

Article

Assessing Combining Abilities of Popcorn Inbred Lines for Agronomic and Root Traits under Contrasting Water Conditions: Towards Developing Drought-Tolerant Genotypes

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Abstract: Developing popcorn genotypes that are adapted to water-deficit conditions is crucial due to the significant impact of this abiotic stress on grain yield. This study aimed to assess the combining abilities of preselected popcorn lines for agronomic and root traits under well-watered and water-stressed conditions. A circulating diallel analysis was conducted to investigate the effects of the general and specific combining abilities of 10 lines and their respective hybrids for various traits, including productivity, popping expansion, expanded popcorn volume, 100-grain weight, ear length, ear width, support root angle, crown root angle, number of support roots, number of crown roots, density of support roots, and density of crown roots. Non-additive action genes predominantly influenced the agronomic traits under both water conditions. In contrast, the root traits displayed a greater proportion of additive action gene expression under both conditions, despite being significantly affected by the environment. Lines L61, L71, and L76 demonstrated positive and high effects for general combining ability. The hybrids L65/L76, L71/L76, and L61/L75, in addition to exhibiting satisfactory effects of their specific combining ability, also displayed the most favorable phenotypic responses for most agronomic and root traits, making them ideal candidates for inclusion in popcorn breeding programs aiming to develop drought-tolerant genotypes.

Keywords: water stress; combining ability; *Zea mays* var. *everta*; diallel analysis; sustainable agriculture

1. Introduction

Climate change, characterized by increasing global temperatures and changing rainfall patterns, has become a significant concern for agricultural producers [1–3]. The possible reduction in average crop yields in the coming years due to these climate changes has generated apprehension among farmers [4–6]. Moreover, with an estimated global population of 9.6 billion by 2050, there will be a substantial increase in demand for food [7]. Drought, induced by climate change, is recognized as a primary factor contributing to crop losses, including maize and its special types, such as popcorn [8–12]. Maize is not inherently tolerant to drought stress, resulting in reduced growth and yield [13]. Consequently, developing cultivars with higher water use efficiency is crucial to mitigate the detrimental effects of water scarcity [14–16].

Agronomic traits in various crops exhibit complex interactions during dry periods as water stress-impaired molecular, biochemical, and physiological processes in plants [17,18], thereby impeding genetic gains. Similarly, popcorn, a highly valued commodity globally, with an annual production chain worth approximately 1 billion dollars in the USA, is directly affected by water scarcity regarding essential agronomic traits, such as grain yield, grain expansion capacity, the volume of expanded popcorn per hectare, grain mass, ear length and width, plant height, and flowering period [14,19,20]. Despite existing studies of the impact of water stress on popcorn cultivation, further evaluation of genetic effects under drought conditions, especially in field settings, is necessary to enhance the understanding of root traits in response to stress.

While a few breeding programs have focused on improving genotype selection based on root phenotyping in maize in recent years, such studies have remained limited for popcorn crops [21–23]. According to [22], identifying and comprehending root phenotypic expressions are crucial for developing drought-tolerant plants. Exploring genotypes that reduce metabolic costs associated with soil exploration and prioritize root growth to enhance water and mineral acquisition from deeper soil layers [24–26] could be key to developing genotypes with improved water deficit adaptation.

Since 2015, the State University of the North Fluminense Darcy Ribeiro (UENF) has been conducting extensive research to gain insights into the adaptation of popcorn to water deficit conditions, with the ultimate goal of developing superior genotypes. The research conducted thus far has yielded several important findings. For instance, specific lines have been identified that demonstrate agronomic efficiency in water usage under water deficit conditions [27]. Additionally, indirect selection methods, such as considering the number of grains per row and chlorophyll concentrations (SPAD index), have been employed to enhance expanded popcorn volume per hectare [14]. Investigations into the inheritance of key agronomic traits and their economic significance in popcorn have also been conducted [19]. Moreover, studies have been conducted to understand the relationships between water stress and various phenotypic responses, including morphological, cellular, epidermal, and stomatal densities; leaf pigments; leaf gas exchange; fluorescence measurements; relative leaf water content; and discrimination via C-isotope [19,20,28]. By decomposing the genetic effects of multiple traits across different combining abilities, researchers have gained valuable insights, such as into heterotic effects and reciprocal effects.

Furthermore, investigations have explored the heterotic impacts and reciprocal effects on diverse physiological, morphological, and root traits [12,29,30]. These studies have provided valuable information about the genetic basis of economically important traits in popcorn. Understanding this genetic foundation is a crucial step in implementing effective genetic improvement programs aimed at increasing the production and enhancing the adaptation of popcorn genotypes resistant to water-stressed environments.

Diallel crosses are a well-established approach, and they have proven to be a promising option in understanding the inheritance of tolerance to water deficit and in generating combinations that consistently perform well under limited water availability [19,20,30]. These crosses offer valuable insights into the genetic mechanisms at work and can aid in the selection and breeding of drought-tolerant popcorn varieties.

In diallel analysis, two types of combinatorial ability are commonly considered: general combining ability (GCA) and specific combining ability (SCA) [31]. GCA refers to the average performance of an inbred line across various hybrid combinations. It is estimated by comparing the average performance of its hybrids with the overall average of all crosses. GCA is primarily associated with the additive effects of genes ($\hat{\phi}^2_g$). On the other hand, SCA represents the specific hybrid combination's performance deviation from the expected value based solely on the GCA of the inbred lines involved (Sprague and Tatum, 1942) [32]. SCA is linked to non-additive gene effects, such as dominance and epistasis ($\hat{\phi}^2_s$) (Hallauer et al., 2010) [33]. These non-additive effects rely on genetic complementation.

With this information in mind, our research aimed to generate insights into the genetic control of economically valuable traits in popcorn, as well as root traits that contribute to

drought tolerance. We sought answers to the following questions. What type of genetic action (additive or non-additive) predominantly influences the expression of agronomic and root traits in popcorn under water deficit conditions? Does the genetic action remain consistent under both well-watered and water-stress conditions? Our ultimate goal was to provide valuable information about the impact of genetic effects on traits of interest. This information could assist in selecting the best breeding strategies to develop superior genotypes that are less susceptible to the negative effects of water restriction.

2. Results

2.1. Agronomic and Root Traits Response to Water Conditions: Significant Differences and Reductions in Phenotypic Responses

Significant differences were observed in all agronomic traits for both water conditions (Table 1). The experimental variation coefficients (C_v) ranged from 5.95 (GW) to 22.81% (PV) for WS and from 5.12 (EW) to 17.59% (PV) for WW. In the combined analysis, genotype (G) and water condition (WC) were significant sources of variation for all agronomic traits, while the G × WC interaction was significant only for GY, PV, and GW (Table 1). Water deficit caused reductions in all agronomic traits when comparing WS and WW conditions. The most significant losses were observed in GY (39.35%) and PV (44.98%), while PE and GW exhibited relatively smaller reductions of 9.74% and 8.24%, respectively (Figure 1).

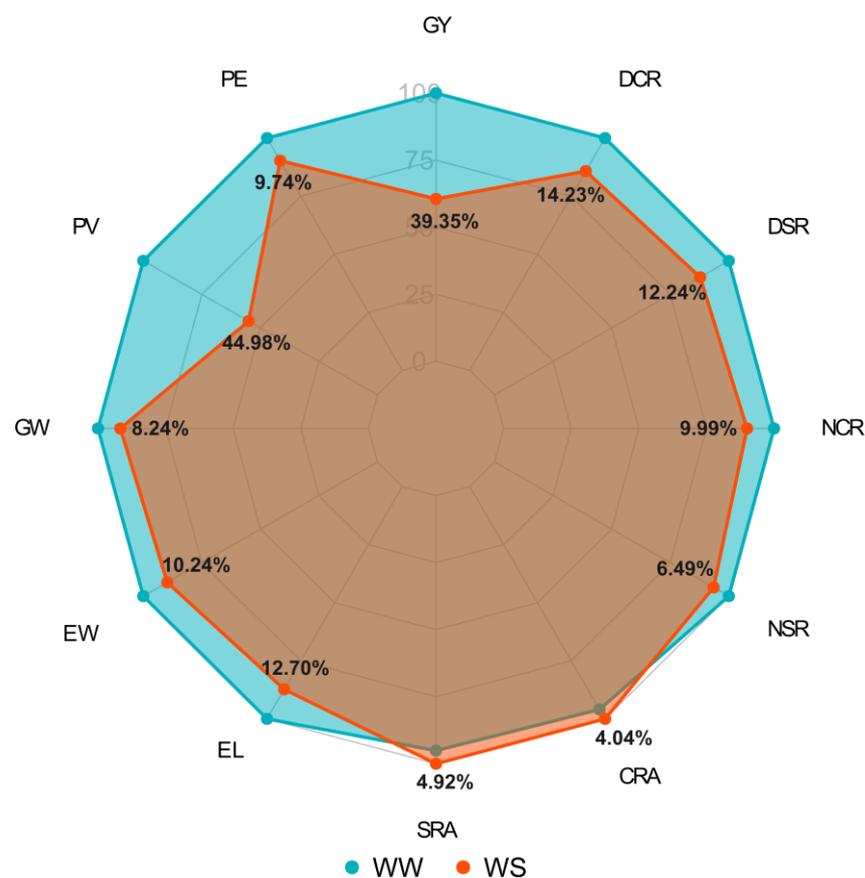


Figure 1. Comparison of agronomic traits and root architecture under water-stressed condition (WS) and well-watered condition (WW). GY: grain yield ($t \cdot ha^{-1}$); PE: popping expansion ($g \cdot mL^{-1}$); PV: expanded popcorn volume per hectare ($m^3 \cdot ha^{-1}$); GW: 100-grain weight (g); EW: ear width (mm); EL: ear length (cm); SRA: support root angle; CRA: crown root angle; NSR: number of support roots; NCR: number of crown roots; DSR: density of support roots; DCR: density of crown roots.

Table 1. Summary of analysis of variance, genotype mean squares, residual mean squares, overall averages, standard deviations, and interactions by joint analysis for agronomic traits and root architecture in popcorn genotypes under water-stressed (WS) and well-watered (WW) conditions.

SV		WS						WW						JA				
		G		RE	MS	AV	SD	CVe	G		RE	MS	AV	SD	CVe	G	WC	G × WC
		(df = 24)	(df = 48)	(df = 24)					(df = 48)									
Agronomic traits	GY	1606.11	5.07	**	1.68	±2.25	13.4	3505.08	99.56	**	2.77	±9.98	11.38	**	**	**		
	PE	40.21	12.69	**	22.71	±3.56	15.69	1469.25	10.78	**	25.16	±3.28	13.05	**	**	ns		
	PV	846	74.17	**	37.75	±8.61	22.81	2027.86	145.7	**	68.61	±12.07	17.59	**	**	**		
	GW	6.34	0.7	**	14.03	±0.84	5.95	7.86	1.51	**	15.29	±1.23	8.03	**	**	*		
	EW	22.62	3.47	**	28	±1.86	6.65	27.59	2.56	**	31.2	±1.60	5.12	**	**	ns		
	EL	6.61	1.1	**	10.65	±1.05	9.85	8.3	1.14	**	12.2	±1.07	8.76	**	**	ns		
Root architecture	SRA	53.25	24.97	*	59.73	±5.00	8.37	69.74	37.42	*	56.93	±6.12	10.74	**	**	ns		
	CRA	47.73	20.11	**	69.23	±4.48	6.48	65.96	47.68	ns	66.54	±6.91	10.38	**	**	ns		
	NSR	2.67	1.43	*	7.4	±1.20	16.19	1.47	1.81	ns	7.91	±1.35	16.99	ns	ns	ns		
	NCR	11.08	3.87	**	13.76	±1.97	14.3	10.3	4.2	**	15.29	±2.05	13.4	**	**	ns		
	DSR	2.42	0.62	**	4.73	±0.79	16.63	2.05	1.07	*	5.39	±1.03	19.21	**	**	ns		
	DCR	1.02	0.3	**	3.48	±0.55	15.76	1.82	0.71	**	4.05	±0.84	20.79	**	*	ns		

WS: water-stressed; WW: well-watered; JA: joint analysis; SV: sources of variation; G: genotype; MS: mean squares; DF: degrees of freedom; RE: residual; AV: average; CVe: experimental coefficient of variation (%); WC: water condition; GY: grain yield ($t \cdot ha^{-1}$); PE: popping expansion ($g \cdot mL^{-1}$); PV: expanded popcorn volume per hectare ($m^3 \cdot ha^{-1}$); GW: 100-grain weight (g); EW: ear width (mm); EL: ear length (cm); SRA: support root angle ($^{\circ}$); CRA: crown root angle ($^{\circ}$); NSR: number of support roots; NCR: number of crown roots; DSR: density of support roots; DCR: density of crown roots; ns = not significant at 5% probability level in the F test; * and ** = significant at 5% and 1% probability levels in the F test; respectively.

All root traits showed significant differences in both water conditions, except for AC and NB in the WW condition (Table 1). In general, comparing the two water conditions, there was a reduction in the phenotypic responses of all traits when subjected to the WS condition, except for SRA and CRA, which showed a small increase in their mean values (4.92% and 4.04%, respectively) under the stress condition (Figure 1).

2.2. Estimates of General and Specific Combining Ability and Quadratic Components under Varying Water Conditions: Implications for Trait Variability

Significant differences were observed for both general combining ability (GCA) and specific combining ability (SCA) estimates in all agronomic traits under both water conditions, except for popping expansion (PE) in the WS condition, which showed significance only for GCA (Table 2). The quadratic components associated with SCA ($\hat{\phi}^2$ s) were found to be the most influential factors in explaining the observed variability in the traits, except for PE (Figure 2).

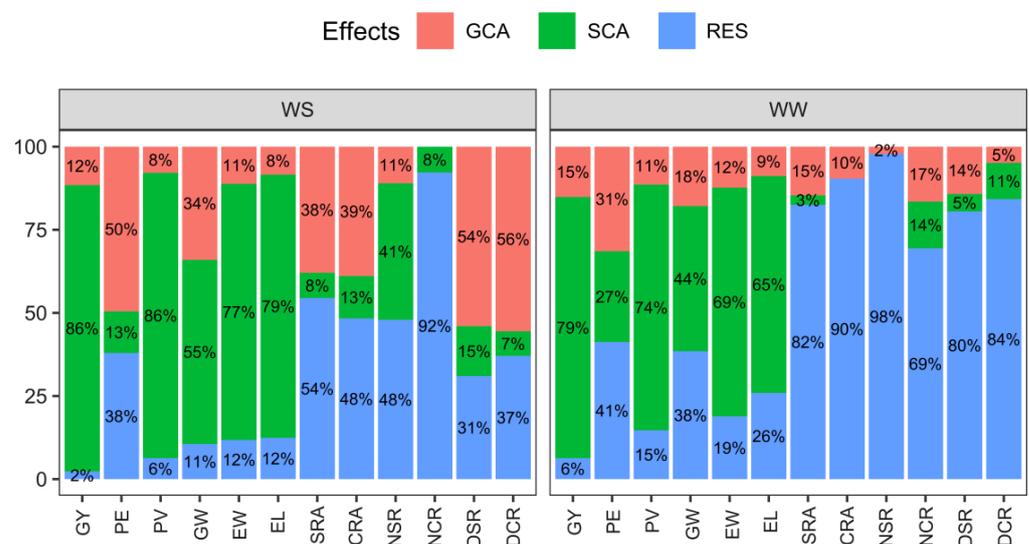


Figure 2. Importance of quadratic components for agronomic traits and root architecture in popcorn genotypes under water-stressed conditions (WS) and well-watered conditions (WW). GCA: general combining ability; SCA: specific combining ability; RES: residual; GY: grain yield ($t \cdot ha^{-1}$); PE: popping expansion ($g \cdot mL^{-1}$); PV: expanded popcorn volume per hectare ($m^3 \cdot ha^{-1}$); GW: 100-grain weight (g); EW: ear width (mm); EL: ear length (cm); SRA: support root angle ($^\circ$); CRA: crown root angle ($^\circ$); NSR: number of support roots; NCR: number of crown roots; DSR: density of support roots; DCR: density of crown roots.

Regarding the root traits, significant differences were predominantly observed only for GCA estimates in the WS condition, except for the number of support roots (NSR), which did not show significance in either of the water conditions, indicating a strong environmental influence on the expression of this trait (Table 2). The quadratic component associated with SCA ($\hat{\phi}^2$ s) was more relevant in explaining the variability observed specifically for the density of crown roots (DCR) in the well-watered (WW) condition, while the other traits showed greater relevance with the quadratic components associated with GCA ($\hat{\phi}^2$ g) (Figure 2).

2.3. General Combining Ability Values in Popcorn Hybrids under Contrasting Water Conditions

In both WS and WW conditions, positive general combining ability (GCA) values were observed in: (i) L76, P2, P3, P6, and P7 for grain yield (GY); (ii) L61, L71, and P6 for popping expansion (PE); (iii) L65, L71, P2, and P3 for 100-grain weight (GW); (iv) L63, L76, P2, and P3 for ear width (EW); and (v) L76, P2, P3, P6, and P7 for ear length (EL) (Figure 3).

Table 2. Mean square estimates of popcorn genotypes for general and specific combining abilities (GCA and SCA), including the residual mean squares of combining ability effects on agronomic traits and root architecture in distinct water conditions.

SV	WS									WW							
	GCA			SCA			Residual			GCA			SCA			Residual	
	MS	$\hat{\phi}^2_g$	%	MS	$\hat{\phi}^2_s$	%	MS	%	MS	$\hat{\phi}^2_g$	%	MS	$\hat{\phi}^2_s$	%	MS	%	
Agronomic traits	GY	**	84,352.97	11.58	**	627,108.88	86.10	50,701.06	2.32	**	239,258.44	15.13	**	1,242,056.56	78.57	99,563.94	6.30
	PE	**	5.53	49.55	ns	1.40	12.54	12.69	37.91	**	8.23	31.47	**	7.14	27.30	10.78	41.23
	PV	**	30.89	7.86	**	337.51	85.85	74.17	6.29	**	113.18	11.42	**	732.20	73.88	145.70	14.70
	GW	**	0.75	34.05	**	1.22	55.39	0.70	10.56	**	0.70	17.87	**	1.71	43.66	1.51	38.47
	EW	**	1.10	11.19	**	7.57	77.06	3.47	11.76	**	1.67	12.32	**	9.33	68.82	2.56	18.86
	EL	**	0.24852	8.40	**	2.34	79.19	1.10	12.40	**	0.39	8.84	**	2.88	65.25	1.14	25.91
Root architecture	SRA	**	5.80	37.95	ns	1.16	7.59	24.97	54.46	**	6.64	14.64	ns	1.30	2.87	37.42	82.50
	CRA	**	5.40	38.92	ns	1.77	12.76	20.11	48.32	*	5.08	9.63	ns	-2.45	0.00	47.68	90.37
	NSR	ns	0.11	11.02	ns	0.41	41.07	1.43	47.91	ns	0.04	2.17	ns	-0.27	0.00	1.81	97.83
	NCR	**	-3.10	0.00	ns	2.17	7.78	77.14	92.22	**	1.00	16.54	ns	0.85	14.06	4.20	69.41
	DSR	**	0.36	54.01	ns	0.10	15.00	0.62	30.99	**	0.19	14.25	ns	0.07	5.25	1.07	80.50
	DCR	**	0.15	55.54	ns	0.02	7.41	0.30	37.05	**	0.13	4.89	*	0.29	10.91	2.24	84.20

WS: water-stressed; WW: well-watered; SV: sources of variation; GCA: general combining ability; SCA: specific combining ability; MS: mean squares; $\hat{\phi}^2_g$: quadratic component associated with GCA; $\hat{\phi}^2_s$: quadratic component associated with a SCA; %: percentage of the total variance; GY: grain yield; PE: popping expansion; PV: expanded popcorn volume per hectare; GW: 100-grain weight; EW: ear width; EL: ear length; SRA: support root angle; CRA: crown root angle; NSR: number of support roots; NCR: number of crown roots; DSR: density of support roots; DCR: density of crown roots; ns = not significant at 5% probability level in the F test; * and ** = significant at 5% and 1% probability levels in the F test; respectively.

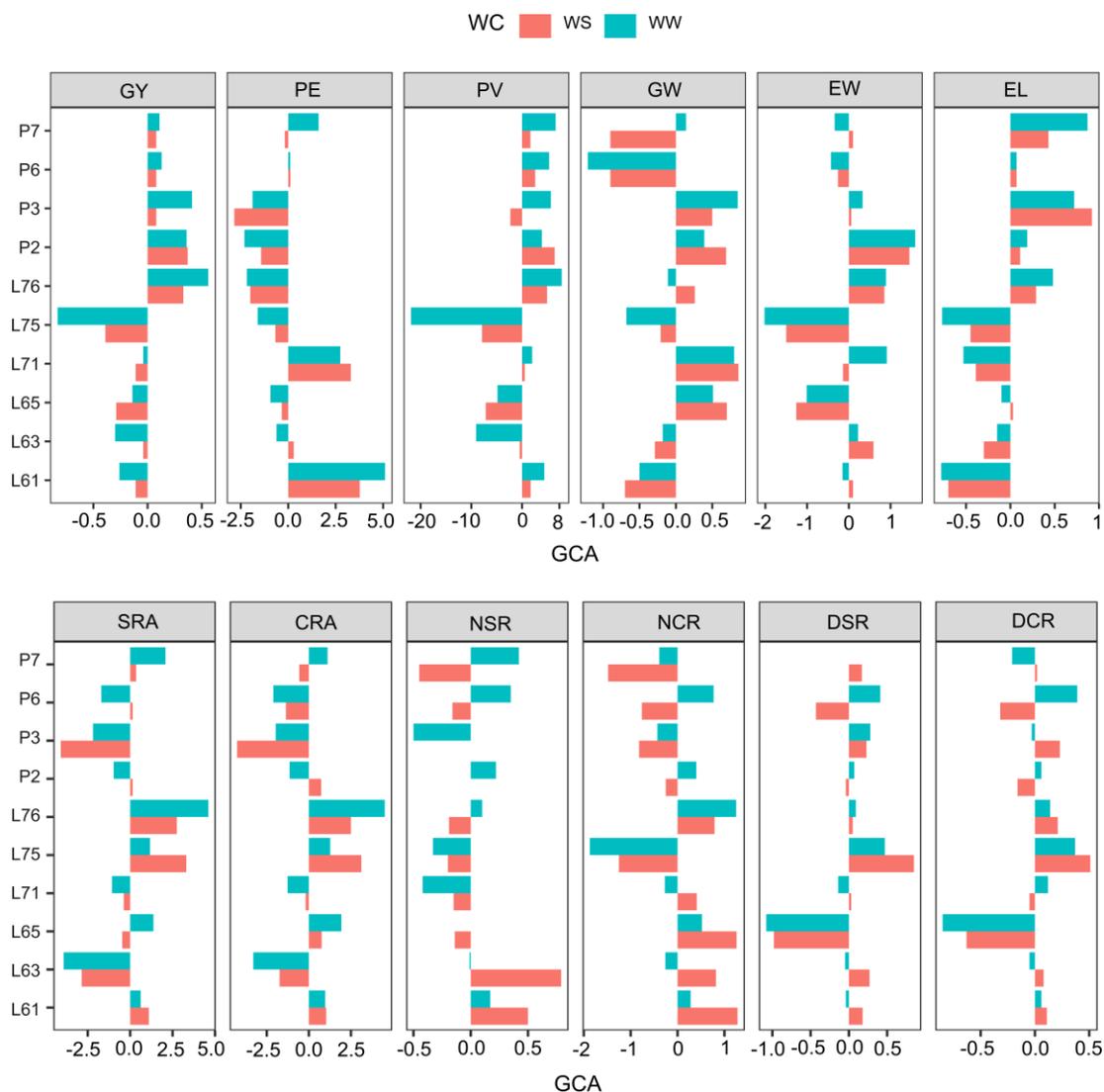


Figure 3. Estimates of the effects of general combining abilities (GCA) for agronomic and root traits of popcorn inbred lines under water-stressed conditions (WS) and well-watered conditions (WW). GY: grain yield ($\text{t} \cdot \text{ha}^{-1}$); PE: popping expansion ($\text{g} \cdot \text{mL}^{-1}$); PV: expanded popcorn volume per hectare ($\text{m}^3 \cdot \text{ha}^{-1}$); GW: 100-grain weight (g); EW: ear width (mm), EL: ear length (cm); SRA: support root angle ($^\circ$); CRA: crown root angle ($^\circ$); NSR: number of support roots; NCR: number of crown roots; DSR: density of support roots; DCR: density of crown roots.

For root traits, in both WS and WW conditions, positive general combining ability (GCA) values were observed in: (i) L61, L75, L76, and P7 for support root angle (SRA); (ii) L61, L65, L75, and L76 for crown roots angle (CRA); (iii) L61 for number of support roots (NSR); (iv) L61, L65, and L76 for number of crown roots (NCR); (v) L75, L76, and P3 for density of support roots (DSR); and (vi) L61, L75, and L76 for density of crown roots (DCR) (Figure 3). These results indicate the potential of specific inbred lines for the improvement of these traits under contrasting water conditions.

2.4. Specific Combining Ability Value in Popcorn Hybrids under Contrasting Water Conditions

For the agronomic traits, significant SCA values were observed in the hybrids under both water conditions. The hybrids that showed highly positive SCA indices are shown in Figure 4. Considering the general averages for both water conditions, the following hybrids stood out: PV, L71/L76 with an average of $69.34 \text{ m}^3 \cdot \text{ha}^{-1}$ in WS and $108.60 \text{ m}^3 \cdot \text{ha}^{-1}$ in WW; GW, L65/P3 with an average of 16.84 g/ha in WS and 17.75 g/ha in WW; EW, L65/L76

with an estimate of 31.53 mm in WS and L61/P2 with an average of 34.81 mm in WW; and EL, L61/L75 with a mean of 12.64 cm in WS and 14.55 cm in WW, as well as L65/L76 with means of 12.64 cm in WS and 14.55 cm in WW (Supplementary Table S1).

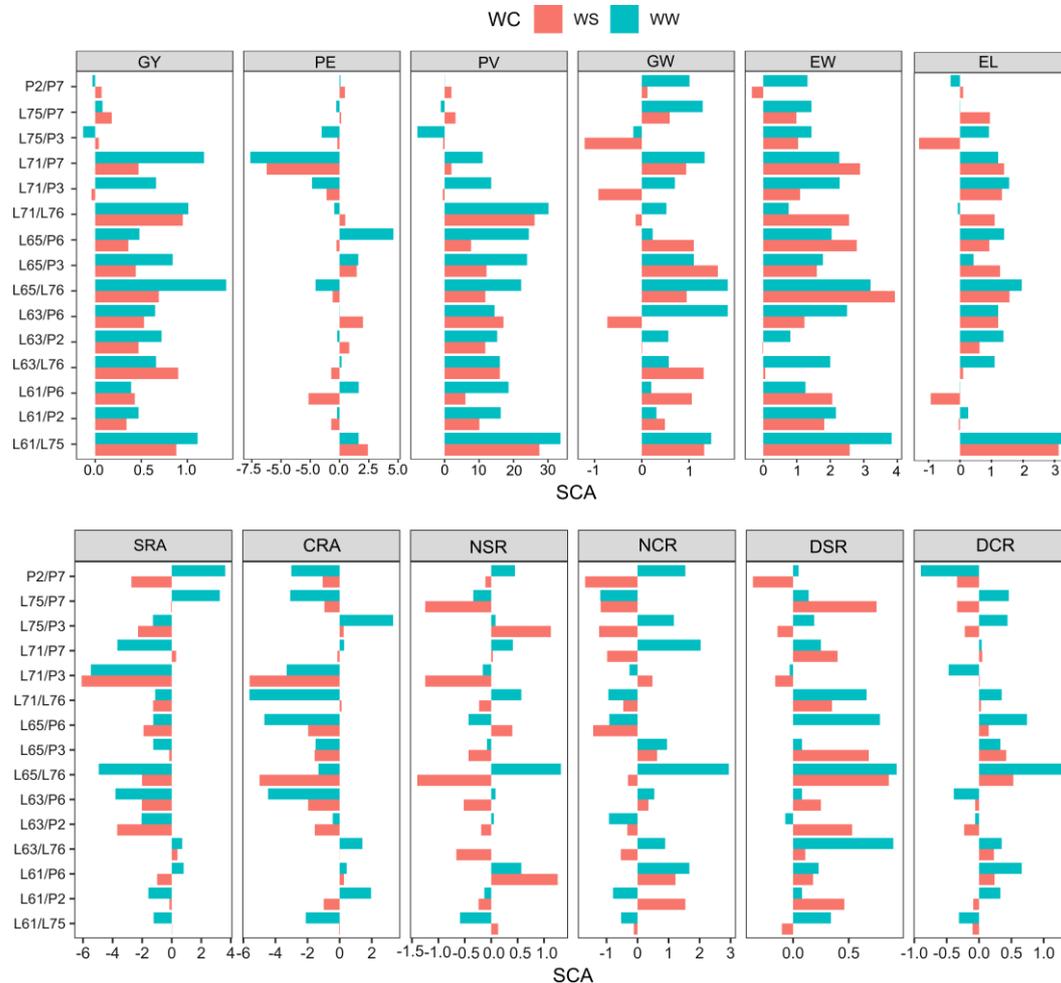


Figure 4. Estimates of the effects of specific combining ability (SCA) of agronomic and root traits of 15 popcorn hybrids under water stressed (WS) conditions and well-watered conditions (WW). GY: grain yield (t ha^{-1}); PE: popping expansion (g mL^{-1}); PV: expanded popcorn volume per hectare ($\text{m}^3 \text{ ha}^{-1}$); GW: 100-grain weight (g); EW: ear width (mm); EL: ear length (cm); SRA: support root angle ($^\circ$); CRA: crown root angle ($^\circ$); NSR: number of support roots; NCR: number of crown roots; DSR: density of support roots; DCR: density of crown roots.

Regarding root traits, the hybrids with the highest SCA values in both water conditions are shown in Figure 4. The best-performing hybrids were L63/L76 with values of 60.0° in WS and 58.33° in WW for SRA; L61/P6 and L75/P3 with values of 69.17° in WS and 65.83° in WW, and 68.33° in WS and 69.17° in WW for CRA; L61/P6 with values of 15.50 in WS and 18.0 in WW for NC; and L65/L76 with values of 3.58 in WS and 4.67 in WW for DCR (Supplementary Table S1).

3. Discussion

3.1. Genetic Variability in Different WCs

Genetic variability was observed among the evaluated genotypes for agronomic traits. Suspending irrigation during the pre-anthesis phase led to significant reductions in trait responses under water-stressed (WS) conditions. Previous studies have indicated that severe drought during the reproductive stages of corn and popcorn can cause substan-

tial grain yield losses [11,12,28]. Water stress during the flowering stage can result in female gamete sterility, floral asynchrony, reduced anther dehiscence, and decreased pollen viability, ultimately impacting flower formation, fertilization, and the number of grains produced on the ear [34–37]. Moreover, water deficit during grain filling directly affects key yield components, such as grain weight and size, involving complex morphological, physiological, and biochemical responses [38,39], resulting in significant crop yield losses and economic implications for producers.

Variability among the evaluated genotypes was observed for root traits, except for CRA and NSR under well-watered (WW) conditions (Table 1). Corn plants have adapted to improve drought tolerance by reducing the number and density of crown roots and increasing rooting depth, enabling water uptake from deeper soil layers [22,25]. The small increase (4.04%) resulting from the difference between WW and water-stressed (WS) regimes did not contribute to variability in CRA traits. The absence of a statistical difference in WC responses could be explained by two rainfall events at 77 days (30.8 mm) and 98 days (65 mm) after planting, temporarily increasing the soil's osmotic potential (Table 4 and Figure 5). As for NSR, the lack of genotypic variability in both individual (WC) and combined (G and WCs) analyses could be attributed to the minimal difference between treatments until day 49 when the WS condition intensified. Consequently, the initial regime difference did not significantly impact the number of support roots (NSR).

Among the 12 traits evaluated and considering the combined analysis of the genotype by water condition ($G \times WC$) interaction, statistical differences were observed only for grain yield (GY), PV, and GW (Table 1). These findings indicate that these traits exhibit complex effects, suggesting that genotype selections based on these traits can be accurately performed by considering each water condition separately. In other words, the performance of genotypes may vary under different water conditions, emphasizing the importance of considering the specific environmental context when making breeding decisions related to GY, PV, and GW traits. This information is valuable for breeders and researchers aiming to develop cultivars with improved performance and adaptability under varying water availability conditions.

3.2. Effect of Water Limitation

For a comprehensive understanding of the impact of water stress on corn growth and development, it is crucial to recognize the intricate nature of various plant responses to water deficiency. These responses encompass morphological changes (reduced plant size, decreased stay-green phenomenon, increased leaf rolling, prolonged anthesis-silking interval, elevated root-to-shoot ratio, etc.), physiological adjustments (stomatal closure, decreased transpiration and photosynthesis rates, enhanced oxidative stress, improved water use efficiency, etc.), and biochemical adaptations (accumulation of abscisic acid and stress-related metabolites, increased activity of antioxidative enzymes, decreased photochemical efficiency, etc.) [40,41]. The collective impact of these responses significantly influences the grain yield in corn, as drought conditions directly and negatively affect grain filling, size, and weight.

In the specific case of popcorn cultivation, previous studies by Kamphorst et al. [28] investigated the effects of water stress on S_7 inbred lines from flowering to physiological maturity and reported substantial reductions of 55.3% in grain yield and 28.76% in popping expansion. Similarly, Leite et al. [41] demonstrated significant decreases in grain yield (59.98%) and popping expansion (21.45%) when evaluating S_7 popcorn inbred lines under water stress conditions. However, studies examining hybrids and inbred lines simultaneously, such as those conducted by Lima et al. and Kamphorst et al. [19,20], reported smaller reductions in grain yield and popping expansion. These findings align with the current study, which observed reductions of 39.35% and 9.74% in grain yield (GY) and popping expansion (PE), respectively. The expansion process is associated with moisture presence in the starch granules of the grain. When heated ($\approx 180^\circ\text{C}$), the moisture exerts pressure on the pericarp, with rupturing subsequently exposing the endosperm [42]. This process

means that water shortages during grain formation can affect physicochemical properties and therefore the capacity of the grain to expand. Moreover, no morphological or chemical traits that could explain this phenomenon have yet been recorded [21].

The traits ear length (EL) and ear width (EW) experienced reductions of 12.70% and 10.24%, respectively, under water stress conditions. These findings are consistent with a study conducted by Ali [43] on corn, in which water stress led to a reduction of 6.98% in ear diameter and 13.99% in ear length. The occurrence of water stress during the pre-flowering period can disrupt the synchrony between tassel and ear growth, causing a delay in anther extrusion and exposing pollen grains to the stigma style [44]. In our study, the water stress regime was implemented close to the flowering period, when the ear is undergoing active development. Consequently, water deficit significantly affected ear formation, resulting in substantial reductions in both ear length and width (EL and EW).

Regarding 100-grain weight (GW), a reduction of 8.27% was observed under water stress (WS) compared to well-watered (WW) conditions. This reduction is comparatively lower than the losses observed in other agronomic traits, which may be attributed to the lower intensity of water deficit during the grain filling period. Ali [43] also reported a smaller reduction in GW (12.17%) in corn genotypes. Sah et al. [40] reported losses of 8.86% in non-drought tolerant and 17.67% in drought-tolerant corn inbred lines subjected to water stress.

Root densities (DSR and DCR) were significantly impacted by water stress, showing the greatest sensitivity among all the root architecture traits. The decrease in root density observed in response to stress can be attributed to genotypes' adaptive responses, in which reduced root competition enhances the metabolic efficiency of soil exploration, promoting drought tolerance [22,25,45,46]. In the context of nutrient acquisition and soil exploitation efficiency, corn and other plant species employ two general mechanisms: enhancing root system distribution and improving transmembrane nutrient absorption [39]. The latter mechanism involves minimizing the metabolic cost of soil exploration under water deficit conditions by developing hypertrophy of root cortical cells while reducing their overall number [47,48]. This adaptation allows for deeper soil exploration, potentially accessing water and nutrients in the lower soil layers.

Overall, the reduced root densities observed in DSR and DCR traits under water stress indicate a strategic adjustment of the root system to optimize resource utilization and enhance drought tolerance in corn plants.

The current study also observed a reduction in the number of crown roots in response to water stress. In corn plants, this reduction indicates a greater rooting depth, facilitating the uptake of nitrogen and water from the subsurface layers of water-deficient soil [24,49]. Furthermore, the SRA and CRA traits showed increases of 4.92% and 4.05%, respectively, under water-stress conditions. A root system with a steeper angle toward the soil enhances the acquisition of water and nutrients by allowing for exploration of deeper soil profiles. This characteristic enables plants to avoid relying solely on the superficial soil layers that are most affected by water deficit [24]. Kamphorst et al. [28] also reported larger root angles in popcorn lines as an adaptive trait of the root system in response to water deficit. The observed reduction in crown roots and the increases in SRA and CRA traits under water stress reflect the adaptive strategies of popcorn plants to optimize water and nutrient uptake under limited conditions. These traits contribute to enhanced drought tolerance and support the efficient utilization of resources in water-deficient environments.

3.3. The Influence of Genetics Effects on Plant Response to Contrasting Water Conditions

The influence of water conditions (WCs) on the estimation of general and specific combining abilities for agronomic traits was observed, with dominance effects ($\hat{\phi}^2_s$) playing a more significant role than additive effects ($\hat{\phi}^2_g$). Non-additive effects accounted for 86% of the total variation in grain yield (GY) under water stress (WS) and 78% under well-watered (WW) conditions. The trait expanded popcorn volume (PV) exhibited a strong influence of non-additive effects, contributing to 86% of the total variation in WS and 74%

in WW. These findings are consistent with previous studies conducted by [15,20,50–53]. Non-additive effects were also prominent for ear width (EW) (77% in WS and 69% in WW) and ear length (EL) (79% in WS and 65% in WW).

Similarly, the substantial non-additive effects observed for the yield components (EW, EL, and GW) under both WCs suggest that harnessing heterosis through careful parental selection is the most effective strategy for enhancing the performance of these traits in popcorn. This finding is in agreement with previous studies highlighting the significant role of heterosis in corn's adaptation to various types of stress [54–57].

The obtained results provide evidence that the additive effect plays a more significant role in determining the expression of popping expansion (PE), as indicated by the substantial magnitude of $\hat{\phi}^2_g$, which accounted for 50% of the total variation under well-watered (WW) conditions. However, under water stress (WS) conditions, the contribution of $\hat{\phi}^2_g$ to the trait's expression was less prominent, explaining only 31% of the total variation. A study conducted by Kamphorst et al. [20] investigating the effects of different water conditions on agronomic traits in popcorn hybrids and lines also identified a significant interaction of specific combining ability (SCA) components for PE, with an average variation of 18% for the trait. This variation can be attributed to the differential expression of alleles controlling the same trait under more severe environmental changes, such as water stress, leading to the activation or suppression of specific genes [58–60].

Popping expansion (PE) is a trait in which additive effects play a crucial role in its expression, as supported by previous studies [19,20,50,61–65]. Therefore, employing breeding methods that prioritize the accumulation of favorable additive alleles becomes essential for achieving genetic gains in PE and other economically important traits in the crop. This goal can be achieved through the development of inbred lines resulting from advanced cycles of intrapopulation selection, followed by the exploitation of heterosis through strategic crosses. These breeding strategies have demonstrated effectiveness in enhancing not only PE but also other valuable traits in popcorn [19,66].

The analysis of the root traits revealed significant general combining ability (GCA) effects in both well-watered (WW) and water-stressed (WS) regimes for most of the traits, except for NRS and DCR under WW conditions, in which additive effects were not statistically significant (Table 2). These findings suggest that the control of the evaluated root traits is predominantly influenced by additive gene action. One significant advantage of traits controlled by additive effects is the possibility of directly selecting parents without the need for prior combinatorial ability studies [33].

However, a contrasting observation was provided by Kamphorst et al. [12], who evaluated different traits in S_7 inbred lines and popcorn hybrids under two water regimes (WS and WW) in a greenhouse. They found that, for most of the quadratic components, there was a predominance of specific combining ability (SCA), indicating that non-additive effects ($\hat{\phi}^2_s$) played a major role in controlling specific root length and root weight density. The authors even recommended harnessing heterosis in both water conditions to enhance the expression of phenotypic responses for root traits.

Considering the conflicting results regarding the genetic effects controlling root traits in popcorn, it is important to approach this discussion cautiously and with careful consideration. It should be noted that the environmental effect is a crucial factor in this equation and can significantly influence the expression of these traits.

3.4. Combining Ability: Exploring Trait Interactions in Contrasting Water Conditions

In this study, the effects of GCA on the lines L76, P2, and P3 were found to have positive and high values for the traits GY, EL, and EW, consistent with previous findings by Kamphorst et al. (2018b) [27]. Positive and high magnitudes of GCA were also observed for the lines L61 (WW) and GW and for the lines P3 (WW) and L71 (in both WCs) regarding the agronomic trait PE (Figure 3). The hybrids L61/L75, L65/L76, and L71/L76 showed the highest magnitudes of $\hat{\phi}^2_s$ for the agronomic traits that expressed the dominance effect, indicating the importance of SCA in these traits (Figure 4 and Supplementary Table S1).

The genotypes L76, L61, and L71 were identified as good progenitors for recombination when considering both GCA and SCA effects together. However, further research is needed to understand the influence of water deficit on the expression of these traits.

In terms of root traits, the inbred line L76 exhibited high magnitudes of GCA for SRA, CRA, and NCR in WW, while line L75 stood out for DSR in WS and DCR in both WCs (Figure 3). Examining the SCA, the hybrid L61/L75 showed a significant increase in SRA, CRA, and DCR under WS conditions (Figure 4 and Supplementary Table S1), indicating its contribution to a root architecture that facilitates enhanced water and nutrient absorption. Genotypes characterized by a greater root angle to the soil, fewer roots, and lower root hair density are known to represent the ideotype for improved drought tolerance, offering adaptive advantages in WS conditions [22,25,28]. Based on these findings, the L61/L75 hybrid emerges as an ideotype and presents a promising option for cultivation in Brazilian agribusiness.

The inbred lines investigated in this study have been extensively utilized in popcorn research, particularly in studies involving various water stress treatments. Previous investigations have demonstrated that these inbred lines exhibit considerable phenotypic plasticity, making them valuable contributors to combining ability assessments under drought conditions [12,19,20,27–30].

According to Wattoo et al. [67], lines displaying positive and high GCA values play a crucial role in breeding programs, as they enhance the likelihood of obtaining hybrids with favorable phenotypic responses. In line with this notion, the findings of this study align with the aforementioned statement since hybrid combinations demonstrating higher magnitudes of SCA were predominantly composed of lines exhibiting substantial GCA estimates.

4. Materials and Methods

4.1. Plant Material

For the current study, 10 inbred lines were selected from previous studies conducted by Kamphorst et al. [28,68] to evaluate their performance under water stress conditions. Among them, four (P2, P3, P6, and P7) were efficient in agronomic water use, while four (L61, L63, L65, and L75) were inefficient, and two (L71 and L76) were intermediate. The five lines derived from the BRS-Angela variety (L61, L63, L65, L71, and L75) have tropical climate adaptations, while P6 and P7 are derived from the Zaeli commercial three-way hybrid. P2 and P3 were obtained from the composite CMS-42, and L76 was derived from the Viçosa variety. All of the last five lines have temperate/tropical climate adaptations, as reported by Vittorazzi et al. [69].

The 10 popcorn inbred lines were then used as parents to obtain 15 hybrids through circulating in diallel, based on the model proposed by Kempthorne and Curnow [70], adopting the value of *s* (crosses) equal to 3 (Table 3). Crosses were performed in pairs so that there were combinations between lines with the same genealogy.

Table 3. Hybrid combinations from the circulating diallel among 10 S7 inbred lines of popcorn with crosses (*s*) = 3.

Inbred Lines	L75	P2	P6	L76	P3	P7
L61	X	X	X			
L63		X	X	X		
L65			X	X	X	
L71				X	X	X
L75					X	X
P2						X

The hybrid seeds were obtained at the Experimental Station of Antônio Sarlo State Agricultural College in Campos dos Goytacazes, RJ, Brazil (21°42'48" S, 41°20'38" W, 14 m altitude).

4.2. Environmental Conditions and Experimental Design

The evaluation trial of 15 hybrids and their respective 10 S₇ inbred lines was conducted during the low rainfall season of the region, from April to August 2018, at the same experimental station where the genotypes were obtained. The experimental design was a randomized complete block with three replications under two distinct water conditions, namely water-stressed (WS) and well-watered (WW). Each plot consisted of a row of 4.8 m, with a spacing of 0.2 m between plants and 0.8 m between rows and a total of 23 plants per plot. For the sowing fertilization, 30 kg.ha⁻¹ of N (urea), 60 kg.ha⁻¹ of P₂O₅ (single superphosphate), and 60 kg.ha⁻¹ of K₂O (potassium chloride) were used. Topdressing fertilization was carried out 30 days after sowing, with an additional 100 kg.ha⁻¹ of N (urea).

Irrigation was applied using a drip system with a “Katif” dripper installed for each plant, having a flow rate of 2.3 mm.h⁻¹. The soil of the experimental station was classified as yellow dystrophic latosolic fragipan argisol, and it contained high clay and silt levels. The soil water content at field capacity and permanent wilting point was 38.21% and 28.41%, respectively. The soil water content was monitored using three Decagon MPS-6 sensors (Decagon, Pullman, WA, USA) installed at a depth of 0.2 m, exactly between two plants in the line of the treatment. In the WW condition, irrigation was performed to maintain the soil water at field capacity (−0.01 MPa), whereas, in the WS condition, irrigation was suspended at the pre-anthesis phenological stage, which was 15 days before male flowering. The plants experienced some rainfall during the trial, with a total of 148.2 mm recorded (Table 4). In the WS condition, the plants received 69.3 mm of water through irrigation, while in the WW condition, additional water corresponding to 186.8 mm was supplied (Table 4).

Table 4. Weekly precipitation and irrigation (mm) applied during the 2018 crop for popcorn genotypes under water-stressed (WS) and well-watered (WW) conditions after planting.

Days after Sowing	Amount of Water (mm)				
	Rainfall (mm)	WS		WW	
		Irrigation (mm)	Total	Irrigation (mm)	Total
1	0.00	2.70	2.70	2.60	2.60
7	17.00	3.50	20.50	3.60	20.60
14	6.00	10.20	16.20	11.00	17.00
21	0.00	9.90	9.90	10.10	10.10
28	10.60	10.30	20.90	10.70	21.30
35	5.20	8.40	13.60	8.40	13.60
42	2.00	12.20	14.20	11.60	13.60
49	0.00	12.10	12.10	12.90	12.90
56	0.00	-	0.00	10.90	10.90
63	0.00	-	0.00	18.80	18.80
70	0.00	-	0.00	18.90	18.90
77	30.80	-	30.80	1.10	31.90
84	0.00	-	0.00	16.70	16.70
91	0.00	-	0.00	14.00	14.00
98	65.00	-	65.00	2.00	67.00
105	0.00	-	0.00	13.50	13.50
112	9.20	-	9.20	10.00	19.20
119	2.40	-	2.40	10.00	12.40
Final Total	148.20 mm	69.30 mm	217.50 mm	186.0 mm	335.10 mm

In the WS treatment area, during the phenological stage of grain filling, the soil reached the minimum osmotic potential values ($\psi_s > -1.5$ Mpa), which corresponded to the permanent wilting point at 70 and 93 days after sowing (DAS) (Figure 5). However, there was an increase in the soil’s osmotic potential values due to a precipitation event recorded during the periods of ψ_s less than -1.5 Mpa (Table 4), as shown in Figure 5.

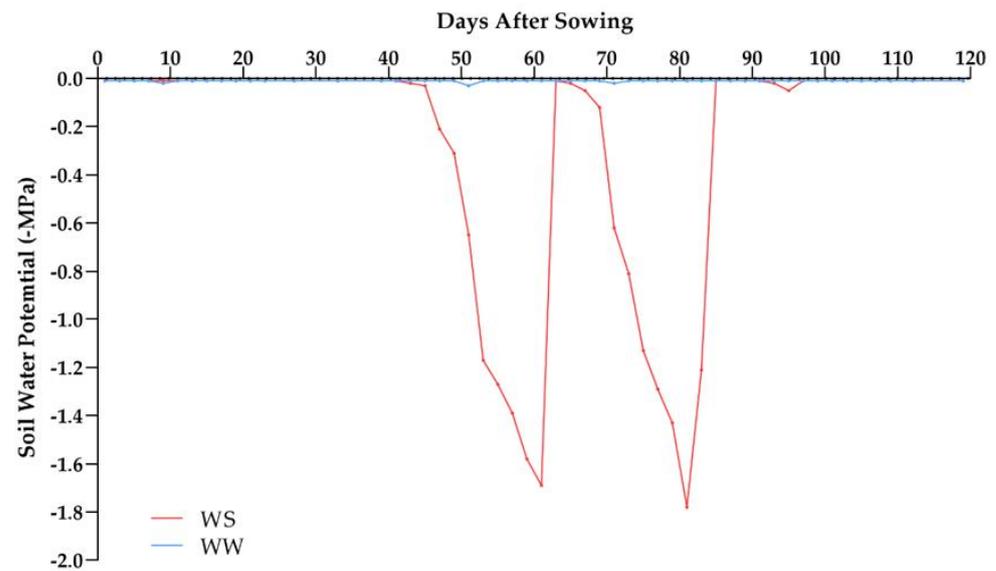


Figure 5. Soil water potential (-MPa) in the days after sowing (DAS) of the experiment carried out in the 2018 crop with popcorn genotypes in the water-stressed (WS) and well-watered (WW) conditions.

During the crop cycle, the average temperature was 21.59 °C, and the relative humidity was 78.45%. The mean solar radiation was approximately 1.189 $\mu\text{mol}/(\text{m}^{-2} \text{s}^{-1})$ (Figure 6). The weather conditions near the experimental area were recorded by a weather station belonging to the National Institute of Meteorology (INMET).

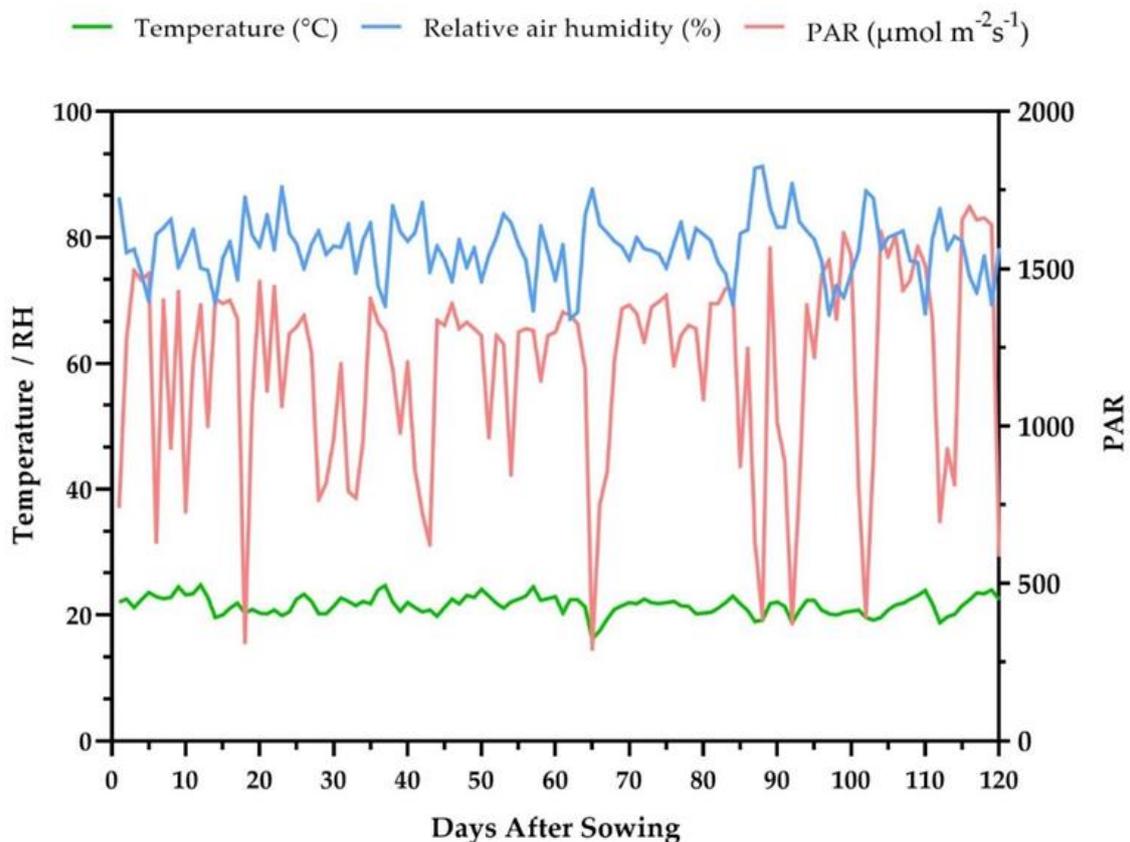


Figure 6. Daily average values of temperature (°C), relative humidity (RH—%), and photosynthetically active radiation (PAR— $\mu\text{mol m}^{-2} \text{s}^{-1}$) throughout the growing period of the experiment with popcorn genotypes in the 2018 crop.

4.3. Evaluated Traits

4.3.1. Agronomic Traits

Grain yield (GY) was determined by threshing the ears of each plot, correcting for 13% moisture and expressing the results in $\text{kg}\cdot\text{ha}^{-1}$. Popping expansion (PE) was calculated as the quotient between the volume of popped popcorn and the mass of grains used for popping (30 g), expressed in $\text{mL}\cdot\text{g}^{-1}$. The grains (30 g) were irradiated in the microwave (1000 W) for 2 min in a Kraft paper bag. The expanded popcorn volume per hectare (PV) was obtained by multiplying GY and PE and converting the results into $\text{m}^3\cdot\text{ha}^{-1}$. Ear length (EL) was measured using a ruler (cm), while ear width (EW) was estimated using calipers (mm). The 100-grain weight (GW) was determined by averaging the weight (g) of two samples of 100 grains per plot. All traits were evaluated for all plants in the plot, except for EL and EW, which were measured based on a random sample of six plants per plot.

4.3.2. Root Traits

The support root angle (SNA) and crown root angle (CRA) were estimated using a protractor and expressed in degrees ($^{\circ}$) relative to the soil surface. The number of support roots (NSR) and number of crown roots (NCR) was determined by direct counting. The density of support roots (DSR) and density of crown roots (DCR) were evaluated based on a rating scale proposed by Trachsel et al. [22], ranging from 0 to 9, with higher values indicating greater density. All root traits were measured and estimated based on a representative sample of three plants per plot.

4.4. Data Analysis

Individual analysis of variance was performed according to the following model: $Y_{ij} = m + G_i + B_j + e_{ij}$, where Y_{ij} is the observation of the i -th genotype in the j -th block; m is the overall mean; G_i is the fixed effect attributed to the i -th genotype; B_j is the random effect of the j -th block; and e_{ij} is the experimental error associated with the Y_{ij} observation, considering NID $(0, \sigma^2)$.

Subsequently, joint analysis of variance was performed to determine possible interactions between the genotypes with the two conditions of water availability, following the following model: $Y_{ijk} = m + B/A_{jk} + A_j + G_i + GA_{ij} + e_{ijk}$, where Y_{ijk} is the observation of the i -th genotype in the j -th block in the k -th block; m is the overall mean; B/A_{jk} is the effect of the k -th block in the j -th environment; A_j is the fixed effect of the j -th environment; G_i is the fixed effect of the i -th genotype; GA_{ij} is the fixed effect of the interaction between the i -th genotype with the j -th environment; and e_{ijk} is the experimental error associated with the Y_{ijk} observation, with NID $(0, \sigma^2)$.

Then, the genetic-statistical analysis was performed using model III, as described by Hallauer et al. (2010): $Y_{ij} = m + g_i + g_j + s_{ij} + e_{ijk}$, where Y_{ij} is the mean of the observation associated with the hybrid combination ij ($i \neq j$) or the i -th parent ($i = j$); m is the overall mean; g_i and g_j are the fixed effects of the general combining ability, respectively; s_{ij} is the fixed effect of the specific combining ability; and e_{ijk} is the mean experimental error.

The quadratic components (ϕ) that express genetic variability in terms of general (g) and specific (s) combining abilities were estimated by: $\phi_g = (\text{MSG} - \text{MSR})/2p$; and $\phi_s = \text{MSS} - \text{MSR}$, where MSG is the mean square of the general combining ability, MSS is the mean square of the specific combining ability, MSR is the mean square of the residue, and p is the number of parents. The GCA and SCA effects were estimated using the following expressions, respectively: $\hat{g} = \frac{1}{n+2} (Y_i + Y_{ii} - \frac{2}{n} Y_{..})$; and $\hat{s} = Y_{ij} - \frac{1}{n+2} (Y_i + Y_{ii} + Y_j + Y_{jj}) - \frac{2}{(n+1)(n+2)} Y_{..}$. Statistical analysis was performed using the GENES computational program [71].

5. Conclusions

In conclusion, it was observed that traits associated with grain yield (GY, PV, GW, EL, and EW) are predominantly influenced by dominance effect genes, while root traits (except

NSR and DCR in WW) and PE are primarily determined by gene additivity. Furthermore, these traits are strongly influenced by the environment, and selection must be performed in each specific environment. Therefore, the formation of a synthetic population is recommended to obtain superior segregants with enhanced drought adaptation. Additionally, the hybrid combinations L65/L76, L71/L76, and L61/L75 exhibited great potential for utilization in non-irrigated agricultural systems, as they displayed superiority across all agronomic traits evaluated. Among these hybrids, special attention should be given to the L61/L75 combination, which demonstrated significant improvements in root traits (SRA, CRA, and DCR) under water stress conditions (WS).

These findings provide valuable insights for breeding programs aiming to develop drought-tolerant popcorn varieties. The identification of genotypes with desirable traits under specific water conditions allows for more targeted and efficient selection strategies to enhance crop performance and agricultural productivity in challenging environments.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/stresses3030041/s1>, Table S1: Estimates of the effects of specific combining ability (SCA) and mean values of agronomic and root architecture traits of 15 popcorn hybrids under water stress (WS) and well-watered (WW) conditions.

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