptera frugiperda* resistance in five popcorn varieties (*Zea mays* L.): final larva weight (FW), food intake weight (IW), relative consumption rate (RCR), apparent digestibility (AD), and leaf area consumed (LAC).

Variance inflation factor (VIF)		Condition index (CI)	
Diagonal	Inverse element (r)	Order	Eigenvalues
1	2.9494	1	2.0070
2	5.2925	2	1.9228
3	3.6100	3	0.8289
4	2.6017	4	0.1538
5	5.7045	5	0.0876
Number of VIFs ⩾10	0	CI (max./min.)	22.9163

Multivariate techniques to select traits related to *S. frugiperda* resistance in popcorn genotypes were also used by Oliveira et al. (2018) and Sanches et al. (2019) and as in this study, the application of multivariate analysis allowed a significant reduction in the number of traits. This raises the chances of a more effective selection, since the smaller number of traits prevents the effect of interrelationships among them, avoiding redundancy and mistakes in the process of selecting promising genotypes (Aaliya et al., 2016).

The selected traits can be described as directly related to the damage caused by *S. frugiperda* larvae and can be considered key traits for the resistance of popcorn genotypes, in that resistant genotypes will have a smaller leaf area consumed (LAC) and a lower food intake weight (IW) and relative consumption rate (RCR), as well as less apparent digestibility (AD), which will result in a lower final larva weight (FW) (Souza Crubelati-Mulat et al., 2020).

In this study, the use of multivariate techniques for selection and grouping was used as a way to validate both the selection of resistant genotypes and the influence of the chosen traits on the identification of resistance.

In multivariate procedures, one of the most widely used techniques is hierarchical clustering (Oliveira et al., 2018; Paiva et al., 2016; Sanches et al., 2019). By these methods, genotypes are grouped by a process that is repeated at several levels, establishing a dendrogram, with no predetermined optimal number of groups. For this case Cruz, Carneiro, and Regazzi (2014) described different forms of representing the clustering structure based on the distance between the genotype pairs, for which UPGMA is the most commonly used method (Sanches et al., 2019; Sathua, Shahi, Mahato, Gayatonde, & Kumar, 2018; Vivodík, Petrovičová, Balážová, & Gálová, 2017).

The relationships between the varieties UEM J1, Zapalote Chico, Composto Márcia, Arachida, and Composto Gaúcho can be observed in a graph of the results of the dendrogram based on Mahalanobis' generalized distance, grouped by the UPGMA method (Figure 1). The high cophenetic correlation coefficient (CCC = 0.93) indicated an optimal fit between the original data and the dissimilarity matrix and high accuracy of the experimental results. The dendrogram shows two main groups, making the discrimination of the resistance and/or susceptibility of each genotype group possible (Friendly & Sigal, 2017; Juárez et al., 2012; Omoto et al., 2016).

The first group contained the variety Zapalote Chico, considered by several authors as resistant to *S. frugiperda* (Oliveira et al., 2018; Sanches et al., 2019), and variety Arachida. The varieties Composto Gaúcho, UEM J1, and Composto Márcia were grouped in the second (Figure 1).

The proximity of the varieties Arachida and Zapalote Chico may suggest resistance of variety Arachida to *S. frugiperda*, since the grouping was based on the same traits for both varieties. The results show (Table 3) that the varieties Arachida and Zapalote Chico had the lowest values for index LAC, IW, and RCR, aside from the low AD and FW, which indicate antixenosis resistance of these two varieties. The cultivar Zapalote Chico is so far the only one treated as resistant to *S. frugiperda*, so the identification of new resistant cultivars can be considered a great gain to the breeding since it allows to explore differents sources of resistance.

Moreover, the performance of variety Composto Gaúcho was the worst between the evaluated cultivars, and it was characterized as the most susceptible to *S. frugiperda*, based on the evaluated traits, since the values of FW, IW, RCR, AD, and LAC were high (Table 3).

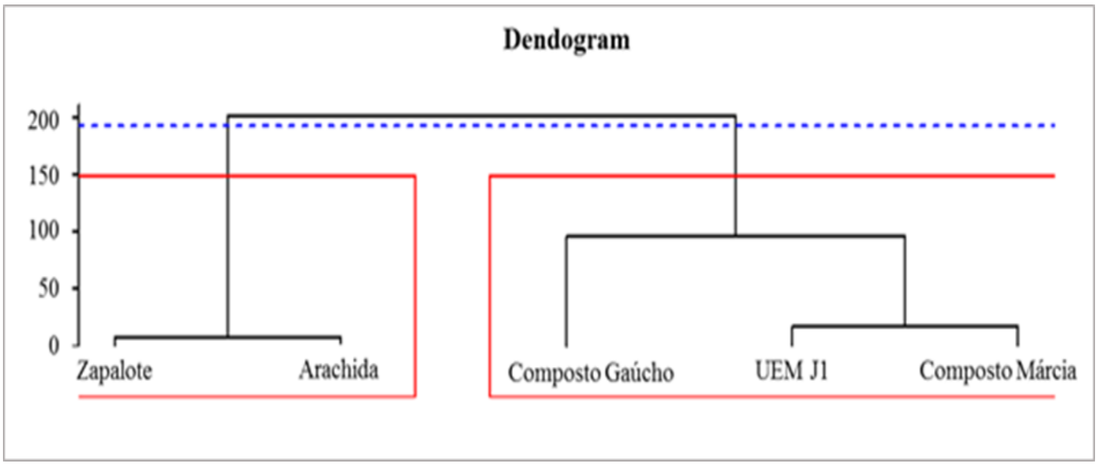

Figure 1. Dendrogram of hierarchical analysis based on Mahalanobis' generalized distance for the traits grouped by the UPGMA method among five popcorn varieties. Cutline established according to Mojena (1977).

Table 3. Means of traits related to *Spodoptera frugiperda* resistance in five popcorn varieties: final larva weight (FW), food intake weight (IW), relative consumption rate (RCR), apparent digestibility (AD), and leaf area consumed (LAC).

Varieties	FW (g)		IW (g)		RCR (g g^{-1})		AD (%)		LAC (cm^2)	
UEM J1	0.5434	ab	2.6850	bc	0.0925	b	37.3388	c	209.6653	b
Zapalote Chico	0.5306	b	2.4318	d	0.0780	d	39.4875	bc	173.8532	d
Composto Márcia	0.5348	b	2.6810	c	0.0862	c	41.0572	ab	209.7829	b
Arachida	0.5547	ab	2.4818	d	0.0763	d	39.5563	bc	186.7935	c
Composto Gaúcho	0.5678	a	2.8366	a	0.1088	a	43.1369	a	222.9237	a

Means followed by the same letter in a column do not differ statistically by the Roy and Bose test at 5% probability.

The dendrogram was confirmed and analyzed in more detail by canonical variable analysis, grouped by Tocher's clustering (Figure 2), which showed the presence of three distinct groups. Tocher's optimization is a clustering method based on the formation of groups whose distances within are shorter than the distances between groups. At the end of the process, the number of groups and accessions contained in each group are computed. This method was applied as suggested by Cruz et al. (2014) and is an important way of determining different groups based on different traits, together with the techniques of dissimilarity analysis and analysis of canonical variables (Paiva et al., 2016).

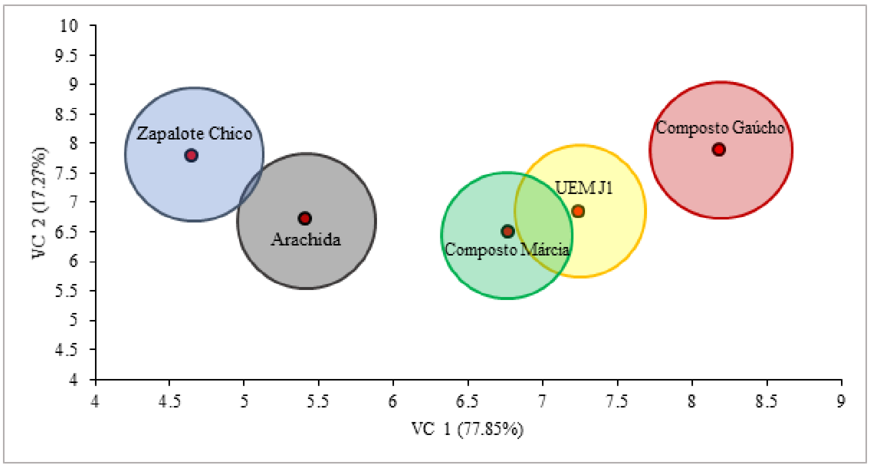

Figure 2. Biplot of canonical variable analysis showing the closest and most distant groups of five popcorn varieties grouped by Tocher's clustering.

The analysis of canonical variables explained 95.12% of the total variation between the five traits. When analyzing the dispersion of the scores of the first two canonical variables, there was an agreement with the previous groupings, confirming the results, as well as the choice of the traits used in the study of *S. frugiperda* resistance. The first canonical variable (VC 1) explained 87.85% of the total variation and the second (VC 2) 25.6% (Figure 2).

Tocher's grouping method, based on the analysis of canonical variables, grouped the varieties Zapalote Chico and Arachida again. Similarly to the variety Zapalote Chico, considered resistant by several authors because of its known resistance classified as antixenosis, i.e., feeding avoidance (Oliveira et al., 2018; Sanches et al., 2019) also in this study, some characteristics of variety Arachida like final larva weight, food intake weight, relative consumption rate, apparent digestibility and leaf area consumed also indicate antixenosis resistance. The varieties UEM J1 and Composto Márcia, which, according to the means of the analyzed variables, were moderately resitant, were contained in the second group. Variety Composto Gaúcho remained isolated from the other evaluated varieties, as the most susceptible to *S. frugiperda*, based on its performance with regard to the analyzed traits (Table 3).

Factor analysis is a multivariate statistical method that has been applied in agronomic studies for a relatively short time (Keith & Reynolds, 2018). This analysis explains the relationships observed between traits and removes possible redundancies or duplications from a set of correlated phenotypic data (Cattell, 1965). The method allows the selection of relevant traits, exploring the relationships and their variations, apart from generating important information about factors and genotypes (Vile et al., 2012). In this study, the factor analysis was directed to the identification of key traits related to resistance to *S. frugiperda*.

By factor analysis, the traits are replaced by a smaller number of latent traits, called factors. These factors group the traits, so that there is little or no variance within groups but maximum variation between groups (Cruz et al., 2014). By this technique, associated with the analysis of canonical variables and canonical correspondence, the traits that best discriminate genotypes for a given objective, here *S. frugiperda* resistance, can be efficiently selected.

In this study, the high commonality (from 0.7012 - A to 0.9912 - RCR), indicated traits with a high relation to the determination of antixenosis resistance, confirming the thesis that the selected traits can be considered key traits (Table 4). In the factor analysis, the first factor was determinant for traits IW, FW, and RCR and the second for AD and LAC (Table 4).

Table 4. Factors and their factorial loads after rotation of the factor axis by the Varimax method for studied traits related to *Spodoptera frugiperda* resistance in the composite varieties UEM J1, Zapalote Chico, Márcia, Arachida, and Gaúcho.

Variables	Factor score coefficients		Loading factors after rotation		Commonality
	Factor 1	Factor 2	Factor 1	Factor 2	
LSt	0.7481	0.1367	0.6362	0.4173	0.8784
IW	0.9849	0.1059	0.6240	0.8694	0.9813
FW	0.9745	-0.1334	0.4302	0.9843	0.9195
MW	0.5249	0.8217	0.1639	0.8612	0.8508
F	0.6063	0.7794	-0.1193	0.9803	0.8751
A	0.8301	-0.5578	0.9820	0.1894	0.7012
M	0.8159	-0.5627	0.9754	0.1760	0.9823
RCR	0.9460	0.1592	0.0645	0.9935	0.9912
RMR	0.7935	0.4367	0.5139	0.4968	0.7721
RGR	0.6952	0.5956	0.0733	0.9126	0.8381
CEI	-0.8723	-0.2911	-0.4136	-0.8213	0.8456
AD	0.1934	0.8863	0.8329	-0.4218	0.9716
CED	-0.8346	0.4910	-0.9381	-0.2400	0.9377
LAC	-0.0728	0.9870	-0.6063	0.9507	0.9625

LSt: larval stage duration, IW: food intake weight, FW: final larva weight, MW: mean larva weight, F: feces, A: assimilated food, M: metabolized food, RCR: relative consumption rate, RMR: relative metabolic rate, RGR: relative growth rate, CEI: conversion efficiency of food intake, AD: apparent digestibility, CED: conversion efficiency of the digested food, and LAC: leaf area consumed.

In this study, estimates above 0.90 were considered for one factor and low estimates for the other factor (Figure 3), which shows a high representativeness of the factor for the respective traits (Keith & Reynolds, 2018). The estimates of the other traits were intermediate between both determined factors, which despite having a certain degree of contribution to resistance, were not as expressive as the described traits. In the study of Sanches et al. (2019), a large number of traits was also reduced, and subsequently divided into two factors by factor analysis.

According to the factor analysis, the chosen traits are directly correlated with the selection of *S. frugiperda* resistant genotypes. Thus, we proceeded to the analysis of canonical correspondence.

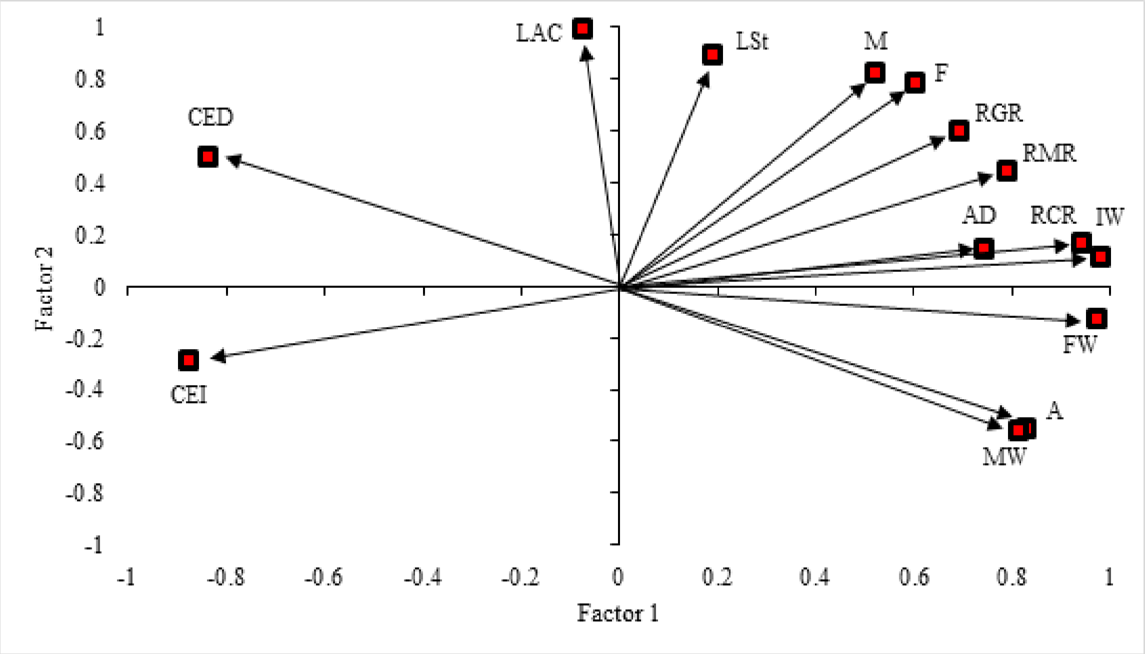

Figure 3. Biplot of factor analysis for traits related to resistance to *Spodoptera frugiperda* in the composites UEM J1, Zapalote Chico, Márcia, Arachida and Gaúcho. LSt: larval stage duration, IW: food intake weight, FW: final larva weight, MW: mean larva weight, F: feces, A: assimilated food, M: metabolized food, RCR: relative consumption rate, RMR: relative metabolic rate, RGR: relative growth rate, CEI: conversion efficiency of food intake, AD: apparent digestibility, CED: conversion efficiency of the digested food, and LAC: leaf area consumed.

Canonical correspondence analysis is an exploratory technique to simplify the structure of multivariate data variability, in which the traits are arranged in contingency tables, taking correspondence measures between rows and columns of the data matrix into account. According to Ter Braak (1987), correspondence analysis is a method to determine an association system between the elements of two or more sets, to explain the association structure of the factors in question. Thus, graphs were constructed with the principal components of the rows and columns, allowing the visualization of the relationship between the sets, where the proximity of the points referring to the row and the column indicates an association and distance indicates repulsion. According to Nyfjäll (2002), one of the great advantages of canonical correspondence analysis is that relationships can be detected by this technique that would not have been perceived if the analysis were based on trait pairs. In addition, it is highly flexible in the data traits, since no theoretical model of probability distribution must be adopted. A rectangular matrix containing non-negative data is sufficient, which in the field of breeding, makes it possible to masterfully relate the effects of different traits on specific genotypes.

Canonical correspondence analysis explained 99.67% of the total variation between the genotypes and the respective traits evaluated. The first canonical correspondence axis (CCA 1) explained 99.20% of the total variation and the second axis (CCA 2) accounted for 0.47% (Figure 4). Most of the total variation was already explained in the first CCA, which is desirable, for increasing the accuracy between the cluster and the estimated scores (Ter Braak, 1987; Nyfjäll, 2002).

The biplot of canonical correspondence analysis shows that the traits IW, FW, and AD were determinant for the resistance expressed by the varieties Zapalote Chico and Arachida, in which variable AD had a greater influence, due to its spatial angular proximity in the graph with the said varieties. For the varieties Composto Gaúcho and Composto Márcia, the traits that most contributed to the determination of resistance or susceptibility were RCR and LAC. For variety UEM J1, the influence of variable LAC was the highest.

Our results showed that the selected traits were efficient in discriminating the varieties regarding resistance and susceptibility to *S. frugiperda* by the applied analyses. The identification of key traits in the description of resistant genotypes can guide future studies, allow greater emphasis on specific traits and consequently a more effective selection regarding resistance in popcorn genotypes.

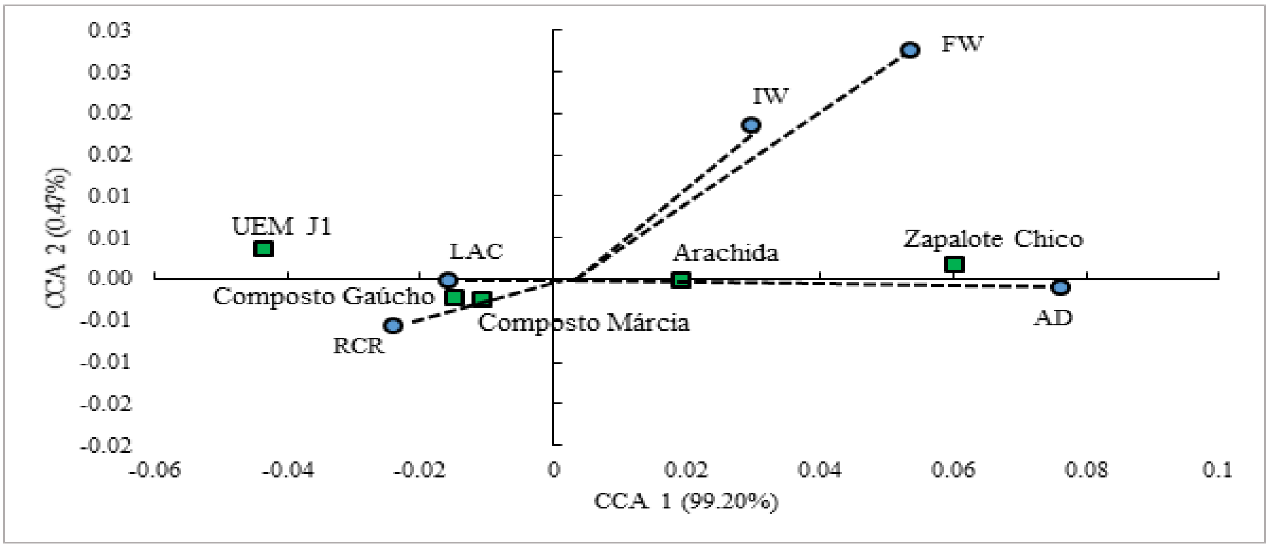

Figure 4. Biplot of canonical correspondence analysis showing the relationship between the five popcorn varieties and the main explanatory traits of resistance to *Spodoptera frugiperda*. FW: final larva weight, IW: food intake weight, RCR: relative consumption rate, AD: apparent digestibility, and LAC: leaf area consumed.

Conclusion

Variety Arachida was identified resistant to *S. frugiperda* by antixenosis and can be used as a source of favorable alleles for the future development of resistant popcorn hybrids. The traits relative consumption rate (RCR), apparent digestibility (AD) and leaf area consumed (LAC) were efficient and considered key traits for the identification of *S. frugiperda* resistant genotypes by antixenosis.

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