Acta Scientiarum
http://www.periodicos.uem.br/ojs/
ISSN on-line: 1807-8621
Doi: 10.4025/actasciagron.v47i1.70904

PLANT BREEDING

Impact of environmental covariates on genotype-environment interactions in a semi-arid region of Rio Grande do Norte State, Brazil

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ABSTRACT. Limited knowledge exists on the impact of environmental covariates on the genotype-by-environment (G × E) interaction in melon cultivated under semi-arid conditions. This study assessed the influence of environmental covariables on G × E interactions and identified melon genotypes demonstrating adaptability and stability. Thirteen yellow melon hybrids were evaluated in randomized blocks with three replications across four municipalities in Rio Grande do Norte State during two distinct seasons. Traits investigated included the number of fruits per plant and soluble solids. Factor regression and principal component analysis were employed to quantify the influence of maximum and minimum temperature, relative humidity, and radiation on the G × E interactions. The Harmonic Mean of Relative Performance of the Genotypic Values method identified adapted and stable genotypes. The covariate-biplot model established relationships between crucial environmental covariables and their impact on the number of fruits per plant and soluble solids. Minimum temperature, relative humidity, and solar radiation significantly contributed to the G × E interactions in melon. Hybrids exhibited distinct sensitivities to environmental covariates, with HA-08 emerging as the most stable and adapted hybrid for both the number of fruits per plant and soluble solids.

Keywords: *Cucumis melo* L.; mixed models, REML/BLUP; multivariate analysis; factor regression.

Received on January 5, 2024.
Accepted on June 29, 2024.

Introduction

When evaluating different genotypes (genetic variations) across diverse environments, genotype-by-environment (G x E) interactions are common. These interactions arise because genotypes perform differently in various environments due to their unique adaptive abilities. This variation can be attributed to mechanisms that influence gene expression, ultimately leading to changes in morphology (Malosetti et al., 2016). "Environment" encompasses all non-genetic variations (Mackay, 2010; Malosetti et al., 2016), with predictable factors (e.g., soil composition and agronomic practices) and unpredictable factors (e.g., rainfall frequency, air and soil temperature, frost) contributing to G x E interaction (Allard & Brashaw, 1964).

Environmental covariates help deepen the understanding of G x E interaction by assessing its effects when environmental information is available (Gauch Jr., 2006). Researchers have employed environmental covariates to elucidate G x E interaction in various crops, including sorghum (Saeed & Francis, 1984), millet (Ramasamy et al., 1996), wheat (Voltas et al., 2005), soybean (Albuquerque et al., 2023), corn (Liu et al., 2013), and sugar cane (Ramburan et al., 2011).

In melon, few studies address the impact of environmental variables on genotype-environment interaction. The sole existing report indicates that average, maximum, and minimum temperatures significantly influence genotype-environment interaction in melon concerning yield (Nunes et al., 2011b). Factorial regression using ordinary least squares has been employed to estimate the contribution of each environmental covariate to the interaction (Van Eeuwijk et al., 1996). An alternative approach involves multivariate techniques, such as principal components or factor analysis, incorporating genotype effects as random variables, successfully applied in cowpea (*Vigna unguiculata* L. Walp) with seasonal and geographic environmental covariates (Carvalho et al., 2017).

This study aims to quantitatively assess the influence of environmental covariates on G × E interaction using multivariate techniques and mixed models and to identify genotypes exhibiting adaptability and stability under Brazilian semi-arid conditions.

Material and methods

Genotypes

Thirteen yellow melon hybrids (HA-01 to HA-12 and Goldex) were evaluated under field conditions. The HA-coded hybrids are experimental varieties from the genetic improvement program at the Federal Rural University of the Semi-arid Region (UFERSA). All hybrids are andromonoecious, with a white mesocarp and smooth yellow exocarp.

Environments

Assessments were conducted in four municipalities within the agricultural pole of Mossoró-Assu in Rio Grande do Norte State, Brazil, namely: Mossoró, Baraúna, Assú, and Apodi (Table 1). Evaluations occurred during two sowing periods in the "dry" season: June to August (SE-1) and September to November (SE-2), resulting in evaluations across eight environments.

Table 1. Location, altitude, soil type, and climatic data for the evaluation sites of yellow melon hybrid in the Mossoró-Assú Agricultural Complex, Rio Grande do Norte State, Brazil.

Environment	Season	City	Altitude	Soil	MaxT	MinT	RH	RAD
MO-01	SE-1	Mossoró	18	ERL	30.96	28.82	83.13	1943.37
BA-01	SE-1	Baraúna	94	QUN	31.71	29.59	71.45	2066.05
AS-01	SE-1	Assú	27	HAC	31.88	29.53	70.98	1868.87
AP-01	SE-1	Apodi	13	HAC	33.11	30.59	64.34	2055.69
MO-02	SE-2	Mossoró	18	ERL	31.60	29.30	66.21	1965.26
BA-02	SE-2	Baraúna	94	QUN	33.40	30.87	55.71	2274.01
AS-02	SE-2	Assú	27	HAC	29.41	27.24	74.70	1879.75
AP-02	SE-2	Apodi	13	HAC	30.73	28.46	65.50	2067.01

E1: (June-July-August); E1: (September-October-November); Altitude (m); ERL: Eutrophic Red Latosol; QUN: Quartzarenic Neosol; HAC: Haplic Cambisol. MaxT: maximum temperature (°C); MinT: minimum temperature (°C), RH: relative humidity (%); RAD: solar radiation (KJ m^{-2}).

Experimental driving

A drip irrigation system was used at all sites, with 2.0 meters between rows and 0.5 meters between drippers, applying approximately 300 m^3 ha^{-1} of water. Fertilizers were applied via fertigation based on soil analysis. Other cultural practices followed recommendations for melon cultivation in the state (Nunes et al., 2016). The experiment employed a completely randomized block design with three replications. Each plot consisted of two 5-meter rows spaced 2 meters apart, with plants spaced 0.5 meters apart, totaling 20 plants per plot. The useful area consisted of the 16 central plants.

Traits evaluated

The number of fruits per plant (NFP) and soluble solids (SS) were assessed. NFP was calculated by dividing the total number of fruits by the number of plants per plot. SS content was measured using a refractometer to extract juice samples from the mesocarp, recorded in °Brix.

Statistical analysis

Successive multiple linear regression analyses using "stepwise" selection assessed the specific effects of environmental covariates on genotype-by-environment (G × E) interaction (Nunes et al., 2011b). Multivariate analysis followed the procedure of Carvalho et al. (2017), using R software (R Core Team, 2023).

For REML/BLUP analysis, the mixed model was expressed as: y = Xb + Zg + Wc + e, wherein: *y*, *b*, *g*, and *c* correspond to the data vectors with fixed effects (block averages across environments), genotype effects (random), genotype × environment interaction effects (random), and random errors; *X*, *Z*, and *W* are the incidence matrices for *b*, *g*, and *c*, respectively. Effects from joint deviance analysis were used to derive predicted genotypic values as μ + gi, wherein: *μ* represents the overall mean, and *gi* is the genotypic effect without genotype × environment interaction. Genotypes were jointly selected for stability and adaptability using the Harmonic Mean of the Relative Performance of Genotypic Values statistic (Resende, 2007). Analyses were conducted using SELEGEN software (Resende, 2016).

Results

A significant effect ($p < 0.01$) was observed for the evaluated melon hybrids, indicating heterogeneity among the hybrids for both traits (Table 2). Additionally, a genotype × environment interaction effect was noted for both traits ($p < 0.05$), signifying varying behaviors of hybrids across different environments.

Table 2. Deviance analysis for variance components and genetic and phenotypic parameters of yellow melon hybrids for number of fruits per plant and soluble solids in eight environments of the agricultural pole of Mossoró-Assu, Rio Grande do Norte State, Brazil.

Component	Trait	
	Number of fruits per plant	Soluble solids (°Brix)
	Estimative (χ^2)	
$\hat{\sigma}_g^2$	0.027** (35.35%)	0.125** (15.73%)
$\hat{\sigma}_{ga}^2$	0.007* (10.24%)	0.176** (22.15%)
$\hat{\sigma}_e^2$	0.041 (54.31%)	0.493 (62.12%)
CV(%)	12.73	5.19
A_S	0.95	0.86
r_g	0.76	0.41

$\hat{\sigma}_g^2$: genotypic variance component; $\hat{\sigma}_{ga}^2$: variance component of the genotype-by-environment (G × E) interaction; $\hat{\sigma}_e^2$: residual variance component; CV(%): coefficient of variation; A_S: selective accuracy; r_g: genotypic correlation between all environments, *, **: significance at (5%) and (1%) respectively.

Regarding the contribution of variance components, the genotype-by-environment (G × E) interaction played a more substantial role in the phenotypic expression of soluble solids compared to the hybrid effect. Conversely, for the number of fruits, the hybrid effect was more significant. In both traits, the variance component associated with experimental error made the most substantial contribution to phenotypic variance (Table 2).

The coefficients of variation were 12.73% for the number of fruits per plant and 5.19% for soluble solids (Table 2). The selective accuracy, representing the correlation between predicted and observed genotypic values, was 0.95 for the number of fruits per plant and 0.86 for soluble solids.

The combined effect of environmental covariates explained a significant portion of the G × E interaction, accounting for 72.45% of the number of fruits per plant and 43.98% for soluble solids. Maximum and minimum temperatures were the most influential factors in explaining the G × E interaction for both traits (Table 3).

Table 3. Contribution of environmental covariates to the yellow melon genotypes for number of fruits per plant and soluble solids in eight environments of the agricultural pole of Mossoró-Assu, Rio Grande do Norte State, Brazil.

Covariate	Contribution (%) – Sum of Squares Type II	
	Number of fruits per plant	Soluble solids (°Brix)
Maximum temperature (°C)	21.41	11.43
Minimum temperature (°C)	22.64	16.49
Relative humidity (%)	14.59	8.44
Solar radiation (KJ m^{-2})	13.81	7.62
Residue	27.55	56.01

The linear regression coefficient estimates of the hybrids obtained through factorial regression of genotype-by-environment interaction for the two evaluated traits concerning environmental covariates are illustrated in Figure 1. For the number of fruits per plant, the hybrids were categorized into three groups (Figure 1A). The discrimination of genotypes was based on the estimates observed at the two temperatures.

The first group comprised hybrids HA-09, HA-06, HA-07, HA-02, HA-01, and HA-08, which were negatively influenced by maximum temperature and positively influenced by minimum temperature (Figure 1A). The second group included genotypes HA-11, HA-10, HA-03, and Goldex, which were positively influenced by maximum temperature and negatively influenced by minimum temperature. The third group encompassed genotypes HA-12, HA-04, and HA-05, showing behavior similar to the second group but with greater amplitude in the hybrid regression coefficient estimates at the two temperatures (Figure 1A).

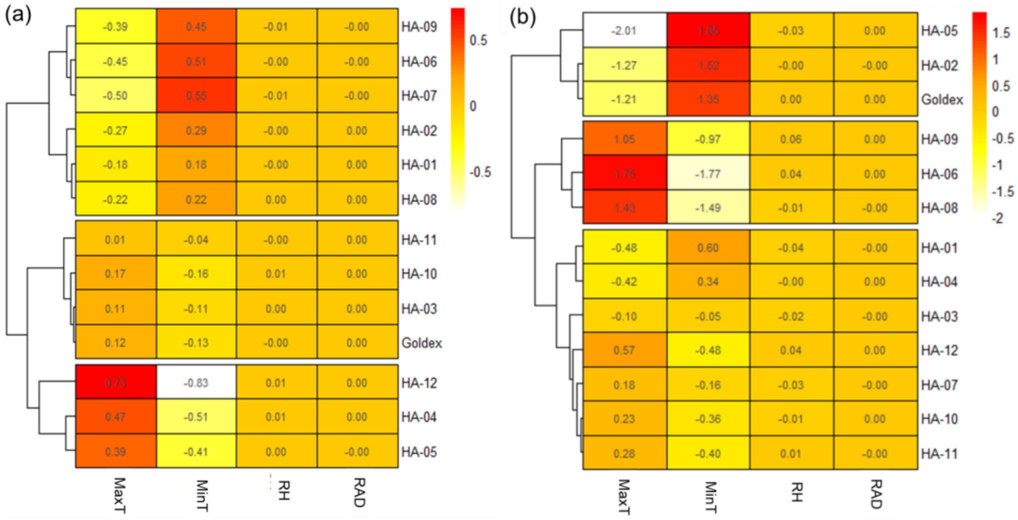

Figure 1. Heatmap with linear regression coefficient estimates for yellow melon hybrids obtained by factorial regression of genotype-by-environment interactions on the number of fruits per plant (A) and soluble solids (B) as a function of the environmental covariates in eight environments of the agricultural pole of Mossoró-Assú, Rio Grande do Norte State, Brazil. MaxT: Maximum temperature (°C); MinT: Minimum temperature (°C), RH: Relative humidity (%); RAD: Solar radiation (KJ m^{-2}).

For soluble solids, a similar pattern of three hybrid groups was identified (Figure 1B). The first group consisted of hybrids HA-05, HA-02, and Goldex, where maximum temperature negatively affected the trait, while minimum temperature had a positive effect. The second group, comprising hybrids HA-09, HA-06, and HA-08, exhibited the opposite behavior. The third group showed minimal variations in the regression coefficient estimates for all environmental covariates.

After the decomposition by singular values (DVS) of the correlation matrix between the BLUPs of the interactions and the covariate values in each environment, it was observed that for the number of fruits per plant, the first two principal components accounted for 84.4% of the variation (Figure 2A). Similarly, for soluble solids, the first two principal components jointly explained 97.3% of the variation (Figure 2B). In both cases, a two-dimensional graph is required to effectively illustrate and interpret the genotype-by-environment interaction.

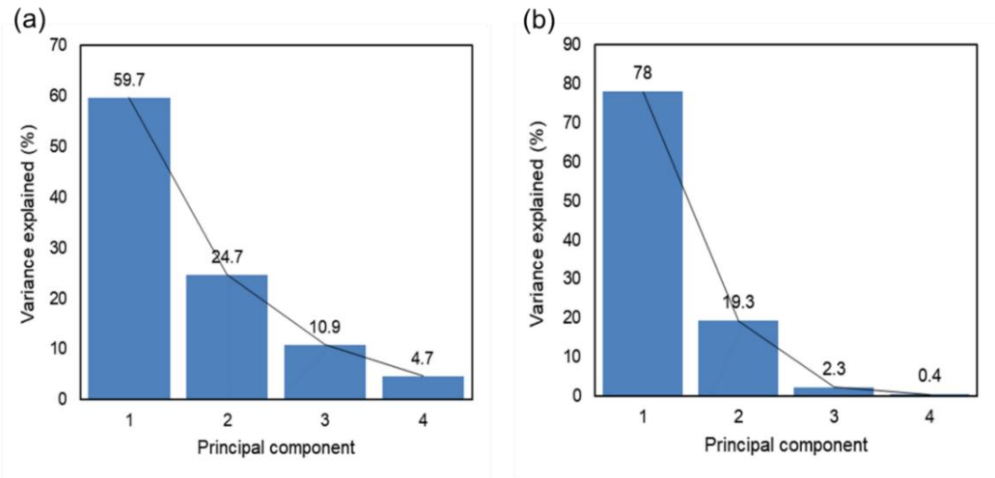

Figure 2. Contribution of the principal components to the total variation in genotype-by-environment interactions for the number of fruits per plant (A) and soluble solids (B) of yellow melon hybrids in eight environments at the agricultural pole of Mossoró-Assú, Rio Grande do Norte State, Brazil.

For the number of fruits per plant, solar radiation, minimum temperature, and relative humidity most influenced the first principal component (Figure 3A). This component contrasts the positive effects of minimum temperature and solar radiation with the negative effects of maximum temperature and relative humidity. Maximum temperature was the main contributor to the second component, interpreted as the combined positive effects of maximum temperature and solar radiation (Figure 3B).

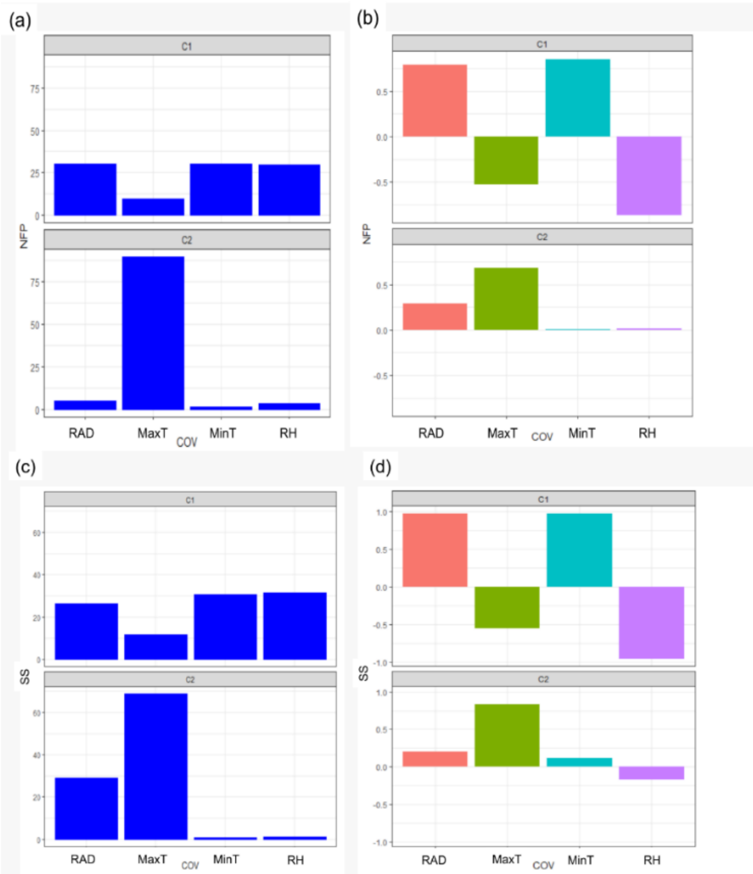

Figure 3. Contribution of the principal components to total variation in genotype-by-environment interactions for the number of fruits per plant (A, B) and soluble solids (C, D) of yellow melon hybrids in eight environments at the agricultural pole of Mossoró-Assu, Rio Grande do Norte State, Brazil. MaxT: Maximum temperature (°C); MinT: Minimum temperature (°C); RH: Relative humidity (%); RAD: Solar radiation (KJ m^{-2}); COV: Covariate; C1: Principal component 1; C2: Principal component 2.

For soluble solids, the first principal component was most influenced by solar radiation, minimum temperature, and relative humidity (Figure 3C). This component contrasts the positive effects of solar radiation and minimum temperature with the negative effects of maximum temperature and relative humidity. In the second principal component, maximum temperature and solar radiation were the most influential covariates, representing their combined positive effects (Figure 3D).

In Figure 4A, the angle cosine between vectors representing any two environmental covariates measures their association concerning their impact on the G × E interaction. For the number of fruits per plant, maximum temperature and solar radiation, positioned at a right angle (90°), show no correlation. Solar radiation and minimum temperature are positively correlated (<90°), while both are negatively correlated with relative humidity (>90°). Maximum temperature and relative humidity have a positive association (<90°).

For soluble solids (Figure 4B), a strong positive association is observed between minimum temperature and solar radiation. These covariates are negatively correlated with both maximum temperature and relative humidity, which display a weak positive association.

Figure 4 highlights the hybrid grouping patterns concerning environmental covariates. For the number of fruits per plant, two distinct hybrid groups were identified. Hybrids HA-03, HA-02, HA-07, HA-05, HA-04, and HA-06 show a positive correlation with maximum temperature and relative humidity and a negative correlation with minimum temperature and solar radiation (Figure 4A). In contrast, hybrids HA-01, HA-08, HA-09, HA-10, and HA-12 exhibit the opposite behavior. Goldex and HA-11 hybrids displayed distinct behaviors, with Goldex positively correlated with solar radiation and maximum temperature, and HA-11 showing the opposite (Figure 4A).

For soluble solids, two hybrid groups emerged (Figure 4B). The first group, including HA-07, HA-12, HA-08, Goldex, HA-09, and HA-10, showed a positive correlation with maximum temperature and relative humidity and a negative correlation with minimum temperature and solar radiation. The remaining hybrids showed the opposite behavior. HA-11 exhibited a negative influence from maximum and minimum temperatures and solar radiation, but a positive correlation with relative humidity (Figure 4B).

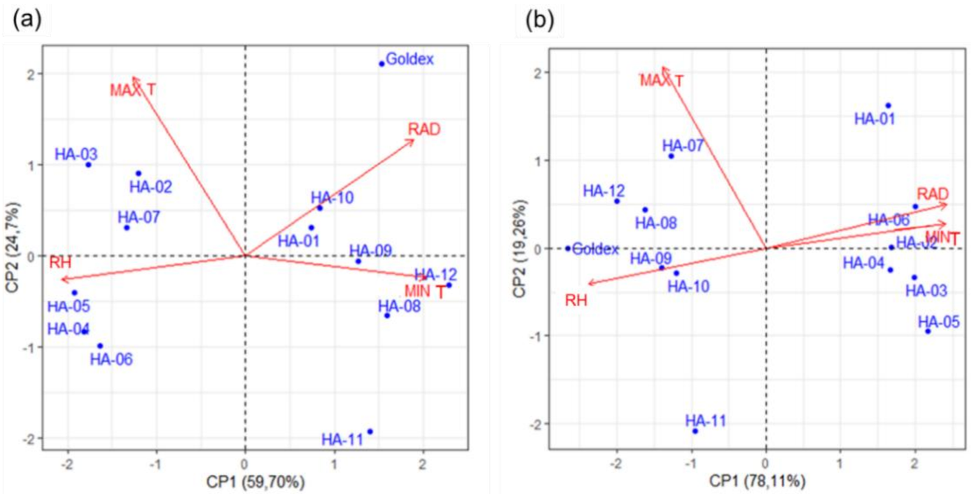

Figure 4. Contribution of the principal components to the total variation in genotype-by-environment interactions for the number of fruits per plant (A) and soluble solids (B) of yellow melon hybrids in eight environments at the agricultural pole of Mossoró-Assú, Rio Grande do Norte State, Brazil. MaxT: Maximum temperature (°C); MinT: Minimum temperature (°C); RH: Relative humidity (%); RAD: Solar radiation (KJ m^{-2}).

Genotype adaptability and stability were assessed using the harmonic mean of the relative performance of the genotypic values (HMRPGV) method. When considering both traits concurrently, four distinct quadrants were delineated (Figure 5). Proceeding clockwise, the first quadrant exclusively contains HA-08 hybrids, with HMRPGV values above the average for both traits. The second quadrant includes hybrids HA-02, HA-05, HA-10, HA-06, and HA-09, with higher-than-average HMRPGV values for the number of fruits but lower for soluble solids. The third quadrant comprises hybrids HA-01, HA-11, and HA-12, with the lowest values for both variables. The fourth quadrant includes hybrids HA-03, HA-07, Goldex, and HA-04, with above-average HMRPGV values for soluble solids and below-average values for the number of fruits per plant.

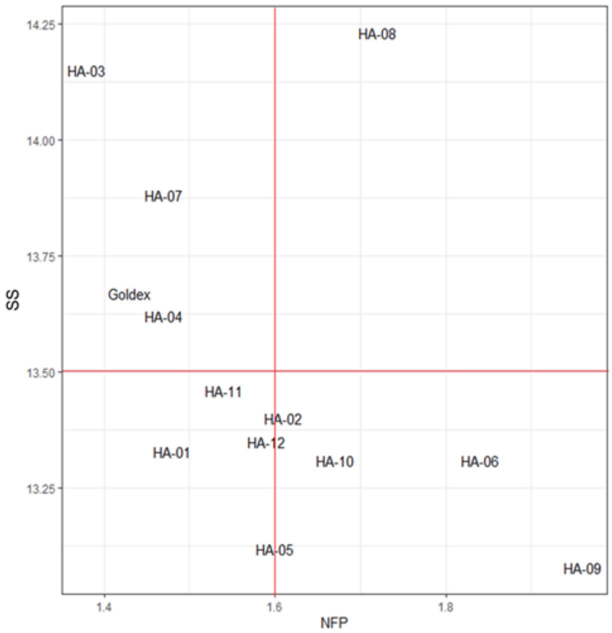

Figure 5. Distribution of HMRPGV values for the number of fruits per plant and soluble solids of yellow melon hybrids in eight environments of the agricultural pole of Mossoró-Assú, Rio Grande do Norte State, Brazil.

Discussion

Multi-environment trials are conducted to identify and recommend the most promising cultivars for specific growing regions. These trials typically involve genotypes with high production performance, requiring high experimental precision, usually measured by the residual coefficient of variation (CVE). In this study, CVE estimates were within the observed range for melon cultivar trials at the agricultural pole of Mossoró-Assú (Nunes et al., 2006; Nunes et al., 2011b; Silva et al., 2011; Guimarães et al., 2016; Oliveira et al., 2019).

Selective accuracy (AS) measures the quality of genotype evaluation experiments, reflecting the correlation between predicted genotypic values and observed values (Resende, 2007). The accuracies in this study are high (Resende & Duarte, 2007), indicating high experimental precision when considering both CVE and AS.

Genotypic variability was identified for both traits, consistent with findings in other melon trials (Nunes et al., 2006; Silva et al., 2011; Aragão et al., 2015; Guimarães et al., 2016; Silva et al., 2019; Oliveira et al., 2019). The presence of G × E interaction indicates a differential response of genotypes to varying environmental conditions. This phenomenon is commonly observed in melon genotype evaluations across different environments for productivity and soluble solids (Nunes et al., 2006; Nunes et al., 2011a; Silva et al., 2011; Aragão et al., 2015; Guimarães et al., 2016; Silva et al., 2019). In this study, the G × E interaction is primarily attributed to the simple part for the average number of fruits and the complex part for soluble solids. The prevalence of cross-interaction results from a reduced genotypic correlation (rg), leading to fluctuations in genotype rankings across the four trials and complicating the cultivar recommendation process (Cruz & Castoldi, 1991; Olivoto et al., 2019). Most cultivar evaluation studies have consistently reported the predominance of the qualitative or crossed part of the G × E interaction over the simple part for both productivity and soluble solids (Nunes et al., 2011a and b; Silva et al., 2011; Aragão et al., 2015; Guimarães et al., 2016).

In this study, four climate covariates were measured across the eight evaluation environments. Understanding the causes and nature of the G × E interaction has been a focal point for researchers. Van Eeuwijk et al. (1996) proposed incorporating environmental covariates in factorial regression to elucidate the G × E interaction. In our investigation, maximum and minimum temperatures made the most significant contributions to the G × E interaction, as determined by factorial regression analysis. Nunes et al. (2011b) found that in Cantaloupe melon hybrids in semi-arid conditions in Rio Grande do Norte, minimum, average, and maximum temperatures accounted for 39%, 35%, and 33%, respectively, of the G × E interaction. Similar observations were made in a corn study by Liu et al. (2013), noting the effects of temperature, rainfall, and solar radiation. In sugarcane, Ramburan et al. (2011) found that seasonal covariates such as temperature and water stress played crucial roles in stalk yield. Each plant species exhibits a unique response to its environment, and even within a species, different cultivars may respond differently to environmental covariates. Consequently, variations in results can be expected across different studies due to these inherent differences and environmental variations.

Factorial regression estimates the sensitivity of each genotype to individual environmental covariates. Genotypic sensitivity, quantified through the factorial regression coefficient, indicates the change in the number of fruits per plant and soluble solids in response to a one-unit change in the evaluated covariates.

The unique impact of each environmental covariate on each hybrid can be discerned by examining the magnitude and sign of the genotype's factorial regression coefficient. Genotypes exhibited distinct responses, aligning with expectations due to the intensity of the G × E interaction. In a study evaluating Cantaloupe melon hybrids, Nunes et al. (2011b) reported high sensitivity of genotypes to average and maximum temperatures.

While factorial regression is useful and commonly employed, it relies solely on regression coefficients to measure genotype sensitivity to environmental effects (Heslot et al., 2014). Approaches that treat the genotype effect as random, coupled with multivariate analysis, can provide valuable insights into the influence of environmental covariates on the interaction.

In this study, all studied covariates contributed to the (G × E) interaction with varying intensities. Minimum temperature, relative humidity, and solar radiation contributed most to the first principal component, while maximum temperature contributed most to the second component. Carvalho et al. (2017) found that seasonal variables such as mean temperature, relative humidity, total insolation, days of precipitation, and total precipitation significantly influenced cowpea genotype productivity. Differences in genotype behavior were attributed to geographic factors like latitude and longitude, and the study encompassed more diverse environments with greater soil and climate variation.

Regarding the responses of genotypes to environmental covariates, variability was observed, revealing groups of genotypes with distinct sensitivities (Figure 5). The diverse responses of cultivars to the four studied covariates highlight that the causes of the G × E interaction are rooted in physiological and biochemical factors unique to each genotype. Given that genotypes develop within dynamic systems subject to constant changes from sowing to harvest, it is expected they will exhibit varying responses to environmental fluctuations. This variability was evident in the different sensitivities of genotypes to environmental covariates when using both methodologies. Examining each genotype's response to the G × E interaction, coupled with environmental covariates, facilitated genotypic discrimination and contributed to understanding the differential behavior of hybrids across the eight environments studied.

However, comprehending the causes of G × E interaction is not sufficient; it is crucial to identify adaptable and stable genotypes for both traits under investigation. Using the HMRPGV statistic allowed for the classification of genotypes into four groups. Notably, the most outstanding hybrid was HA-08 (Figure 5), which exhibited performance above the average for both evaluated characters, making it the most promising among the evaluated group.

Conclusion

Minimum temperature, relative humidity, and solar radiation contributed most significantly to the genotype-by-environment interaction in the semi-arid region of Rio Grande do Norte State, Brazil. The hybrids differed in sensitivity to these environmental covariates, with HA-08 being the most stable and adapted for both the number of fruits per plant and soluble solids.

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