

Phenotypic assessment of genetic gain from selection for improved drought tolerance in semi-tropical maize populations

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Abstract

Most maize production across the globe is rain-fed, and production is set to be negatively impacted as duration and occurrence of droughts increases due to climate change. Development of water-deficit tolerant maize germplasm has been a major focus for most breeding programmes. Here, we sought to assess the genetic gain for grain yield in two maize populations developed for drought tolerance at CIMMYT by evaluating their cycle progeny through hybrid performance. Inbreds derived from different cycles of the Drought Tolerant Population (DTP) and La Posta Sequia (LPS) were mated to a tester (CML550), and resulting hybrids were evaluated under managed water-deficit stress and well-watered conditions. The difference in yield between water-deficit and well-watered treatments was 27% and 36% for the DTP and LPS, respectively. Genetic gain for grain yield across cycles for the two populations was confirmed in the study. Genetic gain was observed for both treatments indicating that selection for water-deficit stress tolerance simultaneously improves grain yield in well-watered conditions. The DTP population had a genetic gain of $0.07 \text{ t ha}^{-1} \text{ cycle}^{-1}$, while the LPS had $0.16 \text{ t ha}^{-1} \text{ cycle}^{-1}$ under water-deficit conditions. Significant genetic gain was also observed in the well-watered treatments for both populations. Anthesis to silking interval was significantly reduced under water-deficit stress conditions in both populations. Plant and ear height were reduced in the LPS population in both treatments, while no reductions were observed for the trait in the DTP population. Potential water-deficit stress tolerance donor lines with yields comparable to commercial check varieties were identified.

KEYWORDS

cycles, DTP, LPS, recurrent, topcross, water deficit

1 | INTRODUCTION

Maize grain production in 2019 was 1.1 billion metric tons (FAOSTAT, 2021), which was higher than any other cultivated grain crop globally. Animal feed takes up 61% of all global production with biofuel production and human consumption accounting for 17% and 13% of

maize use, respectively (Grote et al., 2021). Maize is a staple food in the Americas and Africa with reduced harvests being synonymous with food insecurity (Cairns, Hellin, et al., 2013; Hadebe et al., 2017). Water-deficit stress in the form of drought is a major limiting factor in maize production across the world. Droughts can occur at any point during the growing season; however, the occurrence of drought

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mid-season generally coincides with the reproductive stages of maize crops leading to yield losses of up to 40% (Daryanto et al., 2016). Semi-arid regions where maize is the main source of calorific intake such as Southern Africa are predicted to receive less precipitation in the future due to the impacts of climate change (Shukla et al., 2019).

Having established that drought is a major contributor towards reduced maize grain yield across the world, particularly in semi-arid regions, breeding for drought-tolerant germplasm became a priority in several breeding programmes across the world. Drought is a common feature in semi-tropical regions of the world as a result of irregular rainfall patterns and soils with low water holding capacity (Fischer et al., 1982; Prasanna et al., 2021). The definition of drought tolerance is as difficult as defining drought itself. One definition for drought tolerance generally used in several studies explains it as the ability to produce approximately 30% of potential yield when exposed to water-deficit stress for six weeks before and during grain filling (Lunduka et al., 2019; Magorokosho et al., 2008). Several approaches have been taken towards the goal of breeding drought-tolerant maize. Recurrent selection methods were among the first used in drought-tolerance breeding programmes (Fischer et al., 1982). The general principle behind recurrent selection is the utilization of multiple parents to accumulate favourable alleles while maintaining genetic diversity. The effectiveness of recurrent selection in population improvement has been recorded for different traits and species (Bolaños & Edmeades, 1993; Monneveux et al., 2006; Posadas et al., 2014; Singh et al., 2016).

The International Maize and Wheat Improvement Center (CIMMYT) established a drought-tolerance breeding programme in the 1970s through utilization of elite lowland topical maize germplasm (Cairns, Hellin, et al., 2013). Through breeding for increased grain yield, marked improvements in yield were obtained in the lowland adapted populations with gains of over 100 kg ha⁻¹ year⁻¹ being realized (Edmeades et al., 1999). Drought tolerant improved populations have been used as sources for inbred lines used in the development of hybrids in Africa, central America and Asia by CIMMYT (Prasanna et al., 2021). Weak correlations between inbred lines and testcross performance have brought about the hypothesis that evaluations should be conducted on testcrosses under drought stress in order to identify drought stress-tolerant and climate-resilient hybrids at CIMMYT (Trachsel, Leyva et al., 2016).

The Drought Tolerant Population (DTP) and La Posta Sequia (LPS) maize populations were developed and improved for drought tolerance through successive cycles of recurrent selection by CIMMYT. Selection of grain yield and correlated traits was conducted under managed drought stress (Edmeades & Deutsch, 1994). Known sources of drought tolerance were combined in the development of the DTP population. Full-sib recurrent selection was used to develop the LPS population, while both full and half-sib recurrent selection schemes were utilized in developing the DTP population (Edmeades et al., 1999). Detailed descriptions of the development of the DTP and LPS populations have been provided by several authors (Edmeades et al., 1999; Monneveux et al., 2005; Pandey et al., 1986). Using both the doubled-haploid and conventional methods, inbreds were created

from cycles of the DTP and LPS populations. Some of the DTP and LPS-derived inbreds have been studied and proposed as potential donor lines for drought and heat tolerance (Cairns, Hellin, et al., 2013).

The objectives of this study were to (1) evaluate genetic gains across breeding cycles for grain yield in two maize populations developed for drought tolerance through hybrid performance under two water treatments and (2) assess secondary trait changes occurring across population cycles brought about by recurrent selection for drought tolerance.

2 | MATERIAL AND METHODS

2.1 | Germplasm

Inbred lines derived from two maize populations were used in the experiments. The two populations are La Posta Sequia (LPS) and Drought Tolerant Population (DTP). These populations were developed for drought tolerance using half and full-sib recurrent selection. The development of the LPS and DTP populations has been described (Bolaños & Edmeades, 1993; Edmeades et al., 1999).

Within the DTP population cycles, the number of inbred lines was 51, 48, 38, 53 and 27 for cycles 0, 3, 5, 7 and 9, respectively. In the LPS population cycles, the number of inbred lines was 19, 36, 37 and 30 for cycles 0, 3, 5 and 7, respectively. All inbred lines in cycles 0, 3, 5 and 7, of the DTP and cycles 0, 3 and 5 of the LPS populations were developed using the doubled-haploid technique. Inbred lines from cycle 9 of the DTP and 7 of the LPS were developed through several generations of self-pollination. All inbred lines were mated to inbred line CML550 to create topcross hybrids for evaluation. The inbred line is classified in the CIMMYT heterotic group B. CML550 was used as a male parent because it has excellent combining ability, making it a good tester choice for assessing combining ability of lines derived from heterogenous populations such as LPS and DTP.

2.2 | Trial management and design

The trials were conducted at four locations in Mexico. The locations were situated at San Juan de Abajo (PV) 20.8158887, -105.2119142—Nayarit State, the CIMMYT experiment station at Tlaltizapán (TL) 18.6892406, -99.12799—Morelos State, Collantes (OA) 16.1782130, -97.9856642—Oaxaca State, and Juan Jose Rios (SI) 25.76122, -108.81242—Sinaloa state. Site selection was considered in regions that had a period of no to very low precipitation during prolonged periods of the year. Trials were conducted over a three-year period (2018–2020), and planting was done between the months of December and February. Temperature and precipitation data at all sites are included in the supplementary section (Table S1).

The drought treatments were established using protocols by Trachsel, Leyva, et al. (2016). In brief, drip irrigation was terminated

TABLE 1 Summary statistics for grain yield (GY), plant height (PH), ear height (EH), days to 50% anthesis (AN) and anthesis to silking interval (AS) across all locations

		Water-deficit					Well-watered				
		GY t/ha	PH cm	EH cm	AN days	AS days	GY t/ha	PH cm	EH cm	AN days	AS days
DTP	Min	3.89	194.1	87.4	69.2	0.18	5.75	197.7	84.4	67.5	-0.37
	Max	8.02	251.9	138.4	73.6	2.40	10.57	263.4	140.1	73.4	2.80
	Median	6.12	220.5	112.7	71.1	1.29	8.41	230.7	117.6	70.4	1.17
	Mean	6.08	220.6	113.2	71.2	1.32	8.35	231.2	117.4	70.4	1.15
LPS	Min	4.36	209.7	110.0	72.2	-1.45	6.97	228.3	113.2	73.1	-0.30
	Max	8.23	253.5	253.5	79.2	2.88	11.83	277.0	153.6	79.0	2.56
	Median	5.94	232.9	126.0	75.2	1.30	9.33	253.9	131.9	76.6	1.14
	Mean	5.98	232.7	125.1	75.3	1.26	9.31	277.0	132.9	76.5	1.13

12 days before expected 50% anthesis. An additional irrigation was applied 7 days after completion of anthesis to induce moderate drought stress. In the well-watered treatment, irrigation was maintained throughout the growing season. An alpha-lattice design with two replications was utilized in the drought treatment. At PV, SI and OA, plots were 4 m long for both the drought and well-watered treatments, while at TL, plots with the drought treatment were 4 m long and the well-watered treatment plots were 3 m long. Distance between plants within each row was 0.2 m. Inter-row spacing at all sites was 0.75 m. At all sites, two-row plots were used for all treatments with 67000 plants per hectare. In both the drought and well-watered treatments, agronomic practices as soil analyses recommendations for each location were practised. Nitrogen, phosphorous and potassium were applied at ratios of 195:60:30 at TL, 360:150:00 at SI, 280:90:00 at PV and 250:90:00 at OA. Fertilizers were applied at planting with a second fertilizer application of made 35 days after planting. The quantity of fertilizer applied at each location was based on soil analyses and management requirements.

2.3 | Trait measurement

Days to anthesis and silking were recorded when 50% of the plants had shed pollen and 50% of the plants had silks, respectively. The ASI was calculated as days to silking—days to anthesis. Four representative plants per plot were used in measuring plant and ear height 4 weeks after 50% anthesis. Grain was machine-harvested at all sites providing measures of the grain weight and grain moisture of each plot. Grain weight was adjusted to 15 % moisture content.

2.4 | Statistical analyses

Linear mixed models were used for data analysis using the lme4 package (Bates et al., 2015) in R statistical software (Team, 2013). The linear mixed model used for trait analyses for each location was as follows

$$Y_{ijklm} = \mu + G_i + \text{Year}_j + \text{Ran}_k(\text{Year}_j) + \text{Row}_l(\text{Year}_j) + \text{Blk}(\text{Year}_j) + \xi_{ijklm}$$

where Y_{ijklm} is the response value, μ the overall mean, G_i is the genotype effect ($i = 1, 2, \dots, z$). Ran_k is the effect of the k th Range nested in the j th Year, Row_l is the effect of l th row nested in the j th Year, Blk is the block effect nested in j th Year, and ξ_{ijklm} is the error. All variables except for Year were random.

Yield and secondary trait analyses for all locations across years were performed using the given model.

$$Y_{ijklmn} = \mu + G_i + \text{Loc}_j + \text{Ran}_k(\text{Year}_l \text{ Loc}_j) + \text{Row}_m(\text{Year}_l \text{ Loc}_j) + \text{Blk}(\text{Year}_l \text{ Loc}_j) + \xi_{ijklmn}$$

where Y_{ijklmn} is the response value, μ the overall mean, G_i is the genotype effect ($i = 1, 2, \dots, z$), Loc_j is the j th Location (combination of stress, location and season) effect ($j = 1, 2, \dots, z$), Ran_k is the effect of the k th Range nested in the l th Year and j th Location, Row_m is the effect of m th. Row nested in the l th Year at the j th Location, Blk is the block effect nested in l th year at the j th Location, and ξ_{ijklmn} is the error. Location was fixed with all other variables denoted as random. Heritability was calculated using a method described in a previous drought and heat stress study (Cairns, Hellin, et al., 2013). Pearson's correlation coefficients (r) were calculated using R software. Correlations were conducted for each environment and a combination of all environments. Estimated marginal means obtained from the linear mixed model were used to fit a regression model to assess changes in grain yield (genetic gain) across population cycles in both the DTP and LPS populations.

3 | RESULTS

3.1 | Overall grain yield

The average temperature during the growing season at all sites ranged from 21.5°C to 28.4°C. Precipitation during the months when trials were conducted ranged from 7.5 to 178.2 mm. The mean grain yield of topcrosses in the DTP population was 6.08 t ha⁻¹ under water deficit and 8.35 t ha⁻¹ for the well-watered populations across all four sites (Table 1). Grain yield values ranged from 3.89 to 8.02 t ha⁻¹ for the water-deficit treatment and, 5.75 to 10.57 t ha⁻¹ for the well-watered treatment. In the LPS population, the mean grain yield under water-deficit

and well-watered conditions was 5.98 and 9.31 t ha⁻¹, respectively. The grain yield range for the LPS topcrosses was from 4.36 to 8.23 t ha⁻¹ in the water deficit and 6.97 to 11.83 t ha⁻¹ in the well-watered treatment.

The well-watered treatments had 27% higher grain yield compared with the water-deficit treatments in the DTP population, while in the LPS population, mean grain yield was 36% higher in the well-watered treatments. A broader range of values for grain yield was observed in the water-deficit stress compared with the well-watered treatment for both populations. The mean grain yield difference between the two populations under water-deficit treatment was 0.1 t ha⁻¹, whereas in the well-watered treatment, a mean yield difference of 0.96 t ha⁻¹ was observed between the two populations.

3.2 | Heritability

Combined analyses for all trials indicated moderate-to-high broad-sense heritability values for all traits (Table 2). The water-deficit treatment had higher heritability for grain yield (0.59) compared with the well-watered treatment (0.49). Heritability values for ear height (0.81 vs 0.80), days to 50% anthesis (0.66 vs. 0.64) and, anthesis to silking interval (0.26 vs. 0.26) were the same in the two treatments. Plant height heritability was lower in the water-deficit treatment (0.73) when compared to the well-watered treatment (0.83).

3.3 | Grain yield in the DTP and LPS cycles

The means of grain yield for cycles of the DTP population are shown in Table 3. Grain yield was higher in the well-watered compared with the water-deficit treatments for all cycles. The average values of the DH topcrosses of cycle 0 and cycle 9 were 5.84 t ha⁻¹ and 6.51 t ha⁻¹ respectively. Except for the interval of cycles 0 and 3 in the water-deficit treatment, mean grain yield increased in successive cycles. Cycles 0 and

9 in the well-watered treatment had mean grain yield of 8.80 t ha⁻¹ and 9.35 t ha⁻¹. The top 5 yielding hybrids from each cycle had average grain yield of 6.73 t ha⁻¹ and 7.32 t ha⁻¹ for cycles 0 and 9, respectively, in the water-deficit treatment. As was the trend in the full topcross hybrid compliment, cycle 3 had lower average grain yield than cycle 0, while all later cycles had higher mean grain yield than their preceding cycles.

A consistent increase in grain yield for the water-deficit treatment in the complete set LPS-derived hybrids from cycle 0 to 7 is shown in Table 4. Overall, grain yield for cycles 0 and 7 were 5.20 t ha⁻¹ and 6.41 t ha⁻¹, respectively, in the water-deficit stress trials. Cycle 5 had a higher mean grain yield compared with cycle 7 in the top 5 set of hybrids. Yield differences between the first and last cycle were 1.21 t ha⁻¹ for water-deficit stress and 1.24 t ha⁻¹ for the well-watered treatment. In the top 5 set of hybrids, there was a larger difference between the initial and last cycle in the water-deficit treatment (1.42 t ha⁻¹) than the well-watered treatment (1.00 t ha⁻¹).

Comparisons of the DTP and LPS for grain yield and other traits of topcrosses of cycles are illustrated in Figure 1. There was an alternating shift in ranking between cycles 0 to 5 of the DTP and LPS population in terms of grain yield in the water-deficit treatment. Grain yield of cycle 0 in the DTP population outyielded that of the LPS population. However, yield superiority changed after every cycle between the population. This trend was not observed in the well-watered treatment as cycles of the LPS population had greater grain yield compared with similar cycles of the DTP population.

3.4 | Genetic gain in the maize population cycles

The water-deficit treatment had genetic gain of 1.3% (Table 5). A total of 0.07 t ha⁻¹ cycle⁻¹ was observed in the water-deficit stress treatment. No increase in grain yield between cycles 0 and 3 was observed indicating that no genetic gain was observed between that interval of cycles in the DTP topcross populations. The well-watered treatment yielded

TABLE 2 Variance components and broad-sense heritability (H²) across sites for grain yield (GY), plant height (PH), ear height (EH), anthesis (AN) and anthesis silking interval (AS) in the well-watered and water-deficit treatments

Trait	Genotype	Genoptype:Location	Genotype:Year	Genotype:Location:Year	H ²
Water-deficit stress					
GY	0.26(0.04)	0.04(0.04)	0.08(0.03)	0.33(0.05)	0.59
PH	68.5(6.69)	6.20(4.11)	8.81(3.74)	14.9(5.97)	0.73
EH	49.1(4.95)	0.80(2.09)	6.33(2.01)	12.4(2.98)	0.81
AN	0.81(0.10)	0.28(0.07)	0.21(0.06)	0.40(0.09)	0.66
AS	0.06(0.02)	0.19(0.04)	0.07(0.03)	0.09(0.04)	0.26
Well-watered					
GY	0.35(0.07)	0.14(0.08)	0.09(0.07)	0.43(0.11)	0.49
PH	134(13.2)	8.46(5.95)	4.66(4.81)	61.2(10.2)	0.83
EH	71.7(7.38)	1.05(3.17)	9.19(3.11)	14.3(5.03)	0.80
AN	1.08(0.15)	0.47(0.12)	0.22(0.09)	0.79(0.18)	0.64
AS	0.07(0.02)	0.18(0.04)	0.01(0.03)	0.16(0.07)	0.26

[†]Brackets indicate standard errors of variance components estimates.

TABLE 3 Mean and range of grain yield (t/ha) of DTP cycles for the water-deficit and well-watered treatments at individual and combined locations

Site	OA			PV			SI			TL			Overall	
	n	Mean	Range	n	Mean	Range	n	Mean	Range	n	Mean	Range	Mean	Top 5 mean
Water-deficit														
C0	51	5.49	3.46–7.71	51	6.60	5.00–8.28	48	5.89	4.13–7.70	49	4.95	2.72–6.48	5.84	6.73
C3	48	5.61	3.40–7.42	48	6.54	4.19–8.67	48	5.79	2.21–8.46	48	4.94	2.80–6.71	5.82	6.61
C5	38	5.85	4.30–9.15	38	6.91	5.21–8.79	34	6.32	4.65–8.10	36	5.20	3.52–6.46	6.16	6.85
C7	53	6.01	4.04–7.18	53	6.79	5.14–8.50	51	6.62	4.55–8.21	51	5.32	3.62–7.24	6.23	7.06
C9	27	5.85	4.56–7.22	27	7.14	3.83–8.38	26	7.01	5.07–8.63	27	5.87	4.00–7.24	6.51	7.32
Well-watered														
C0	51	8.49	3.74–12.90	51	7.10	4.48–9.85	48	7.77	5.33–10.44	49	8.78	6.17–11.53	7.97	8.80
C3	48	8.65	6.32–12.42	48	7.19	5.25–9.88	48	7.54	4.15–9.59	48	9.12	5.79–12.84	8.05	8.74
C5	38	8.63	5.59–11.81	38	7.77	5.63–12.98	34	8.56	5.85–11.06	34	9.39	7.53–12.88	8.47	8.90
C7	53	9.36	6.12–12.37	53	7.57	5.63–10.02	51	8.82	6.48–11.07	50	9.52	7.64–11.33	8.69	9.29
C9	27	9.13	7.67–12.13	27	7.57	4.01–9.19	26	8.96	7.22–10.55	26	9.73	7.96–13.08	8.70	9.35

[†]n = number of genotypes from each cycle tested.

TABLE 4 Mean and range of grain yield (t/ha) of LPS cycles for the water-deficit and well-watered treatments at individual and combined locations

Site	OA			PV			TL			Overall	
	n	Mean	Range	n	Mean	Range	n	Mean	Range	Mean	Top 5 mean
Water-deficit											
C0	18	5.81	4.45–8.51	18	5.95	5.01–7.70	18	5.00	3.80–5.89	3.84	6.10
C3	36	6.51	4.05–9.37	36	6.64	4.34–8.64	36	6.00	4.05–7.61	4.20	6.59
C5	27	6.28	2.98–9.29	25	6.28	4.50–8.77	26	6.43	5.10–8.69	4.24	7.02
C7	29	6.99	4.54–10.91	28	6.82	5.63–8.04	28	6.71	4.67–8.42	4.72	7.52
Well-watered											
C0	18	11.08	6.84–14.70	18	8.37	5.17–10.36	17	9.42	7.30–11.46	5.49	9.07
C3	36	11.68	8.71–15.02	36	8.93	6.76–11.37	36	9.73	7.83–11.85	6.32	9.41
C5	27	11.41	7.11–15.62	25	8.79	6.88–12.89	26	9.79	7.74–11.97	6.55	10.33
C7	29	11.80	8.85–16.42	28	9.57	7.65–11.87	29	10.11	8.24–12.63	6.99	10.07

[†]n = number of genotypes from each cycle tested.

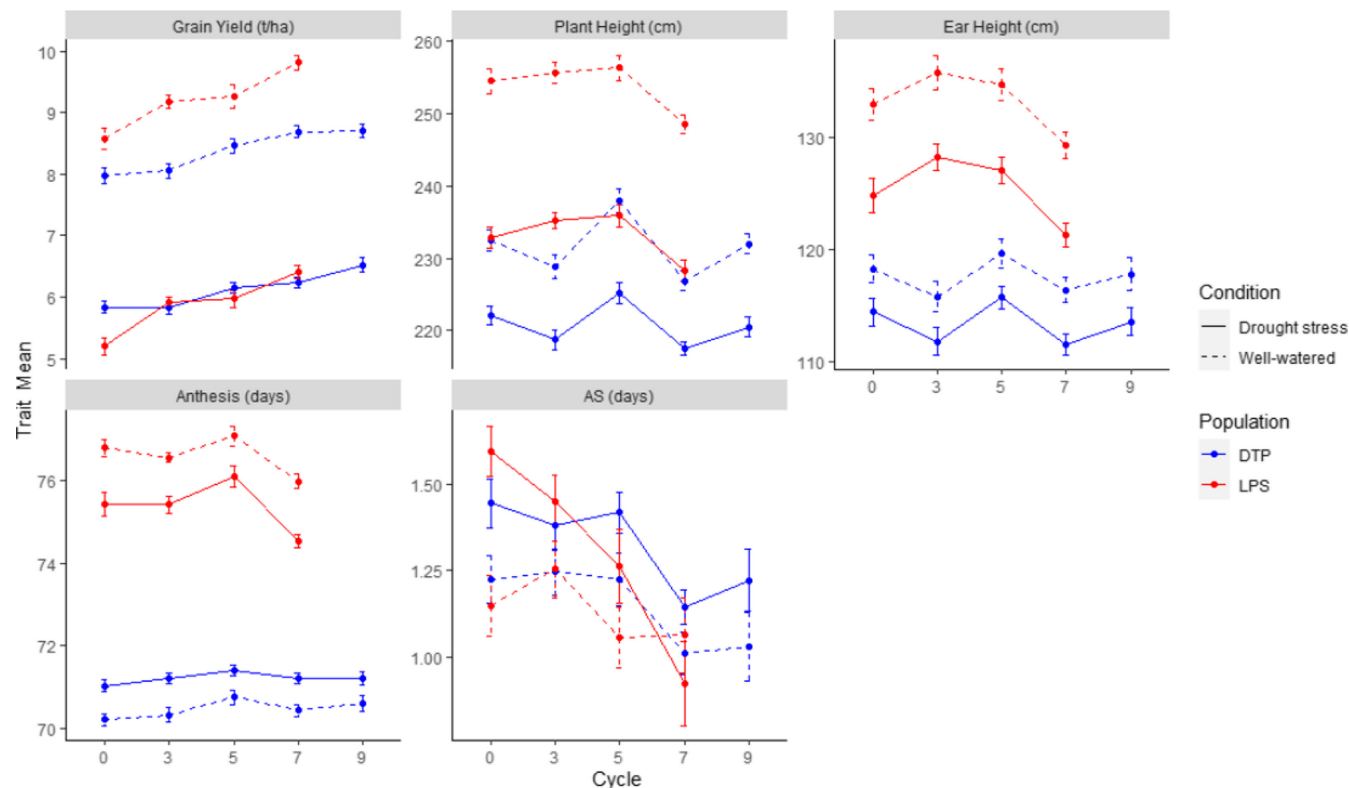


FIGURE 1 Comparisons of trait means for the DTP and LPS populations across cycles

Water-deficit					
Site	GY (t/ha)	PH (cm)	EH (cm)	AN (days)	AS (days)
OA	0.07 (1.2)***	−0.3 (0.1)	−0.3 (0.2)	0.05 (0.1)	−0.05 (4.2)**
PV	0.05 (0.9)***	−0.5 (0.1)*	−0.2 (0.2)	0.00 (0.0)	0.00 (0.0)
SI	0.13 (2.2)***	0.2 (0.1)	0.2 (0.2)	0.00 (0.0)	−0.03 (1.1)
TL	0.12 (2.5)***	−0.2 (0.1)	0.0 (0.0)	0.04 (0.1)	−0.04 (2.7)*
All sites	0.07 (1.3)***	−0.3 (0.1)	−0.1 (0.1)	0.02 (0.0)	−0.03 (2.2)**
Well-watered					
Site	GY (t/ha)	PH (cm)	EH (cm)	AN (days)	AS (days)
OA	0.08 (0.9)***	−0.4 (0.2)	0.1 (0.1)	−0.03 (0.1)	−0.02 (2.3)
PV	0.07 (1.1)***	−0.4 (0.1)	−0.1 (0.1)	0.00 (0.1)	−0.03 (6.0)**
SI	0.154 (2.0)***	0.6 (0.2) [†]	0.2 (0.2)	0.07 (0.1)	0.00 (0.0)
TL	0.10 (1.2)***	−0.3 (0.1)	−0.2 (0.2)	0.05 (0.1)	−0.07 (5.4)***
All sites	0.10 (1.2)***	−0.2 (0.1)	−0.1 (0.1)	0.04 (0.1) [†]	−0.03 (2.2)**

Significant at $p < .001$ ***, $.01$ **, $.05$ *, $^{\dagger}0.1$.

TABLE 5 Genetic gains per cycles in the DTP population in the water-deficit and well-watered trials for grain yield (GY), plant height (PH), ear height (EH), days to 50% anthesis (AN) and anthesis to silking interval (AS) with percentage changes given in brackets

genetic gains of 1.2% which was just 0.1% lower than the water-deficit stress treatment (Table 5). Genetic gain for grain yield under the well-watered conditions was $0.10 \text{ t ha}^{-1} \text{ cycle}^{-1}$ from cycle 0 to 9.

The genetic gains realized in the LPS population are indicated in Table 6. In the water-deficit treatment, the genetic gain observed was 0.16 t ha^{-1} or 3% across the cycles. Figure 1 shows a rapid gain in grain yield from cycle 0 to 3 in the LPS population in both treatments. The interval of cycle 5–7 also had a drastic increase in genetic gain in both

the well-watered and water-deficit treatment. Genetic gain of 2% and $0.17 \text{ t ha}^{-1} \text{ cycle}^{-1}$ was observed in the well-watered treatment.

3.5 | Morphological traits

Under water deficit, mean plant and ear height were lower than that of well-watered treatment for the DTP population (Table 2). A smaller

TABLE 6 Genetic gains per cycles in the LPS population in the water-deficit and well-watered trials grain yield (GY), plant height (PH), ear height (EH), days to 50% anthesis (AN) and anthesis to silking interval (AS) with percentage changes given in brackets

Water-deficit					
Site	GY (t/ha)	PH (cm)	EH (cm)	AN (days)	AS (days)
OA	0.14 (2.4)***	-0.7 (0.3)†	-0.7 (0.5)†	0.05 (0.1)	-0.12 (10.4)**
PV	0.11 (1.5)***	-1.0 (0.3)†	-0.9 (0.6)*	-0.12 (0.1)*	0.02 (6.0)
SI	0.23 (3.5)***	-0.1 (0.0)	-0.5 (0.3)	-0.18 (0.2)**	-0.14 (3.7)**
TL	0.11 (2.3)***	-1.0 (0.3)**	-0.8 (0.5)**	-0.17 (0.2)**	-0.19 (5.9)***
All sites	0.16 (3.0)***	-0.8 (0.3)*	-0.7 (0.5)**	-0.11 (0.2)*	-0.10 (6.0)***
Well-watered					
OA	0.08 (0.7)***	-1.2 (0.5)*	-0.6 (0.5)	0.03 (0.0)	-0.05 (4.8)*
PV	0.18 (2.1)***	-0.8 (0.3)†	-0.6 (0.4)	0.00 (0.0)	0.00 (0.0)
SI	0.11 (1.1)***	-1.1 (0.4)*	-0.3 (0.2)	-0.02 (0.2)*	0.03 (1.4)
TL	0.20 (3.5)***	-0.8 (0.3)	-1.0 (0.7)*	-0.18 (0.2)**	-0.11 (8.7)**
All sites	0.17 (2.0)***	-0.9(0.4)**	-0.7 (0.5)*	-0.09 (0.1)*	-0.02 (1.8)

Significant at $p < .001$ ***, .01 **, .05*, † 0.1.

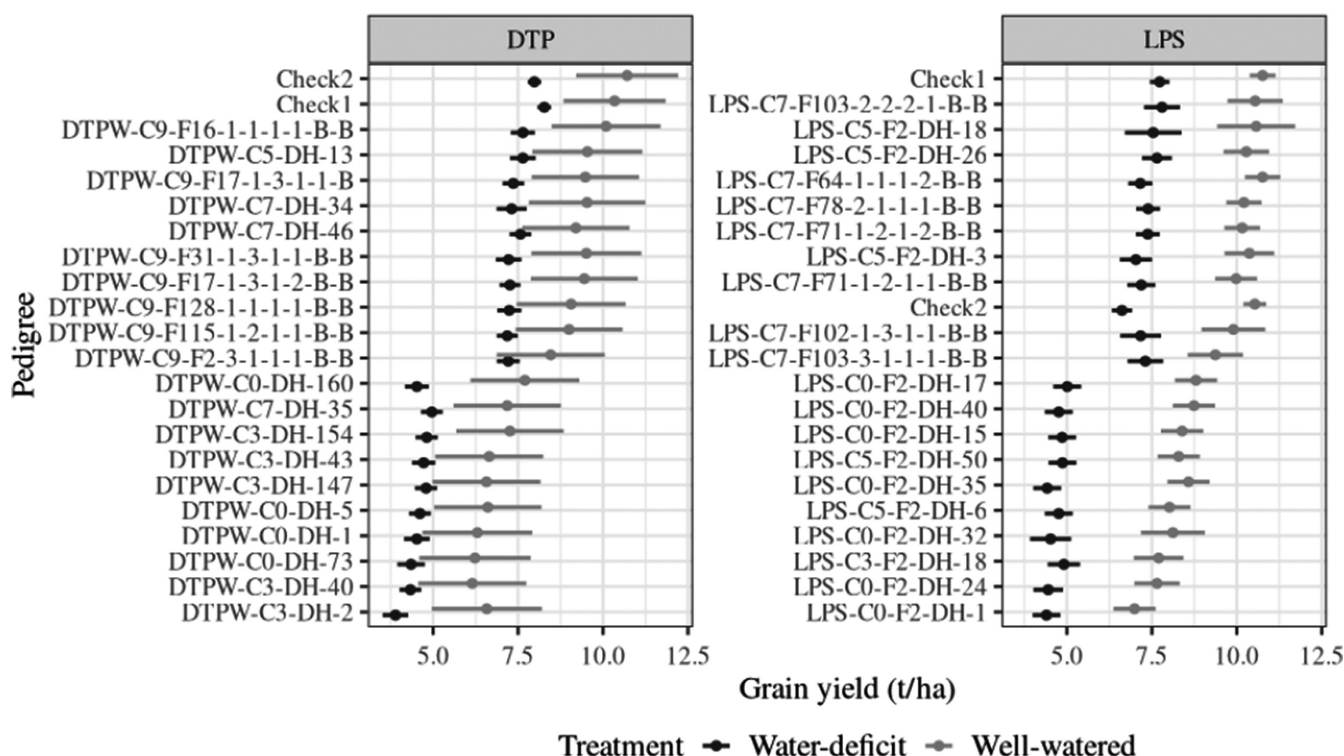


FIGURE 2 Top and bottom 10 ranked genotypes of the DTP and LPS by yield (\pm SE) based on grain yield in water-deficit stress conditions

mean of 1.15 days for anthesis to silking interval was observed in the well-watered compared with the water-deficit treatment with 1.32 days. Days to 50% anthesis (71.2) were greater in the water-deficit treatment compared with the well-watered (70.4) conditions. There were no significant changes in plant height, ear height and days to 50% anthesis in topcross hybrids across the DTP cycles. A reduction in anthesis to silking interval took place in all treatments for the DTP population (Table 5). The greatest reduction in anthesis to silking interval for DTP took place between cycles 5 and 7 for both treatments (Figure 1).

The LPS population also had higher plant and ear height means in the well-watered treatment compared with the water-deficit treatment (Table 1). Anthesis to silking interval percentage reduction per cycle of 6% was observed in the water-deficit treatment of the LPS population (Table 6). There were, however, no changes observed for anthesis to silking interval across cycles in the LPS population in well-watered conditions. All other measured traits in the LPS population recorded significant changes from cycle 0 to 7 (Table 6). Ear height decreased in all treatments with a similar percentage margin (0.5%) per cycle. Plant height was reduced across cycles at a percentage reduction rate

of 0.3 and 0.4% in water-deficit stress and well-watered conditions, respectively.

3.6 | Ranking topcrosses

Figure 2 shows that seven of the top ten yielding hybrids under water-deficit stress conditions were derived from cycle 9. Cycles 7 and 5 made up the remaining three top-yielding DTP hybrids under water-deficit stress conditions. A similar pattern was observed in the LPS population where 7 of the 10 best yielding hybrids had lines from the last cycle of selection (cycle 7). The earlier cycles (0–3) contributed 90 % of the bottom 10 hybrids in the DTP and 80 % of the LPS population. Only one hybrid from both populations, LPS-C7-F103-2-2-2-1, had higher grain yield than Check 1.

3.7 | Correlation of grain yield and other traits

Correlations between grain yield and secondary traits for all cycles are shown in Table 7. High positive correlations with plant height were observed from cycles 0 to 7 in the DTP populations under both treatments. The correlation between grain yield and all other traits except for anthesis to silking interval was highest in cycle 9 of the water-deficit stress treatment of the DTP population. Anthesis to silking interval was negatively correlated to grain yield in the earlier cycles (0, 3 and 5) of the DTP population while in the later cycles (7 and 9), no correlations with grain yield were observed. In the well-watered treatment, both ear and plant height were positively correlated to grain yield. In contrast to the water-deficit treatment, only cycle 9 of the well-watered treatment was significantly correlated to grain yield for anthesis to silking interval.

Moderate negative correlations with grain yield were observed in cycles 0 and 3 of the LPS population for anthesis to silking interval and days to 50% anthesis in water-deficit stress treatment, while cycles 5 and 7 had no significant correlation. There was no correlation with ear height in the water-deficit treatment for all cycles of the LPS population. Plant height was negatively correlated to grain yield in cycle 5 of the LPS population, while the rest of the cycles were not correlated to grain yield for the water-deficit treatment. In the well-watered treatment, ear height in cycles 0, 3 and 7 of the LPS population were negatively correlated to grain yield. Apart from ear height, no other trait had a cycle correlated with grain yield in the well-watered treatments of the LPS population.

4 | DISCUSSION

4.1 | Grain yield

The effectiveness of the treatments is shown by the higher grain yield of the well-watered compared with the water-deficit trials. The differences in grain yield between the two treatments in both populations (LPS: 36%; DTP: 27%) can be attributed to the

TABLE 7 Correlations between grain yield and secondary traits for the DTP and LPS populations

	DTP	C0	C3	C5	C7	C9	C0	C3	C5	C7	C9	
	Water-deficit						Well-watered					
DTP	AS	-0.19**	-0.30***	-0.20*	-0.09	0.09	0.06	-0.06	0.07	0.09	0.20*	
	AN	0.05	-0.02	0.08	0.15*	0.33***	-0.15*	-0.26***	-0.02	-0.10	0.00	
	EH	0.00	0.20**	0.01	0.13	0.37***	0.16*	0.28***	0.33***	0.18**	0.36***	
	PH	0.21**	0.29***	0.24**	0.37**	0.40***	0.24***	0.22*	0.30***	0.33***	0.30**	
LPS	AS	-0.36**	-0.41***	-0.14	-0.06	-0.06	0.03	-0.07	0.12	0.07		
	AN	-0.32***	-0.23**	-0.03	-0.07	-0.07	-0.07	-0.17	-0.11	-0.05		
	EH	-0.17	-0.07	0.16	-0.15	-0.15	-0.27*	-0.40***	-0.16	-0.19*		
	PH	0.06	0.05	0.32***	0.14	0.14	0.16	0.11	0.17	0.10		

Significant at $p < .001$ ***, .01 **, .05*.

severity of the stress imposed by the water-deficit treatment. Mean grain yield of topcross hybrids generally increased from cycle 0 to 9 in both water-deficit and well-watered treatments. The largest difference in grain yield between the populations was observed in the well-watered treatment with a previous study confirming greater discrimination for grain yield between maize genotypes under well-watered compared with water-deficit conditions (Messina et al., 2020).

4.2 | Heritability

The moderately high broad-sense heritability value for grain yield under water-deficit conditions could possibly indicate good trial management as low heritability values are generally the norm under such conditions. Moderately higher heritability value (0.64) was observed in a combined site analyses for grain yield under water-deficit conditions (Cairns, Hellin, et al., 2013). The lower heritability value of grain yield under well-watered conditions compared with the water-deficit stress is contrary to several studies that have indicated that heritability values under water-deficit stress conditions will tend to be lower than those of trials conducted in non-stress environments (Bolaños & Edmeades, 1996). Lower heritability for grain yield under water-deficit environments has been attributed to a more rapid decline in genetic variance for yield compared with environmental variance. However, in this study, the higher heritability values for grain yield in the water-deficit stress treatment can be as result of similar environments (lowland) used in the trials which leads to a lower environmental variance. Our results show that trials for grain yield conducted under water deficit can be as effective as those under well-watered conditions, hence it could be worthwhile conducting selections for drought in water-limited conditions.

4.3 | Genetic gain in the maize population cycles

There was substantial evidence that the recurrent selection for grain yield in water-deficit environments was effective for improving grain yield for both populations in both water-deficit and well-watered environments. Treatments were effective with grain yield for the well-watered treatments higher than that of the water-deficit treatments at the four sites. Genetic gain in the DTP population was confirmed in the study.

Across all sites, the percentage genetic gain was within a narrow range of 0.9%–2.5 % for both treatments. Direct evaluation of cycles 0, 3 and 6 of the DTP populations under water-limited conditions realized higher genetic gain of 0.16 t ha^{-1} which amounted to 14.3% gain per cycle (Monneveux et al., 2005). There was no noticeable genetic gain observed between cycle 0 and 3 of the DTP topcross populations. Intriguingly, very low genetic gain was observed in the same cycles in water-deficit conditions in a previous study (Monneveux et al., 2005). This was unraveled as a product of mild

half-sib selection utilized in the progenitor cycles, which was coupled by the relatively unimproved, and poorly adapted germplasm, combined in the early stages of developing the populations. It is interesting to note that low genetic gains on the per se performance of the cycles is manifested in the topcross hybrids in water-deficit conditions.

The study showed relatively similar rates of genetic gains for the topcross hybrids of DTP under both treatments. Various studies differ on whether selection under drought conditions confer a yield penalty under well-watered conditions. Our study shows no yield penalty on the DTP population when grown under optimal conditions. In contrast with our observations, several studies have reported no genetic gain in drought-tolerant maize populations when they are grown in well-watered conditions. Selection for the DTP populations was conducted under three water regimes offering well-watered, flowering and grain-filling stress (Edmeades et al., 1999; Monneveux et al., 2005).

Genetic gains of 3% across cycles observed in this study were lower than the average genetic gain of (12.4%) recorded in previous studies on per se performance of the first three LPS cycles under drought stress (Edmeades et al., 1999). However, if we factor in only the first three cycles of LPS topcrosses in this study, previous reports of a 12.4% genetic gain are congruent with the drastic gain in grain yield between cycles 0 and 3 in our study. High selection intensity coupled with full-sib recurrent selection can be attributed to this high genetic gain the first three cycles of the LPS in both treatments. Selection for the LPS population was conducted under well-watered, intermediate and severe water-stress with an index of increased grain yield in the two stress treatments and constant grain yield in the well-watered regime applied in picking superior progeny (Edmeades et al., 1999). The use of these three selection treatments could explain simultaneous genetic gain for grain yield in both water-deficit and well-watered treatments in topcross hybrids evaluated in this study.

In this study, both DTP and LPS populations exhibited significant genetic gains ($p < .001$) for grain yield in both treatments at relatively similar rates. Some studies have observed greater genetic gain for grain yield under well-watered compared with water-stress conditions with this being attributed to reduced genetic variance and reduced heritability of grain yield with increased water-deficit stress (Beyene et al., 2016; Edmeades et al., 1996). However, in this study, broad-sense heritability values were moderately high. In other studies, higher increases of genetic gain under water-deficit stress than well-watered conditions for populations developed for drought tolerance have been observed (Edmeades et al., 1999).

4.4 | Morphological traits

Plant height and ear height were lower in the water-deficit treatments of the DTP population. Reduction in plant and ear height is an obvious symptom of water-deficit stress during the vegetative growth stages of maize plants (Hussain et al., 2019; Yang et al.,

2021). Selection for yield had no significant effect on plant height, ear height and days to 50% anthesis in the DTP population for both the water-deficit stress and well-watered treatments. Our findings on plant height are consistent with a study assessing the per se performance of some cycles of the DTP populations which revealed no significant changes in plant height under both water-deficit and well-watered conditions (Monneveux et al., 2005). Anthesis to silking interval was significantly shortened in both treatments for the DTP topcrosses. This is consistent with previous drought studies including those that evaluated related DTP populations where anthesis to silking interval was significantly reduced by a margin of -11% per cycle in DTP1 and -7.2% per cycle in DTP2 under drought conditions while in well-watered conditions, anthesis to silking interval was reduced in the DTP1 (12.3%) population with no changes in DTP2 (Edmeades et al., 1999; Monneveux et al., 2005). However, we observed lower percentage reduction per cycle (2.2%) in both the water-deficit and well-watered treatment for anthesis to silking interval. Consistency in reduction in anthesis to silking interval under drought conditions highlights the contribution of a reduced anthesis to silking interval in drought avoidance.

As would be expected, selection for drought tolerance led to a reduction in anthesis to silking interval across the cycles of LPS. There was however no changes observed for anthesis to silking interval in the LPS population in well-watered conditions. Anthesis to silking interval has been observed to increase in maize under severe drought, and breeding has focused on reducing it to improve drought tolerance. The selection of early vigorous silking is pursued as it is advantageous for seed formation, particularly under water-deficient conditions that occur during flowering (Bruce et al., 2002; Liu et al., 2021). It is, therefore, expected that the observed increase in grain yield in successive cycles of LPS under drought stress is accompanied by a decrease in the anthesis to silking interval. Although it is unlikely that plant height would have been used as a selection criterion in the improvement of the LPS population, a reduction in the trait has been associated with improved drought tolerance (Byrne et al., 1995; Fischer et al., 1982). No changes in ASI under well-watered conditions for the LPS population come as no surprise as non-stressed plants would synchronize their pollination well.

4.5 | Ranking of lines

The later cycles of selection in both populations provided the best yielding hybrids. Having the majority of DTP cycle 9 inbreds in the top 10 ranking further shows the effectiveness of recurrent selection in population improvement through the accumulation of favourable alleles. In the case of this study, the effectiveness of recurrent selection in providing germplasm that can contribute to the development of successful maize hybrids for drought tolerance has been confirmed. Consistent with the DTP population, the latter two cycles of the LPS population contributed all the inbreds that made up the top ranking LPS-derived topcrosses. Inbreds from these two

populations can be potential donor sources for drought tolerance in lowland tropical/subtropical environments. Due to the relatively large number of plots used in this experiment, a single tester line CML550 assigned to the CIMMYT heterotic group B was used. This raises a challenge in the form of confounding genetic differences with heterotic groups (Cairns, Hellin, et al., 2013). This is, however, not a major concern as CIMMYT lines do not perfectly fit into distinct heterotic groupings and lines from LPS and DTP have been identified as fitting into CIMMYT heterotic group A (Cairns, Hellin, et al., 2013; Wen et al., 2011).

4.6 | Correlation of grain yield and other traits

The use of secondary traits in breeding for drought tolerance has been suggested to circumvent the challenge of slow genetic gain for grain yield in water-deficient selection environments due to low heritability values (Bänziger et al., 2000; Edmeades et al., 1996; Monneveux et al., 2008). Water-deficit stress during flowering has been accompanied by an undesirable increase in anthesis to silking interval in maize whose mechanism is still unclear. Suggestions have been made for breeders to consider using the trait as a selection criterion for maize in trials under water-deficient conditions because selecting for grain yield directly in water-stressed environments can be inefficient because genetic variance declines faster than environmental variance (Ribaut et al., 1996). Under water deficit stress, there is moderate negative correlation between grain yield and anthesis to silking interval for both populations in cycle 0 and 3. This is to be expected as the earlier cycles would not have undergone several cycles of selection to reduce the anthesis to silking interval. No correlation in the later cycles may imply that germplasm has been selected for reduced anthesis to silking interval with several loci fixed.

4.7 | Implications for breeding drought-tolerant maize

This study differs from most previous population genetic gain studies for drought tolerance in maize as evaluations were conducted on hybrids. DTP- and LPS-derived semi-tropical hybrids have shown significant increase in grain yield across cycles indicating the effectiveness of recurrent selection in shifting the frequency of favourable alleles for grain yield in topcrosses that are a product of germplasm selected for drought tolerance. The use of multiple water regimes (well-watered, intermediate and severe stress) with greater emphasis on performance under stress during selection has been shown to be effective in simultaneously improving grain yield in in topcrosses in water-deficit and well-watered conditions. Breeding for water-deficit stress does not result in a yield penalty under well-watered conditions as signified by simultaneous genetic gain for grain yield in the two treatments. The study has determined that genetic gains under recurrent selection for water-deficit stress tolerance in maize

population cycles transferrable and manifested in hybrid performance. Mean grain yield of hybrids increased from earlier to later cycles accompanied by a reduction in anthesis to silking interval. The importance of a reduced anthesis to silking interval in improving grain yield under water deficit has been solidified by this study.

5 | CONCLUSION

The use of recurrent selection in improving hybrid performance of drought-tolerant maize inbred lines has been confirmed. Genetic improvements in grain yield were determined under both well-watered and drought conditions. Potential donor lines for drought tolerance from the two study populations were also identified.

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DATA AVAILABILITY STATEMENT

Data available on request from the authors

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