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Genetic effects of physiological and morpho-agronomic traits in popcorn under water stress

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KEYWORDS

Diallel analysis, water-stress, *Zea mays* var. *everta*

HIGHLIGHTS

- Identification of genetic effects controlling morphophysiological and agronomic traits in popcorn maize aids in designing strategies for superior gains, especially under water stress.
- Normalized difference vegetation index and relative chlorophyll content effectively revealed phenotypic differences during critical crop stages under water stress.
- Canopy temperature depression provided insights into stomatal closure.
- Dominance effects prevailed for most traits, except for popping expansion capacity and stem diameter, where additive effects were slightly stronger with and without water stress.

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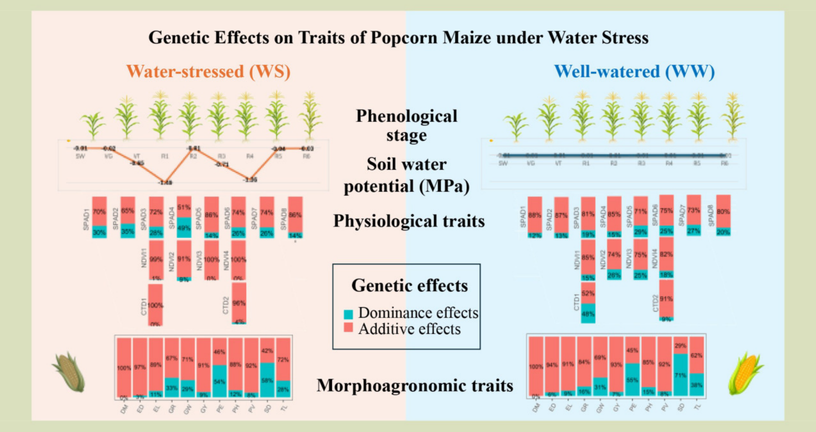
GRAPHICAL ABSTRACT



ABSTRACT

Understanding the genetic basis of agronomic, morphological and physiological traits in popcorn is key to developing effective breeding strategies under water-limited conditions. This study evaluated additive and dominance effects on 25 traits in 10 S7 inbred lines and their 45 diallel hybrids under water-stressed and well-watered conditions. Water stress was applied 15 days before male flowering by ceasing irrigation. Significant genetic variability was observed, with reductions in grain mass and popping expansion under water stress. Normalized difference vegetation index and relative chlorophyll content effectively detected phenotypic differences during critical growth stages, while canopy temperature depression provided insights into stomatal closure. Some genotypes possessed greater drought resilience, maintaining high chlorophyll levels, associated with the stay-green trait, extending active photosynthesis and increasing biomass accumulation. Dominance effects were predominant for most traits, except for popping expansion and stem diameter, where additive effects were slightly higher under both water regimes. Lines L76, L61 and P3 had high potential for grain yield and drought tolerance. Hybrids L61 × L76 and L71 × L76 performed well under both watering treatments, underscoring the role of heterosis due to dominant allelic interactions. This research highlights the importance of exploring genetic variation for yield and drought-related traits, offering insights for developing popcorn cultivars resilient to water stress.

1 Introduction

Water deficit is a major constraint on global agricultural production, affecting essential crops, such as maize, particularly in tropical and subtropical areas, where water deficit is often accompanied by elevated temperatures. This combination exacerbates the negative impacts on crop performance and yield[1,2]. This scenario is even more concerning, considering climate change projections, which indicate an increase in the frequency and severity of droughts[3,4]. In Brazil, droughts have significantly impacted water, food and energy security, affecting various regions of the country[5,6]. Given this reality, there is an urgent need to develop cultivars that are better adapted to water-limited conditions[7].

Developing drought-tolerant maize genotypes is a substantive challenge for breeding programs, given the complex genetics of this trait, which involves the interaction of multiple morphological, agronomic and physiological factors[7]. Understanding the genetic effects that influence these traits under water stress is crucial for improving the efficiency of selection programs.

In recent decades, several breeding strategies have been developed to enhance drought tolerance in crops, ranging from classical approaches to advanced quantitative and molecular methods. Of the long-practiced strategies, diallel analysis has been widely used to investigate gene action and combining ability[8]. More recently, the application of multivariate selection indices such as the multitrait genotype-ideotype distance index and drought risk index has allowed breeders to identify drought-tolerant genotypes across multiple traits and environments[9,10].

Mixed linear models, especially those based on BLUP (best linear unbiased prediction) and BLUE (best linear unbiased estimates), have gained prominence in multi-environment trials for their ability to account for unbalanced data and improve selection accuracy[11,12]. In addition, molecular tools such as quantitative trait loci mapping and genome-wide association studies have enabled the identification of genomic regions associated with yield, physiological efficiency and drought tolerance[10,13].

Although these approaches were not used in the present study, they provide a comprehensive framework for future genetic analyses in popcorn breeding programs. This study focused on the estimation of genetic effects using a full diallel scheme under two contrasting water regimes, which remains a robust strategy for understanding the inheritance of drought-related traits in early generations of selection.

Within this context, several physiological and morpho-agronomic traits have been associated with drought tolerance and used to improve selection efficiency in common maize[14–17]. Traits such as ear size, number of kernels per ear, kernel size, plant height and tassel length are directly impacted by water deficit but can vary depending on the timing of stress and serve as determinants of grain yield[15,17]. Additionally, physiological traits such as canopy temperature (CTD), normalized difference vegetation index (NDVI) and relative chlorophyll content (SPAD) have proven to be useful options for identifying more drought-tolerant genotypes[18,19]. CTD enables the estimation of leaf temperature increases due to stomatal closure whereas NDVI and SPAD assess canopy vigor and the relative chlorophyll content in leaves, correlating them with the ability of the plant to maintain photosynthesis under adverse conditions[18,20]. The stay-green trait, an indicator of high relative chlorophyll content at the end of the cycle, has been correlated with greater drought tolerance[21,22].

Despite the importance of these traits, studies focusing on drought adaptation in popcorn remain scarce, particularly with regard to the genetic control of morphophysiological responses[23–26]. Diallel analysis remains a valuable tool for dissecting the genetic architecture of such traits and for defining appropriate breeding strategies aimed at maximizing genetic gains[27,28].

This study aimed to use the diallel procedure to assess the influence of genetic effects on morphophysiological traits of popcorn inbred lines and hybrids cultivated under contrasting water availability, in an attempt to identify favorable allelic complementation, as well as breeding strategies to obtain superior genotypes, thereby providing more precise guidelines for implementing breeding programs focused on developing cultivars adapted to low water availability environments.

2 Material and methods

2.1 Plant material

Forty-five simple popcorn hybrids and their 10 parental lines were evaluated using a complete diallel design without reciprocals under two contrasting water regimes. The parental inbred lines were selected from a panel of 20 lines from the UENF Germplasm Bank[23] and assessed under water deficit conditions. These included four with higher grain yield (P2, P3, P6 and P7), four with lower grain yield (L61, L63, L65 and L75) and two with intermediate performance (L71 and L76).

The experiment was conducted during the cool season, from May to August (autumn/winter), a period characterized by low rainfall and temperatures within the optimal range for popcorn development. It was conducted at the State Agricultural Technical School Antônio Sarlo, located in Campos dos Goytacazes, Rio de Janeiro, Brazil (2°34′31″ S and 4°54′40″ W). According to the Köppen-Geiger climate classification, Campos dos Goytacazes is categorized as Aw, which corresponds to a tropical savanna climate with a dry winter. During the period from May to August, average daytime temperatures are around 24 °C, characterized by milder weather conditions and reduced rainfall. The soil at the experimental site is classified as a Dystrophic Yellow Argisol, featuring fragipan horizons and latosolic characteristics, according to the Brazilian Soil Classification System. Physically, the soil has high clay and sand content, friable or very friable consistency when moist and slightly hard to hard consistency when dry. The average macroporosity is about 0.17 $m^3 \cdot m^{-3}$ and the microporosity is 0.33 $m^3 \cdot m^{-3}$, both relatively uniform throughout the soil profile.

2.2 Water stress monitoring

Phenotypic evaluation was conducted under two water regimes: water-stressed (WS) with irrigation suspended 15 days before flowering (R1) until physiological maturity (R6) and well-watered (WW) being maintained at field capacity (−0.01 MPa). The soil was classified as a Latossolic Dystrophic Fragic Yellow Argisol, with high macroporosity (0.17 $m^3 \cdot m^{-3}$) and microporosity (0.33 $m^3 \cdot m^{-3}$). Irrigation was controlled by a drip irrigation system with Katif emitters (2.3 $mm \cdot h^{-1}$) under both watering treatments. Soil water potential in each watering treatment was monitored using Decagon MPS-6 tensiometers installed at a depth of 0.20 m (Fig. 1). The WW regime received 335 mm of water and the WS regime 218 mm (Fig. 1). Climatic data were recorded by the INMET meteorological station located in the experiment, with detailed precipitation detailed in Table 1, and temperature, relative humidity and solar radiation shown in Fig. 2. The average temperature was 22 °C, the relative humidity was 77% and the solar radiation was 3,150 $MJ \cdot m^{-2}$ (Fig. 2).

The imposition of water deficit was interrupted by rainfall, resulting in two periods where the soil had a water potential below −1.5 MPa, characterized as the permanent wilting point (PWP). The first water deficit (WD1) occurred during the flowering phase (R1), beginning 68 days after planting, while the second (WD2) occurred during the dough stage (R4), starting 90 days after planting. During the WD1 period, 4 days after suspension of irrigation, the soil had a potential of −0.21 MPa and reached the PWP 15 days after irrigation cutoff, coinciding with male flowering. Twenty-one days after suspension of irrigation, with a potential of −1.80 MPa, 30.8 mm of rain interrupted the water deficit, restoring the soil to field capacity. In the WD2 period, the soil began losing water potential again (−0.05 MPa) 7 days after the rain and reached the PWP 19 days later. This phase was again interrupted by 65 mm of rain 24 days after planting (Fig. 2).

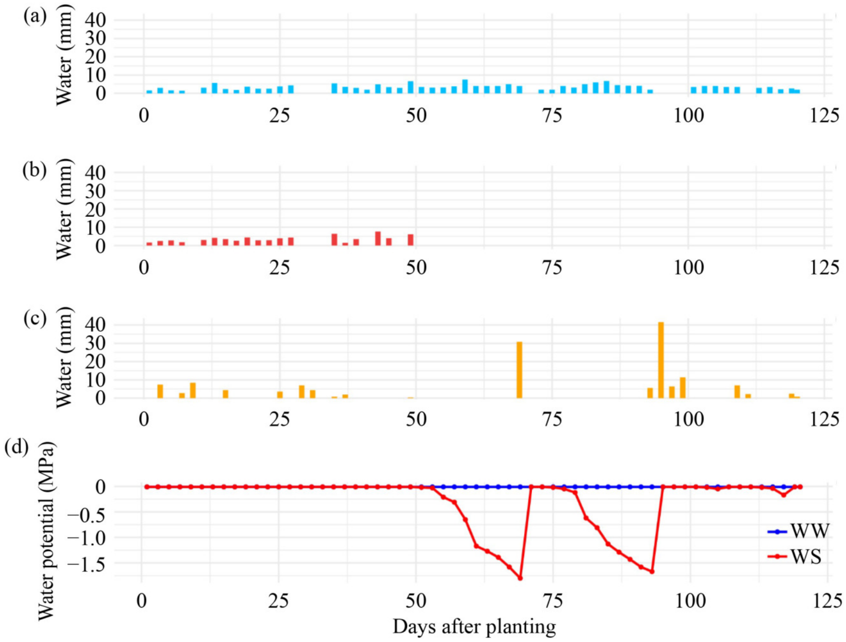


Fig. 1 Amounts of water applied for irrigation under: (a) water-watered and (b) well-stressed conditions, (c) precipitation and (d) soil water potential in days after planting for a complete diallel experiment involving 10 parental lines and 45 popcorn hybrids over time.

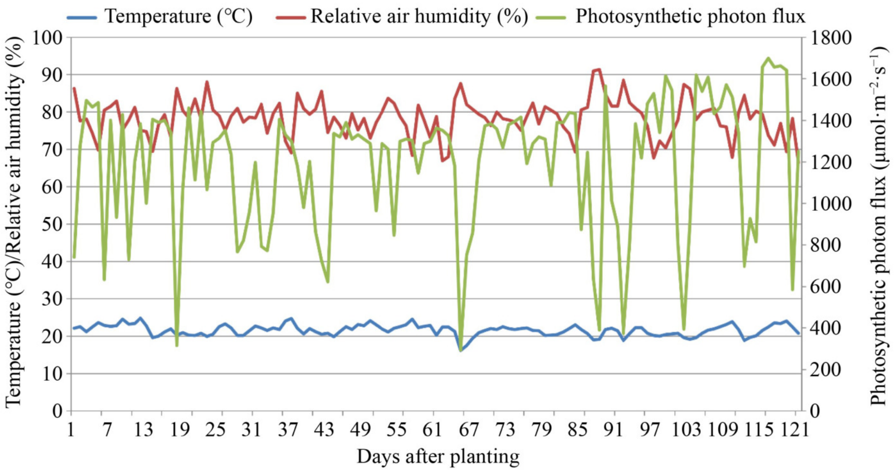


Fig. 2 Variation, in days after sowing, of temperature, relative humidity and solar radiation over the period of a complete diallel evaluation with 10 parents and 45 popcorn hybrids.

2.3 Evaluated traits

2.3.1 Morphological traits

Morphological traits were assessed at the grain filling stage including tassel length (TL), plant height (PH) and stem diameter (SD). TL was the distance from the flag leaf to the tip of the tassel, PH was distance from the soil to the flag leaf, and SD was measured at the internode below the primary ear.

Measurements were collected from five plants per plot. Dry matter was obtained after drying five plants from the usable area until constant weight was reached.

2.3.2 Agronomic traits

The number of kernels per row (GR) was determined by direct counting. Ear diameter (ED) was measured in the central region and ear length (EL) from one end to the other. These traits were evaluated using a sample of five ears collected from the effective area of the plot. The 100-kernel weight (GW) was calculated by weighing two subsamples of 100 kernels. Grain yield (GY) was obtained after shelling the ears from each plot, adjusted to 13% moisture.

The popping expansion (PE) was measured by microwaving (1000 W for 130 s) 30 g of kernels and calculating the ratio of the popcorn volume to the kernel mass. Additionally, the expanded popcorn volume per hectare (PV) was obtained by multiplying the average plot yield by the expansion capacity, resulting in the average expanded popcorn volume per hectare of planting.

2.3.3 Physiological traits

NDVI was measured using a portable optical sensor, FIELDSCOUT CM1000. Ten measurements were taken per plot, with the sensor positioned at a height of 60 cm above the canopy. NDVI was calculated using the standard formula:

$$\mathrm{NDVI} = (\mathrm{NIR} - \mathrm{Red}) / (\mathrm{NIR} + \mathrm{Red}) \tag{1}$$

where NIR and Red represent the reflectance in the near-infrared and red spectral bands, respectively. The SPAD was determined in six plants per plot by averaging three readings, taken from the middle third of the upper ear leaf, using the portable SPAD-502 Soil Plant Analysis Development meter.

CTD was assessed using a FLIR i50 thermal camera, capturing images at 60 cm above the plant canopy and processed with the FLIR Tools/Tools + software.

$$\mathrm{CTD} = T\_\mathrm{air} - T\_\mathrm{canopy} \tag{2}$$

where $T_$air is the ambient air temperature and $T_$canopy is the canopy surface temperature. CTD assessments were taken only at times when soil water potential was close to or below −1.5 MPa (Fig. 3).

All physiological measurements (NDVI, SPAD and CTD) were taken between 10:00 and 14:00 h to minimize diurnal variation. The measurement dates and corresponding phenological stages are detailed in Fig. 3, which includes days after in days after planting, phenological stages and soil water potential (MPa) corresponding, with descriptions of the phenological stage at each evaluation point.

2.4 Diallel analysis of griffing and determination of combining ability

The combining ability analysis was performed according to Method II of Griffing (1956)[29], where the $p(p + 1)/2$ treatments corresponding to the inbred lines and their hybrids were evaluated, excluding reciprocal F_1 hybrids. The treatment effects were decomposed into general combining ability (GCA) and specific combining ability (SCA).

Genotypes and experimental error were considered random effects, following model:

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + e_{ij} \tag{3}$$

where Y_{ij} is the mean value of the hybrid combination ($i \neq j$) or the parent ($i = j$), μ is the overall mean, g_i and g_j are the effects of the GCA of the i-th and j-th parent ($i, j = 1, 2, ..., 10$), s_{ij} is the effect of the SCA for the crosses between the parents of order i and j, and e_{ij} is the experimental error associated with the observation of order ij with NID $(0, \sigma^2)$.

2.5 Experimental design and statistical analyses

The experimental design used was a randomized complete block design with three replicates. Each plot consisted of a 4.80-m row with 0.80 m spacing between rows and 0.20 m between plants, totaling 23 plants per row.

The individual and joint analyses of variance for the experiments (water regimes) were performed using the GENES software[30], considering the genotype effect as random. The individual analysis of variance was conducted according to the following statistical model:

$$Y_{ij} = \mu + G_i + B_k + \varepsilon_{ij} \tag{4}$$

where Y_{ij} is the observed value of the i-th genotype in the j-th block, μ is a general constant; G_i is the random effect assigned to the i-th genotype, B_k is the effect of the k-th block, and ε_{ij} is the random error associated with the observation Y_{ij} with NID $(0, \sigma^2)$.

Subsequently, the joint analysis of variance was performed for the genotypes and environments, with environments formed by the combination of WS and WW conditions. The main

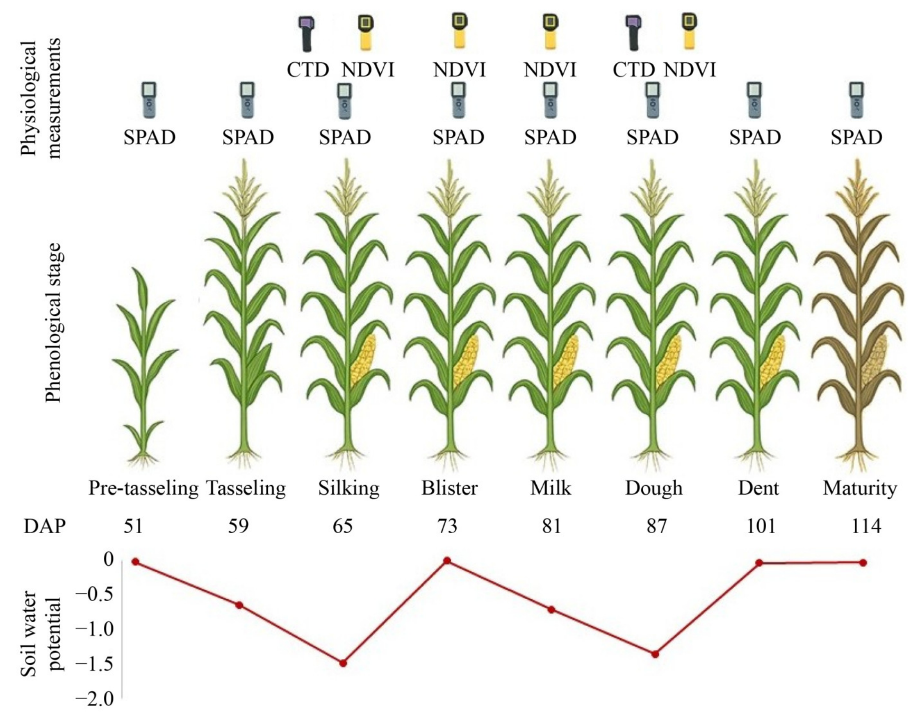


Fig. 3 Physiological measurements, normalized difference vegetation index (NDVI), relative chlorophyll content (SPAD), and canopy temperature depression (CTD) presented in days after planting (DAP), phenological stages and soil water potential (MPa) corresponding to the time of the assessments.

objective was to determine potential genotype-by-environment interactions, using the following statistical model:

$$Y_{ijk} = \mu + G_i + B/A_{jk} + A_j + GA_{ij} + \varepsilon_{ijk} \tag{5}$$

where Y_{ijk} is the observation of the i-th genotype in the j-th environment in the k-th block, μ is a general constant; G_i is the random effect of the i-th genotype, B/A_{jk} is the effect of the k-th block within the environment j, A_j is the fixed effect of the j-th environment with NID (0, σ^2), GA_{ij} is the random effect of the interaction between the i-th genotype and the j-th environment with NID (0, σ^2), and ε_{ijk} is the experimental random error associated with the observation Y_{ijk} with NID (0, σ^2).

3 Results

3.1 Characterizing and comparison environments and genetic variability under water deficit and normal irrigation

Male flowering occurred 69 days after planting under WW conditions and 67 days after planting under WS conditions. A shortening of 1 week in the phenological cycle of the genotypes was observed under WS conditions, with harvest maturity reached 1 week earlier than under WW conditions.

There was significant genetic variability for all traits. The environmental effect was significant for most traits, except for SPAD at stage 1 (VF). The interaction between watering treatments and genotype was significant for RG, VP, CPT and SPAD at stages 3 (R1), 4 (R2), 7 (R5) and 8 (R6), NDVI at stages 1 (R1) and 4 (R6), and CTD under both watering treatment (Table 1). The greatest percentage decreases were observed for RG and VP (39.8% and 44.5%, respectively) whereas the smallest decreases were for P100, CE and CP (8.83%, 8.82%, and 8.01%, respectively) (Fig. 4). Among the traits related to leaf indices, the highest SPAD decreases occurred during the DH1 phase (R1, 27.0%), shortly after rainfall (R2, 24.0%), and in the final stages of the cycle (R5 and R6, 20.4% and 23.5%, respectively). The greatest increase in CTD occurred during the WD1 period (R1, 89.2%) and also in

Table 1 Summary of the analysis of variance for morphological, agronomic and physiological traits of popcorn under water-stressed (WS) and well-watered (WW) conditions, with their respective significance values (*p*-values), means and experimental coefficient of variation (CV%)

Trait	Joint analysis			WS			WW		
	Gen	Env	Gen× Env	Gen	Average	CV%	Gen	Average	CV%
GY	0.00^{**}	0.00^{**}	0.00^{**}	0.00^{**}	1.80	18.8	0.00^{**}	3.0	12.0
PE	0.00^{**}	0.00^{**}	1.00^{ns}	0.00^{**}	23.35	13.0	0.00^{**}	25.6	12.5
PV	0.00^{**}	0.00^{**}	0.00^{**}	0.00^{**}	42.36	25.3	0.00^{**}	76.3	17.6
GR	0.00^{**}	0.00^{**}	0.27^{ns}	0.00^{**}	18.70	20.4	0.00^{**}	26.0	14.5
ED	0.00^{**}	0.00^{**}	0.48^{ns}	0.00^{**}	28.50	6.5	0.00^{**}	31.8	5.2
EL	0.00^{**}	0.00^{**}	0.39^{ns}	0.00^{**}	10.75	9.6	0.00^{**}	12.5	8.4
GW	0.00^{**}	0.00^{**}	0.11^{ns}	0.00^{**}	14.25	7.0	0.00^{**}	15.6	6.8
PH	0.00^{**}	0.01^{**}	0.19^{ns}	0.00^{**}	1.24	7.9	0.00^{**}	1.6	7.0
TL	0.00^{**}	0.02^{*}	0.00^{**}	0.00^{**}	42.35	6.8	0.00^{**}	46.0	5.2
SD	0.00^{**}	0.00^{**}	1.00^{ns}	0.00^{**}	11.43	7.5	0.00^{**}	12.7	8.4
DM	0.00^{**}	0.00^{**}	1.00^{ns}	0.01^{*}	0.20	14.4	0.00^{**}	0.2	13.6
SPAD1	0.00^{**}	1.00^{ns}	1.00^{ns}	0.00^{**}	41.09	6.9	0.00^{**}	40.9	8.0
SPAD2	0.00^{**}	0.00^{**}	0.10^{ns}	0.00^{**}	38.54	7.3	0.00^{**}	43.4	6.9
SPAD3	0.00^{**}	0.00^{**}	0.00^{**}	0.00^{**}	32.40	8.7	0.00^{**}	44.4	6.6
SPAD4	0.00^{**}	0.00^{**}	0.00^{**}	0.00^{**}	34.40	8.4	0.00^{**}	45.3	7.0
SPAD5	0.00^{**}	0.00^{**}	0.37^{ns}	0.00^{**}	39.89	8.6	0.00^{**}	45.4	6.7
SPAD6	0.00^{**}	0.00^{**}	0.28^{ns}	0.00^{**}	39.27	7.4	0.00^{**}	44.2	6.9
SPAD7	0.00^{**}	0.00^{**}	0.00^{**}	0.00^{**}	32.55	9.9	0.00^{**}	40.9	10.1
SPAD8	0.00^{**}	0.00^{**}	0.00^{**}	0.00^{**}	25.42	15.3	0.00^{**}	33.2	12.8
NDVI1	0.00^{**}	0.00^{**}	0.01^{*}	0.00^{**}	0.68	6.7	0.00^{**}	0.8	5.5
NDVI2	0.00^{**}	0.00^{**}	0.38^{ns}	0.00^{**}	0.74	3.4	0.00^{**}	0.8	2.9
NDVI3	0.00^{**}	0.00^{**}	0.25^{ns}	0.02^{*}	0.72	7.7	0.00^{**}	0.8	4.5
NDVI4	0.00^{**}	0.00^{**}	0.00^{**}	0.00^{**}	0.60	15.0	0.01^{*}	0.8	5.1
CTD1	0.00^{**}	0.00^{**}	0.00^{**}	0.00^{**}	–1.70	35.8	0.00^{**}	–0.2	272.4
CTD2	0.05^{*}	0.00^{**}	0.00^{**}	0.00^{**}	–3.65	24.4	0.00^{**}	–2.0	38.7

Note: GY, grain yield; PE, popping expansion; PV, volume of expanded popcorn per hectare; GR, number of grains per row; ED, Ear diameter; EL, ear length; GW, 100-kernel weight; PH, plant height; TL, tassel length; SD, stem diameter; SPAD, relative chlorophyll content index, measurements 1–8, at the planting, pre-tasseling, tasseling, silking, blister, milk, dough and dent, respectively; NDVI: normalized difference vegetation index, measurements 1–4, at the silking, blister, milk and dough, respectively; and CTD, canopy temperature depression measured, measurements 1 and 2, at the silking and dough, respectively. ANOVA significance level: ns, not significant, *, $p \leqslant 0.05$ and **, $p \leqslant 0.01$.

WD2 (44.7%). In contrast, the highest NDVI decrease occurred during the WD1 period (22.5%). Water stress resulted in a 39.8% decrease in grain yield and a 28.1% decrease in the number of grains per row on the ear, especially due to stress during flowering (WD1), which impacted fertilization. The decrease in grain weight was smaller (8.83%), reflecting the lesser impact of the WD2 phase during grain filling (Fig. 4).

In the individual ANOVA, genetic variability was observed for all traits under both watering treatments (Table 1). For the morpho-agronomic traits evaluated, the CV% values were consistently lower under WW conditions, the variation ranged from 5.18% to 17.6% than under WS conditions, which ranged from 6.45% to 25.3%. The physiological traits SPAD and NDVI also had the highest CV% values under WS conditions, except for SPAD at stage 1. For these traits, CV% values ranged from 2.91% to 12.8% under WW conditions and from 3.39% to 15.3% under WS conditions. Under both watering treatments,

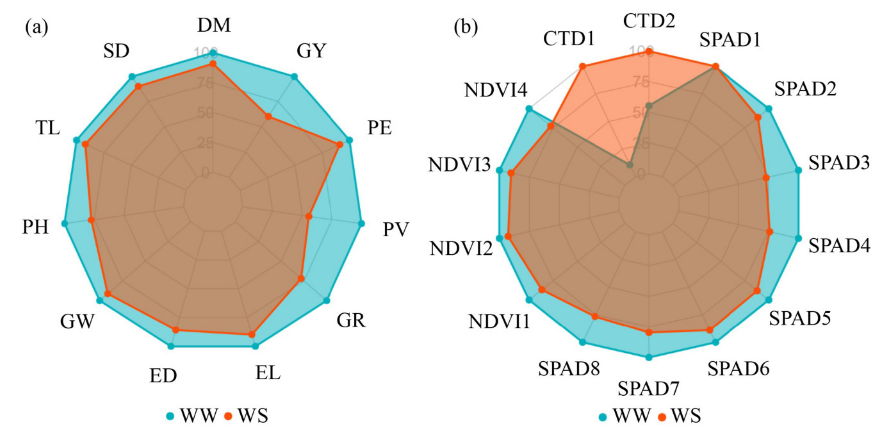


Fig. 4 Percentage decrease of morphological, agronomic and physiological traits of popcorn maize lines and hybrids grown under water-stressed (WS) and well-watered (WW) conditions. (a) GY, grain yield; PE, popping expansion; PV, volume of expanded popcorn per hectare; GR, number of grains per row; ED, Ear diameter; EL, ear length; GW, 100-kernel weight; PH, plant height; TL, tassel length; SD, stem diameter. (b) SPAD, relative chlorophyll content index, measurements 1–8, at the planting, pre-tasseling, tasseling, silking, blister, milk, dough and dent, respectively; NDVI: normalized difference vegetation index, measurements 1–4, at the silking, blister, milk and dough, respectively; and CTD, canopy temperature depression measured, measurements 1 and 2, at the silking and dough, respectively. ANOVA significance level: ns, not significant, *, $p \leqslant 0.05$ and **, $p \leqslant 0.01$.

the highest CV% values occurred for SPAD at the end of the growing season. In contrast, the two CTD evaluations had the highest CV% under WW conditions to WS. This same trait had the largest magnitudes of CV% among all evaluated traits, with estimates of 272 and 38.7 under WW conditions and 35.8 and 24.4 under WS conditions (Table 1).

Under WS conditions, genetic variability was observed for most traits, except for SPAD at stages 1 and 2 (VT), NDVI at stages 2 (R2) and 3 (R3), and CTD at stages 1 (R1) and 2 (R4). Under WW conditions, only NDVI at stages 2, 3 and 4, and CTD at stage 2 (R4), did not have significant genetic variability (Table 1).

3.2 Inference of the combining ability effects of the diallel under water deficit and normal irrigation

In the diallel ANOVA, the GCA effects were significant for most of the morpho-agronomic traits, except for PV, EL and dry matter under both watering treatments, and GY and ED under WW conditions (Table 2). For physiological traits, the GCA effects were significant for all SPAD evaluations, except at stage 1 under WW conditions. For NDVI, the GCA effects were significant only under WW conditions at stages 2 and 3. Similarly for CTD, the GCA effects were significant only under WW conditions and only in the first evaluation. In contrast, the SCA effects were significant for all physiological traits, except for NDVI at stage 4 under WW conditions (Table 2).

Overall, the magnitudes of the quadratic components indicated that the dominance effects were the most influential for nearly all traits evaluated under both watering treatments (Figs. 5 and 6). Only for PE and SD were the additive effects more relevant under both watering treatments, GCA to SCA ratios above one (Table 2), though with percentages close to those of the dominance effects. Under WW conditions, the dominance effects accounted for over 50% of the variation in GY and its components. Under WS conditions, except for GR, the dominance effects also explained more than 46% of the genetic variation in these traits.

Under WW conditions, the SPAD index exhibited about 40% of the total variation explained by dominance effects, particularly in post-flowering evaluations. Under WS conditions, the evaluation stages closer to leaf senescence showed more expressive dominance effects, ranging from 36% (R4) to 54% (R6). For NDVI and CTD, dominance effects did not exceed 23% of the total variation under WW conditions but reached around 30% under WS conditions, especially for NDVI at stage 4 and for CTD under both watering treatments (Figs. 5 and 6).

Table 2 Summary of the diallel analysis (*p*-values) and GCA/SCA mean square rations of morpho-agronomic and physiological traits evaluated in 10 parental lines and 45 popcorn hybrids cultivated under water-stressed (WS) and well-watered (WW) conditions

Traits	WS			WW		
	GCA	SCA	GSA/SCA	GCA	SCA	GSA/SCA
GY	0.05*	0.00**	0.10	0.09^{ns}	0.00**	0.07
PE	0.00**	0.00**	1.18	0.00**	0.00**	1.22
PV	0.08^{ns}	0.00**	0.09	0.08^{ns}	0.00**	0.09
GR	0.00**	0.00**	0.50	0.01*	0.00**	0.19
ED	0.05*	0.00**	0.13	0.06^{ns}	0.00**	0.10
EL	0.26^{ns}	0.00**	0.03	0.15^{ns}	0.00**	0.06
GW	0.00**	0.00**	0.41	0.00**	0.00**	0.45
PH	0.04*	0.00**	0.14	0.02*	0.00**	0.17
TL	0.00**	0.00**	0.39	0.00**	0.00**	0.62
SD	0.00**	0.03*	1.38	0.00**	0.11^{ns}	2.44
DM	1.00^{ns}	0.00**	0.00	1.00^{ns}	0.00**	0.00
SPAD1	0.01*	0.03*	0.43	0.07^{ns}	0.00**	0.14
SPAD2	0.00**	0.03*	0.54	0.04*	0.00**	0.14
SPAD3	0.00**	0.00**	0.39	0.01*	0.00**	0.23
SPAD4	0.00**	0.01	0.96	0.02*	0.00**	0.18
SPAD5	0.05*	0.00**	0.16	0.00**	0.00**	0.41
SPAD6	0.00**	0.00**	0.35	0.00**	0.00**	0.34
SPAD7	0.00**	0.00**	0.35	0.00**	0.00**	0.37
SPAD8	0.02*	0.00**	0.17	0.00**	0.00**	0.24
NDVI1	0.42^{ns}	0.00**	0.01	0.07	0.00**	0.17
NDVI2	0.18^{ns}	0.01*	0.09	0.01*	0.00**	0.35
NDVI3	0.45^{ns}	0.03*	0.00	0.03*	0.05*	0.34
NDVI4	1.00^{ns}	0.00**	0.00	0.08^{ns}	0.06^{ns}	0.22
CTD1	1.00^{ns}	0.00**	0.00	0.00**	0.05*	0.93
CTD2	0.26^{ns}	0.00**	0.05	0.17^{ns}	0.01*	0.09

Note:GY, grain yield; PE, popping expansion; PV, volume of expanded popcorn per hectare; GR, number of grains per row; ED, Ear diameter; EL, ear length; GW, 100-kernel weight; PH, plant height; TL, tassel length; SD, stem diameter; SPAD, relative chlorophyll content index, measurements 1–8, at the planting, pre-tasseling, tasseling, silking, blister, milk, dough and dent, respectively; NDVI: normalized difference vegetation index, measurements 1–4, at the silking, blister, milk and dough, respectively; and CTD, canopy temperature depression measured, measurements 1 and 2, at the silking and dough, respectively. ANOVA significance level: ns, not significant, *, $p \leqslant 0.05$ and **, $p \leqslant 0.01$.

3.3 Concentration of additive effects in the parental lines and dominance effects in the hybrids under water deficit and normal irrigation conditions

The GCA and SCA were estimated for agronomic, morphological, and physiological traits with significant variance for each watering treatment. Due to the complexity and volume of data, only the most relevant results for the research are presented here, as GCA and SCA estimates are crucial for the breeding program in question. However, the complete GCA and SCA estimates are available in the Supplementary Material.

The GCA estimates revealed that inbred line L76 stood out with the highest values for GY under both watering treatments, along with high values for PV, GR, ED, EL and GW. Parent L61 had the highest GCA estimate for PE and high values for PV

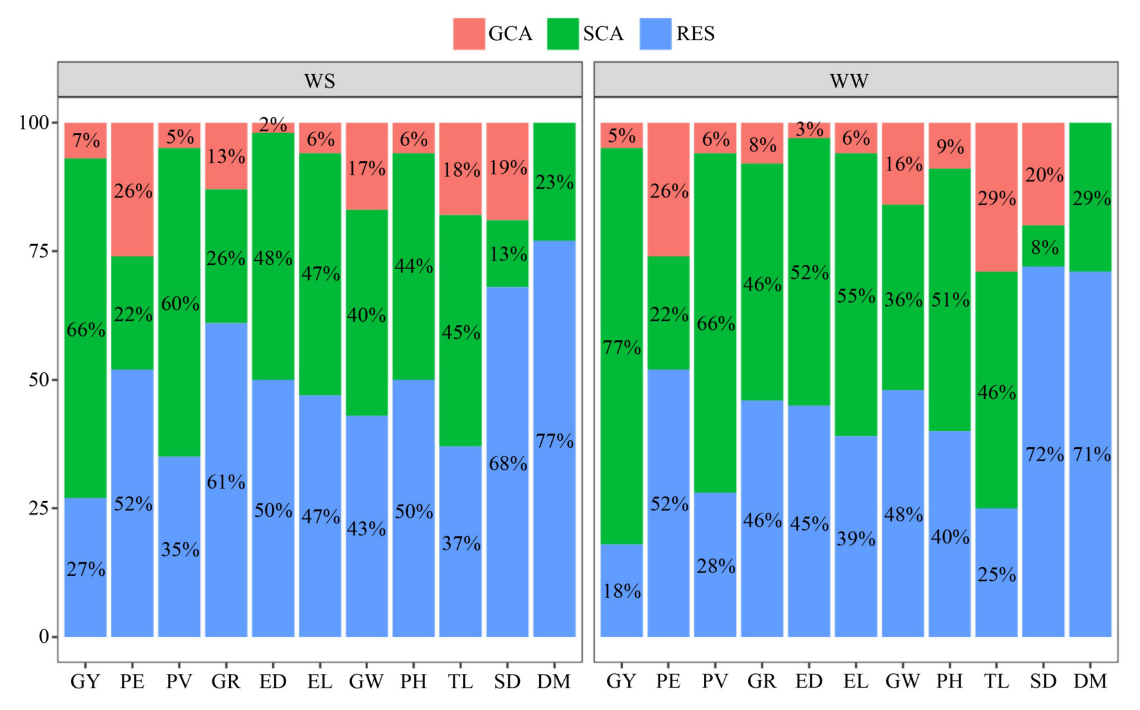


Fig. 5 Percentage contribution of the quadratic components of general combining ability (GCA), specific combining ability (SCA), and residuals for morpho-agronomic traits evaluated in 10 parents and 45 popcorn hybrids grown under water-stressed (WS) and well-watered (WW) conditions. GY, grain yield; PE, popping expansion; PV, volume of expanded popcorn per hectare; GR, number of grains per row; EL, ear length; GW, 100-kernel weight; PH, plant height; TL, tassel length; SD, stem diameter; and DM, dry matter.

under both watering treatments. Other inbred lines, such as P7, L65 and P3, also had high GCA estimates for different traits. Regarding physiological evaluations, parents L71 and P3 were notable, particularly for the SPAD, with P3 being associated with delayed senescence (stay-green) due to its higher SPAD estimates at the end of the cycle (Tables S1 and S2).

For SCA estimates, hybrids L65 × L76 and L76 × P7 had the highest magnitudes for GY under WS and WW conditions, respectively, in addition to high values for PV, PE, GR and TL. Hybrid L71 × L76 was the only one with high GY estimates under both watering treatments, while L61 × L76 had the highest estimates for PV under both watering treatments. For PE, hybrid L65 × P7 had the highest SCA estimates, along with high values for PV. The combinations L61 × L75, L65 × L75 and L65 × P7 also had significant SCA estimates for several traits, notably for SPAD under both watering treatments. Specific hybrids also stood out individually for grain yield components and morphological traits, as shown in Tables S3–S6.

4 Discussion

4.1 Characterizing the environments under water deficit and normal irrigation

The shortening of the phenological cycle of genotypes under WS compared to WW aligns with the pioneering studies of Kamphorst et al.[23,24], which evaluated popcorn maize lines under water deficit. The occurrence of rainfall during the water deficit period did not mitigate the stress effects on productivity, as evidenced by a significant 39.8% decrease in grain yield. Water deficit had a more pronounced impact during flowering (DH1), resulting in a reduction in the number of kernels per ear, which is a direct indicator of pollination failure due to water scarcity.

Compared to the innovative work of Kamphorst et al.[23], the impact on kernel weight was lower in this study (8.83% versus 23.5%), which can be attributed to the fact that, in their study, stress was more severe during the grain-filling stage. Also, the

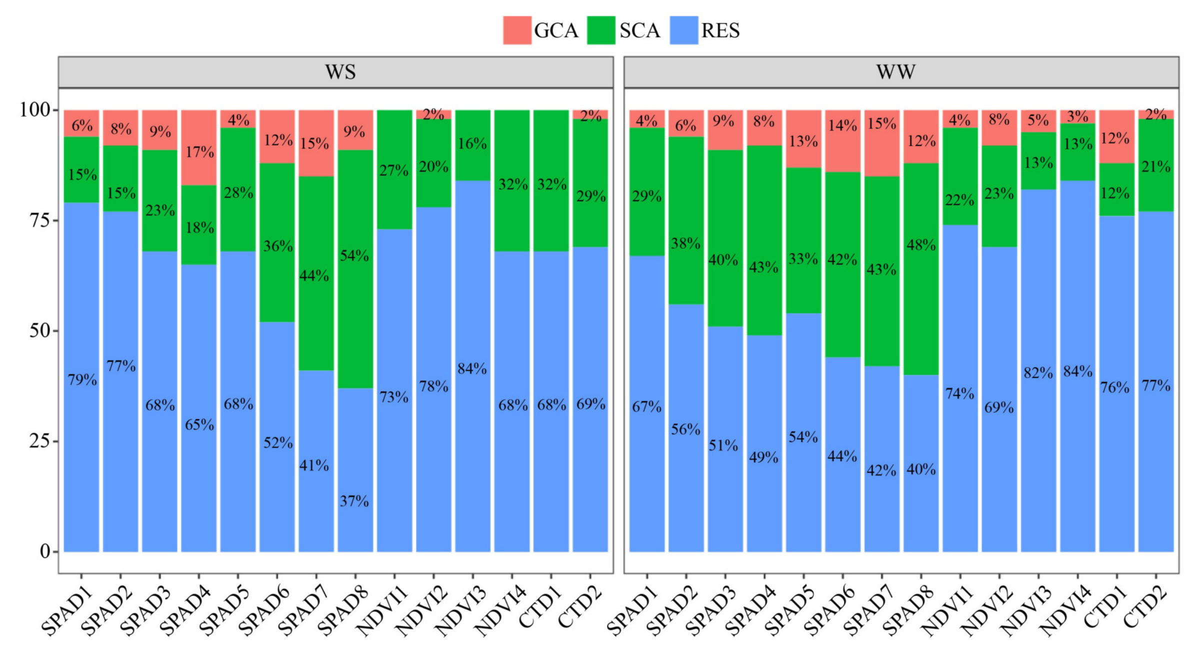


Fig. 6 Percentage contribution of the quadratic components of general combining ability (GCA), specific combining ability (SCA), and residuals for physiological traits during the growing cycle of popcorn inbred lines and hybrids under water-stressed (WS) and well-watered (WW) conditions. SPAD, relative chlorophyll content index, measurements 1–8, at the planting, pre-tasseling, tasseling, silking, blister, milk, dough and dent, respectively; NDVI: normalized difference vegetation index, measurements 1–4, at the silking, blister, milk and dough, respectively; and CTD, canopy temperature depression measured, measurements 1 and 2, at the silking and dough, respectively. ANOVA significance level: ns, not significant, *, $p \leqslant 0.05$ and **, $p \leqslant 0.01$.

total reduction in grain yield observed in this study (39.8%) was lower than that reported by Kamphorst et al.[23] (55.3%), even when considering the average decreases among the lines. Nevertheless, both studies demonstrated the significant effects of water deficit on popcorn maize production, emphasizing the impacts of irregular or absent precipitation on successful cultivation.

4.2 Comparison of environments and genetic variability under water deficit and normal irrigation

Highly significant effects were observed for the genotype source of variation in nearly all evaluated traits, highlighting the presence of genetic variability, which indicates the potential for successful selection of parents and superior combinations under both WS and WW conditions. Only SPAD1 did not show a significant difference between conditions, an expected outcome since irrigation was interrupted at the time of measurement.

The interaction between watering treatments and genotype was significant for key traits such as GY, PV, tassel length (TL), and the physiological indices SPAD and NDVI, particularly during stress evaluation periods and at the end of the cycle. The significance of these traits indicates that both water deficit and the genetic potential of the genotypes directly influenced plant performance, especially during critical developmental stages. The tested genotypes responded differently to water stress, with some demonstrating greater resilience and maintaining productive performance even under water deficit.

Physiological indices, such as SPAD and NDVI, were significant at specific developmental stages, indicating that genotypes have varying capacities to maintain leaf pigmentation under water stress. CTD also showed a significant interaction, indicating differences among genotypes in their sensitivity to stomatal closure and the resulting increase in plant temperature under water deficit or their mechanisms for maintaining cooling.

The high sensitivity of popcorn maize to water stress is evident from the substantial decreases in grain yield (39.8%) and expanded popcorn volume per hectare (44.5%). These reductions are consistent with studies on common maize, highlighting the adverse effects of water stress, particularly during reproductive phases[17,31]. Water deficit during critical reproductive stages, such as pollination, ear formation, and early grain development, significantly impairs grain formation and yield, with decreases exceeding 93% in dry years, depending on drought severity and interactions with other stress factors[1,17,31,32].

For the grain yield components, GR had the greatest decrease (28.08%), which can be attributed to the vulnerability of pollination under water deficit conditions in this study, ultimately compromising fertilization. According to Venman et al.[17], water stress during the flowering phase in maize reduces the emergence of styles (silks), the length of the styles, and the fresh weight of the styles, leading to a significant reduction in the number of grains.

However, other grain yield components, such as EL and GW, had smaller reductions, possibly due to rainfall during the R2 and R3 phases, which partially mitigated the effects of water stress. In contrast, in the study by Kamphorst et al.[23], GW was the most affected component, as grain filling occurred almost entirely under water deficit (R2-R5). According to Venman et al.[17], these latter components are less affected when stress occurs during the flowering period, but when stress occurs during grain filling, grain weight is the most affected component.

PE was also significantly affected, although to a lesser extent. Kamphorst et al.[23] observed a decrease of 28.8% for PE, while the reduction in the present study was only 8.82%. Even in this case, although only the reduction in PE was observed in the lines (data not shown), there was no greater decrease compared to the results obtained by Kamphorst et al.[23]. In both cases, the decreases in GW and PE were equivalent. However, these two characteristics are typically negatively correlated and the reduction in one often leads to an increase in the other[33]. However, under the conditions tested, the decreases in GW and PE were primarily caused by poor grain formation due to the lack of water, resulting in a reduction in mass and the capacity of the grain to expand. Thus, the reduction in grain size due to drought serves as a good indicator of the lower expansion capacity of the grain.

The physiological indices, such as SPAD and NDVI, proved valuable for detecting the impact of water deficit on plants. The sharp decline in SPAD values during the R1 stage reflects an accelerated degradation of chlorophyll in older leaves, while NDVI, with a more moderate decrease, indicates greater resilience in the vigor of younger leaves. It is important to note that SPAD and NDVI were measured in different ways and on different leaves, which may contribute to subtle variations in the results. SPAD was measured on the ear leaf, whereas NDVI was measured on the canopy of the upper leaves, therefore capturing different aspects of plant physiology. These measurements from different leaves provide complementary insights into plant physiology, with SPAD directly reflecting leaf chlorophyll content and NDVI capturing overall vegetation vigor.

SPAD evaluations during the first stress period (assessments 2 and 3) showed greater chlorophyll degradation in the ear leaf compared to the second stress period (assessments 5 and 6). Conversely, NDVI evaluations during the second stress period (assessments 3 and 4) revealed more pronounced chlorophyll decline in the upper canopy leaves than the earlier NDVI assessment under the first stress event (assessment 1). Also, SPAD measurements at the end of the crop cycle (assessments 7 and 8) also indicated a high chlorophyll decline, this time primarily associated with natural leaf senescence, showing considerable variation among genotypes and allowing for the identification of superior stay-green capacity in some lines. Finally, measurements conducted outside the stress periods (SPAD 1 and 4; NDVI 2), when no water deficit was present, exhibited minimal chlorophyll degradation. As a result, these indices can serve as important indicators for selecting genotypes that are more tolerant to water deficit, with SPAD providing an early signal of water stress and NDVI assessing the overall plant vigor throughout its growth cycle.

There was also a significant increase in CTD under more severe WS conditions (DH1), resulting in stomatal closure and the subsequent rise in plant temperature. Stomatal closure occurs to prevent water loss, reducing transpiration, and consequently, increasing leaf temperature[19,34]. This greater depression under stress is an important indicator of plant sensitivity to water deficit conditions and negatively impacts productivity[19]. However, CTD exhibited the highest coefficient of variation (CV%) under WW conditions, influenced by very low averages. This instability can be attributed to high environmental variability and suggests that, while relevant, CTD may not be a particularly reliable trait for selecting genotypes under water stress conditions.

The CV% was consistently higher under WS conditions for all the evaluated traits, indicating greater instability in the results due to water stress. This response is typical under stress conditions, where plants tend to respond in various ways[7]. However, CTD evaluations showed the highest CV% under WW conditions. This can be explained by the fact that, under adequate irrigation, plants maintain a temperature closer to the ambient environment, resulting in CTD values near zero. This proximity reduces the range of variation, which increases the CV% due to small fluctuations in the data. Unlike what is observed under WS conditions, this variation does not reflect physiological plasticity but rather a greater tendency for thermal stability in well-irrigated plants[19].

4.3 Inference of the diallel combining ability effects under water deficit and normal irrigation conditions

The GCA and SCA effects were significant for most of the evaluated traits under both water conditions. This significance highlights the importance of both additive and dominance effects in the study. The significance of $\hat{g}_i$ suggests variation in the number of alleles between the parents, while the significance of $\hat{s}_{ij}$ points to variation in allele complementation between parents at loci exhibiting some degree of dominance[35,36]. Therefore, the magnitudes of the quadratic components Φg and Φs, which represent the mean squares of the $\hat{g}_i$ and $\hat{s}_{ij}$ effects, respectively, can determine whether the concentration of favorable alleles in the parents or the allele complementation between the parents is more efficient for selecting superior genotypes.

Estimates of the quadratic components revealed that dominance effects have a fundamental role in the expression of most morpho-agronomic and physiological traits in popcorn, both under WS and WW conditions. This is consistent with reports suggesting that non-additive effects often have a major role in the genetic control of agronomic traits under varying water availability[7,37]. However, other studies have reported that additive gene action can become more prominent under water-limited conditions[8,37], depending on the target trait and species.

In an earlier study using Hayman’s diallel analysis in popcorn, it was reported that overdominance effects predominantly influence GY and its components (PV, GR, EL and ED)[38]. Dominance, being the main factor determining high heterosis, can maximize genetic gain under water deficit conditions[37]. Thus, the use of hybrids may be the most effective strategy for improving traits related to drought stress adaptation in popcorn maize breeding programs. Under WW conditions, over 50% of the variation in GY was attributed to dominance effects and this trend remained in WS, with 46% of the variation explained by these effects, except for GR, highlighting that water stress increases the importance of specific genetic interactions.

For traits such as PE and SD, additive effects were predominant under both watering treatments, indicating that these traits are associated with the direct action of parental alleles, enabling more predictable transmission to the next generation. For PE, this is a trait of high commercial value for popcorn maize and selecting lines with high PE is an efficient way to achieve rapid genetic progress. Similar results were found by Hassani et al.[8], who observed a greater contribution of additive effects for root and sugar traits in sugar beet.

It is important to note that the quadratic components of the SCA for PE were similar to the GCA effects, despite popping expansion typically being a trait associated with additive effects. In an earlier study involving parental lines and diallel hybrids of popcorn, Hayman’s analysis identified the occurrence of dominance effects for PE under both WS and WW conditions, as well as GW under WS conditions. Additionally, there was a joint influence of dominance and additivity for PE, indicating a mixed effect for this trait[38]. Although dominance effects may eventually prevail, previous studies suggest that the inheritance of PE may involve a major gene with an additive effect combined with polygenes exhibiting both additive and dominance effects[39]. Therefore, both additive and dominance effects should be considered when selecting genotypes for this trait.

Regarding physiological traits, the changes in the SPAD index reinforces the importance of dominance effects, especially during the more critical phases of the crop cycle, such as flowering and leaf senescence. The genetic variation attributed to dominance effects for SPAD, which reached up to 54% at the R6 stage under WS, demonstrates that specific genotypes have greater resilience to water deficit. The ability to maintain high chlorophyll levels throughout the growth cycle, associated with the stay-green trait, indicates a competitive advantage in water-limited environments by prolonging the period of active photosynthesis, leading to increased biomass and, consequently, better grain formation[40,41]. Therefore, selecting genotypes with this trait may be an effective strategy for developing cultivars with greater tolerance to water deficit.

For NDVI and CTD, the low contribution of genetic effects under both WW and WS conditions indicates that these traits are strongly influenced by environmental factors. However, the slight increase in the influence of dominance effects under WS for these physiological traits indicates the possibility of selecting genotypes with better adaptation to water stress conditions, especially when seeking greater stability in performance.

The observed increase in additive effects under WS conditions, though small, is a noteworthy finding. Typically, under stress, such as water deficit, dominance and epistatic effects are expected to have a more prominent contribution to the expression of traits due to the complexity of genetic interactions aiding plant adapt to these adverse conditions[7]. However, the increased additive contribution under drought, as also observed by Hassani et al.[8], points to a potential for more predictable inheritance and greater selection efficiency. Indeed, additive control under stress can lead to higher narrow-sense heritability, improving the response to selection.

This finding has strong implications for breeding programs. It shows that even under water deficit, it is possible to identify lines with superior performance whose favorable alleles are reliably transmitted across generations. Therefore, although dominance effects remain important under stress, the observed reinforcement of additive variance supports the inclusion of inbred line development as a viable drought adaptation strategy.

Although heritability estimation was not a primary objective of this study, its value in assessing the genetic potential of traits is undeniable. In previous work[38], high and stable heritability estimates were obtained across water regimes for yield components. This observation is supported by other studies, such as Sobhaninan et al.[42], Hassani et al.[8] and Archangi et al.[11], which also identified high heritability for drought-adaptive traits, reinforcing their potential for indirect selection in breeding for drought tolerance.

4.4 Concentration of additive effects in parental lines and dominance effects in hybrids under drought and well-watered conditions

The concentration of additive effects in the parents and dominance effects in the hybrids reveals an important trend for the breeding program, particularly under water deficit conditions. Additive effects, reflected in high GCA values, signify the presence of additive genes responsible for the direct transmission of desirable traits to subsequent generations. In this sense, parents such as L76, L61 and P3 have strong potential to contribute to traits related to yield and drought tolerance, including GY, PV, GR and PE. These parents are fundamental for the development of new lines and hybrid combinations with greater stability and productive potential.

Conversely, dominance effects, represented by SCA estimates, were predominant in many hybrids, indicating that heterosis is crucial for maximizing grain yield, water use efficiency and drought tolerance. This was evidenced by the hybrids L61 × L71, L71 × L76, L61 × L75, L65 × L75 and L65 × P7, which performed well under both WS and WW conditions. These results reinforce the importance of accounting for both additive and dominance effects during parent selection, especially in breeding programs focused on adapting to water deficit conditions.

4.5 Implications of the research for plant breeding

The results of this research provide significant insights for advancing the genetic improvement of popcorn maize with a focus on drought tolerance. The use of a complete diallel model, combined with an in-depth analysis of agronomic, morphological and physiological traits, demonstrates how genetic variation can be harnessed to improve the performance of lines under severe water stress conditions. The findings obtained for both water conditions were quite similar, and the same breeding methods can be applied under both conditions. Dominance effects were predominant, and the exploration of hybrids is the best option for adapting popcorn maize to drought stress. Also, the identification of lines with high GCA and hybrids with superior SCA under both WS and WW conditions highlights the potential to select genotypes that are more efficient in water use and have favorable agronomic traits.

In addition, the analyses of traits such as CTD and the SPAD index indicate their potential as phenotypic markers for identifying superior genotypes. The relationship between these traits and drought stress tolerance contributes to the development of more resilient cultivars with greater resource-use efficiency and adaptability to water-limited environments.

These findings reinforce the importance of genetic variability in enhancing key traits in popcorn maize and indicate that the use of selected lines can accelerate the development of hybrids with greater drought tolerance, without compromising agronomic performance under full irrigation conditions.

5 Conclusions

The results of this study demonstrate that both additive and dominance gene effects contribute to the expression of morphophysiological traits in popcorn under contrasting water regimes. However, dominance effects played a predominant role in the expression of morphophysiological traits in popcorn under both WS and WW conditions. This indicates that similar breeding strategies, particularly those based on hybrid development, can be effectively applied across contrasting environments. Water deficit during flowering significantly impacted grain number, while the reduction in grain weight led to a proportional decrease in popping expansion. The SPAD index proved to be a useful physiological marker for identifying superior genotypes under drought stress. Notably, lines L76, L61 and P3 had high GCA for grain yield and drought tolerance. Additionally, the hybrids L61 × L76 and L71 × L76 stood out across both watering treatments, highlighting the importance of heterosis for drought adaptation and productivity.

Supplementary materials

The online version of this article at https://doi.org/10.15302/J-FASE-2025647 contains supplementary materials (Tables S1–S6).

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Compliance with ethics guidelines

Valter Jário de Lima, Antônio Teixeira do Amaral Junior, Samuel Henrique Kamphorst, Rosimeire Barboza Bispo, Talles de Oliveira Santos, Carolina Macedo Carvalho, Uéliton Alves de Oliveira, Flávia Nicácio Viana, Eliemar Campostrini, de Monique de Souza Santos, Lauro José Moreira Guimarães, and Marcelo Vivas declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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