Grain yield gains and associated traits in tropical × temperate maize germplasm under high and low plant density

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Abstract Development of ideal breeding and crop management strategies that can improve maize grain yield under tropical environments is crucial. In the temperate regions, such yield improvements were achieved through use of genotypes that are adapted to high plant population density stress. However, tropical germplasm has poor tolerance to high plant population density stress, and thus it should be improved by introgressing temperate maize germplasm. The aim of this study was to estimate the genetic gains and identify traits associated with such gains in stable and high yielding temperate × tropical hybrids under low and high plant population densities. A total of 200 hybrids derived from a line × tester mating design of tropical × temperate germplasm were developed. These hybrids were evaluated for grain yield and allied traits under varied plant population densities. High yielding and stable hybrids, such as 15XH214, 15XH215 and 15XH121, were resistant to lodging and had higher number of leaves above the cob. The high genetic gains of 26% and desirable stress tolerance indices of these hybrids made them better performers over check hybrids under high plant population density. At high plant population density yield was correlated to stem lodging and number of leaves above the cob. Future gains in grain yield of these hybrids derived from temperate × tropical maize germplasm can be achieved by exploiting indirect selection for resistance to stem lodging and increased number of leaves above the cob under high plant density conditions.

Keywords Adaptability · Genetic gains · Maize population density · Indirect selection · Root and stem lodging

Introduction

Increasing maize yield under stress and non-stress conditions is important in sub-Saharan Africa (SSA) (Masuka et al. 2017). Tolerance to higher planting densities has contributed to yield increase in temperate germplasm (Duvick 2005). High population density is
an important factor limiting maize production in SSA, because as the number of plants in a planting pattern increases, distance between plants decreases and competition for water and nutrients among individuals increases (Lee and Tollenaar 2007). Maize yield improvement has been strongly associated with improvements in stress tolerance, particularly to increased interplant competition (Duvick 2005). As a result, modern hybrids are able to produce kernels at high plant population densities. A stress tolerance index (STI) is more useful in order to select favourable maize hybrids under stress and non-stress conditions. Rosielle and Hamblin (1981) suggested stress tolerance index and defined it as the difference between the production obtained in conditions without stress (Yp) and stress (Ys).

Breeding for direct increase in maize grain yield is complicated due to the fact that maize grain yield is the end-product of interactions among many contributing traits (Raghu et al. 2011). An alteration in a particular trait results in changes in another trait as explained by Ahmad and Saleem (2003). In order to improve gains from selection, it is desirable to have positive significant correlations between yield and agronomic characteristics that contribute towards higher yield (Gasura et al. 2014). Yusuf (2010) observed several positively correlated secondary traits, such as number of leaves per plant with plant height, days to silking with tasselling, and plant height with ear height. These pairs of correlated traits could be simultaneously selected for. Knowledge of the association of yield components can improve selection efficiency (Raghu et al. 2011). Path coefficient analysis is a statistical method capable of partitioning correlations into direct and indirect effects, as well as distinguishing between correlation and causation (Singh and Chaudhary 2004). Path coefficient estimates are useful in understanding the contribution and roles played by different plant traits in establishing growth pattern and behaviour in a particular environment (Gasura et al. 2014).

A successful plant breeding program is directly related to the superiority of the new cultivars. Studies have shown that the average annual maize yield gain in east and southern Africa is around 2% (Masuka et al. 2017). Studies done by Masuka et al (2017) reported that genetic gain in east and southern Africa under optimal conditions, managed drought, random drought, low nitrogen, and maize streak virus disease conditions were estimated to have increased by 109.4, 32.5, 22.7, 20.9 and 141.3 kg ha\(^{-1}\) year\(^{-1}\), respectively. In contrast, Cardwell (1982) showed that the annual maize yield increase in Minnesota, USA was 85 kg ha\(^{-1}\), with 43% of this increase due to the introduction of new cultivars. The aim of this study was to estimate the genetic gains and identify traits associated with such gains in stable and high yielding temperate x tropical maize hybrids.

### Materials and methods

**Germplasm**

In this study, inbred lines were derived from F\(_2\)-crosses between tropical and temperate lines. The USA temperate lines contributed genes for early physiological maturity and good standing ability (stiff stalk source), while the tropical germplasm lines provided water stress tolerance. Self-pollination was applied to advance the materials with concomitant pedigree selection for good agronomic traits and seed parent characteristics. This was achieved in a shuttle programme involving winter nurseries at the Makhathini Agriculture Research Station (27°23’15.04” S and 32°09’31.01” E) and Ukulinga Research Farm (29°39’57.41” S and 30°24’21.34” E) in South Africa from 2011 to 2013. The seed from the F\(_4\) generation of each family was bulked and used for the current study. Seed of the two tester inbred lines DTAB32 and Tester 9 were bulked at both stations. The DTAB32 was derived from a subtropical synthetic population which is adapted to South African conditions. It is a white grain inbred line which has high level of ear prolificacy and medium maturing period. It also has good standing ability and adaptation to abiotic stress environments, including drought. On the other hand, the Tester 9 was derived from a synthetic temperate maize population. The Tester 9 lacks drought tolerance, but it is a very early maturing maize inbred line. It has white grain, produces single ears and has high yield potential under non-stress conditions.
Testcross hybrids were generated at the Makhathini Research Station, in South Africa, during the 2014 winter (May–October) season under irrigation. The experimental materials consisted of 100 test inbred lines which were crossed to two testers (DTAB32 and Tester 9). The 100 inbred lines were crossed with the two testers based on the line x tester mating scheme to generate 200 F1 testcross hybrids. Both tester inbred lines and test inbred lines were used interchangeable as both male and female donors for pollen during pollination. However, at harvest the seed from reciprocal crosses was combined to obtain sufficient seed for planting in trials. For the study, the 93 testcrosses of Tester 9 which had sufficient seed for planting in trials were designated 15XH45 to 15XH135. The other 93 testcrosses of DTAB32 were designated 15XH136 to 15XH228. Two standard commercial maize hybrids, PAN6Q-345CB and BG5285, which are widely grown in South Africa, were included as the commercial controls. In addition five promising experimental hybrids which had been tested extensively for the three previous years (11C1774, 11C1579, 11C2245, 11C1483 and 10HDTX11) in the East and Western South Africa were included as additional control hybrids to obtain the desired 100 entries for the study based on each tester.

Site and test environment description

The hybrids were evaluated across three sites in KwaZulu-Natal province of South Africa, during the 2014/15 summer cropping season. The sites used were Ukulinga Research Farm (UKZN), Dundee Research Station (28° 10’ 13.1219” S and 30° 31’ 45.2365” E) and Cedara Research Station (29° 32’ 38.1624” S and 30° 15’ 59.8536” E). The geographical description for the three sites is presented in Table 1. Four test environments, which were designated as Env-1 to Env-4, were created for the study by varying the population density of the hybrids at Ukulinga Farm, resulting in two testing environments at that station (Tables 1 and 2). The two test environments at Ukulinga Farm were designated Ukulinga 1 and Ukulinga 2 experiments. The experiments at Ukulinga 1 and Ukulinga 2 were planted on the 26th of November 2014 and the 5th of December, 2014, respectively. Only one test environment was created at Dundee and Cedara Agricultural Research Stations. At Dundee Agricultural Research Station, the experiment was planted on the 27th of November, 2014, while at Cedara Agricultural Research Station, the experiment was planted on 09th of December, 2014 depending on the effective rains received.

The climate conditions of Ukulinga Research Farm are characterized by low and erratic rainfall with unimodal pattern of precipitation. The mean annual rainfall at Ukulinga is 678.17 mm. The soil in the testing field of Ukulinga Research Farm is sandy clay-loam, fertile and friable with good water drainage (Cambisol). It is composed of 35% sand, 44% silt, 21% clay, 7.4 pH, 1.2% organic matter, 10.32 ppm available phosphorous (P), and cation exchange capacity (CEC) of 22.34 (meq/100 g). However it is susceptible to cracking and crusting under flooding. Cedara Research Station is characterised by sandy clay soils which are reasonably fertile and well drained. The mean annual rainfall at Cedera is 696.96 mm. Chances of flooding were very low due to a good slope and ground cover. The fields at Ukulinga 1 and 2, and Dundee planting fields were ploughed and disced before planting. The avalon soil type is found at Dundee, and the rainfall is 782.80 mm

| Test environment (Env) | Location | Plant density (plants ha⁻¹) | Latitude | Longitude | Altitude (m.a.s.l) | Total season rainfall (mm) | Temperature range (°C) |
|------------------------|----------|-----------------------------|----------|-----------|-------------------|---------------------------|------------------------|
| Env-1 Ukulinga 1       | 37,037   | 29.67S                      | 30.41E   | 809       | 676.17            | 13.65–24.83               |
| Env-2 Cedara           | 44,444   | 29.76S                      | 30.26E   | 1068      | 696.96            | 9.85–24.41                |
| Env-3 Ukulinga 2       | 74,074   | 29.67S                      | 30.41E   | 809       | 676.17            | 13.65–24.83               |
| Env-4 Dundee           | 74,074   | 28.13S                      | 30.31E   | 1219      | 782.80            | 9.70–24.10                |
per annum. The Cedara field had high organic matter from the stover of preceding maize crop, and minimum tillage was done at Cedara. The ground cover also provided mulch and helped in moisture conservation.

Experimental design and management

The testcrosses were organised into two trials based on the tester, hence two field trials were conducted at each of the three different locations and four test environments at Ukulinga Farm, during the 2014/15 summer season in KwaZulu natal, South Africa. The 100 entries in two replicates for the Tester 9 and DTAB32 testcrosses including the seven control hybrids in each set were laid out as $10 \times 10$ simple lattice design at all sites and test environments. Plot sizes at each environment, had single rows of 5 m long but the spacing varied as follows: 0.9 m inter-row spacing and 0.3 m intra-row spacing at Dundee and Ukulinga 1 and 2, and 0.75 m inter-row and 0.3 m intra-row at Cedara. The use of single row plots was extensively used by several researchers in maize grain yield assessment in sub-Saharan Africa (Annor et al. 2020; Awata et al. 2021; Dao et al. 2020; Koyejo et al. 2021; Musundire et al. 2021; Mutimaamba et al. 2020; Olayiwola et al. 2021; Osuman et al. 2020). The single row plots had 17 planting stations in a row resulting in 34 plants before thinning at all sites and test environments. This is because two seeds were planted per station by hand and later thinned down to one at 21 days after planting to give the desired plant population of 44,444 and 37,037 plants per hectare, at Cedara and Ukulinga 1, respectively. The second planting was not thinned at Ukulinga 2 and Dundee research station resulting in a population density of 74,074 plants per hectare. This was considered to be high plant population density because the average planting density for the area is 37,000 to 45,000 plants per hectare. In the fields where thinning was done, the first and the last stations in the rows were not thinned to minimise the competition advantages along the edges. The experiments at Cedara and Dundee had two border rows planted at either side of the field, while at Ukulinga 1 and Ukulinga 2 there was one border row on both sides.

Crop management including fertilizer, chemical and herbicide application and weed control followed the standard practice for maize trials. The experiments were conducted under rain fed conditions at all sites. The total amount of the monthly rainfall for the growing season and the temperature range data is shown in Table 1. Fertilizer was applied as basal at planting in the form of compound (NPK) 2:3:4 at 250 kg ha$^{-1}$ (56 kg ha$^{-1}$ of N, 83 kg ha$^{-1}$ of P and 111 kg ha$^{-1}$ of K). Nitrogen fertilizer was applied at four weeks after crop emergence in the form of LAN (Lime Ammonium Nitrate, 28% N) at the rate of 250 kg ha$^{-1}$. The herbicides, Gramoxone, Dual, Basagran, and 2,4-D were applied to control weeds. This was augmented by hand weeding to keep the fields relatively clean of weeds throughout the season. Insecticide granules were applied in the maize leaf whorls for stalk borer control. An insecticide, Karate, was applied to control cutworms at planting and seedling emergence.

| Test environment (Env)                     | Planting date       | Row spacing (inter $\times$ intra) (m) | Plant population density (Plants ha$^{-1}$) | Water source                                      |
|-------------------------------------------|---------------------|----------------------------------------|---------------------------------------------|--------------------------------------------------|
| Ukulinga Research Farm 1 (Env-1)          | 26 Nov 2014         | $0.9 \times 0.3$                       | 37,037                                      | Rainfed                                          |
| Cedara Agriculture Research Station (Env-2)| 09 Dec 2014         | $0.75 \times 0.3$                      | 44,444                                      | Rainfed                                          |
| Ukulinga Research Farm 2 (Env-3)          | 05 Dec 2014         | $0.9 \times 0.3$                       | 74,074                                      | Rainfed                                          |
| Dundee Agriculture Research Station (Env-4)| 27 Nov 2014         | $0.9 \times 0.3$                       | 74,074                                      | Rainfed, but was irrigated in the first week after planting |
Data collection

Data for maize traits was collected following the standard protocols which are used at the International Maize and Wheat Improvement Center (CIMMYT) (Magorokosho et al. 2009). Data was recorded for yield and related component traits. Grain moisture content (MOI) was measured as percentage water content of grain measured at harvest using the moisture meter (Eaton, Model 500). Grain yield was estimated using the measured field weight as cob weight per plot adjusted to 12.5% grain moisture content and 80% shelling percentage using the following formula: 

\[ \text{GY} = \text{Field weight (kg)} \times 10,000 \times (100-\text{MOI}) \times \text{shelling} \% / 1000 \times \text{plot area (m}^2) \times (100-12.5\%), \]

where: 
- \( \text{GY} \) = Calculated grain yield per ha, 
- \( \text{MOI} \) = measured grain moisture content at harvest, 
- \( \text{shelling} \% \) = assumed to be 80% for all genotypes. 

The number of ears per plant (EPP) was computed as the proportion of the total number of ears at harvest divided by the total number of plants harvested. Plant height (PH) (cm) was measured as the distance from the base of plant to the insertion point of the top tassel. It was measured when all the plants had flowered, since plants reach their maximum height at flowering. Ear height (EH) (cm) was measured as height from ground level up to the base of the upper most ear. Ear position (EPO) was measured as the ratio of ear height to plant height. Small values indicate low ear position and large values indicate high ear position.

Anthesis-silking interval (ASI) (days) was determined by finding the difference between the number of days after planting when 50% of the plants shed pollen (anthesis date, AD) and the number of days after planting when 50% of the plants show silks (silking date, SD). Root lodging (RL) was measured as a percentage of plants that showed lodging by being inclined 45°. Stem lodging (SL) was measured as a percentage of plants that were broken below the ear. Total plant lodging (TL) was measured as the percentage mean value of the root and stem lodging. Number of tassel branches (NTB) was measured by counting the number of the main tassel branches. Number of leaves above the cob (NLAC) was measured by counting all the main leaves above the cob. DCD = was determined as the number of days when 50% of the ears in a plot dries, calculated from day of planting to drying.

Data analysis

Analysis of variance, hybrid ranking and genetic gains

Analysis of variance was conducted using Genstat Software for all traits. The statistical model used in the analysis was 

\[ Y_{ijkl} = h_i + E_j + h_iE_j + E_j(r_k) + e_{ijkl}, \]

where, 
- \( Y_{ijkl} \) is the performance of the \( i \)th hybrid evaluated in the \( k \)th replication nested within the \( j \)th environment, 
- \( h_i \) is the effect of the \( i \)th hybrid, 
- \( E_j \) is the effect of the \( j \)th environment, 
- \( h_iE_j \) is the interaction between \( i \)th hybrid and the \( j \)th environment, 
- \( E_j(r_k) \) is the effect of the \( k \)th replication nested within the \( j \)th environment, 
- \( e_{ijkl} \) is the random error. 

Hybrids were ranked according to grain yield from the highest yielding to the lowest yielding hybrids across all the sites and within sites. The gains were estimated as a difference in yield between the experimental hybrids and checks, and this was expressed as a percentage. Stress tolerance index was estimated based on formula suggested by Bouslama and Schapaugh (1984) by finding the quotient between the hybrid mean yield under stress condition and the mean yield under the optimal condition according to the formula: 

\[ \text{STI} = \frac{Y_p}{Y_s} \]

where, 
- \( Y_p \) = mean of each hybrid under non-stress conditions, 
- \( Y_s \) = mean of each hybrid under stress condition, 
- \( Y_{pi} \) = mean of all the hybrids under non-stress conditions.

Correlation and path coefficient analysis

The phenotypic correlation coefficients between secondary traits and grain yield were calculated using Genstat software as described by Singh and Chaudhary (2004). The PATHSAS micros was used with the Statistical Analysis Software (SAS) version 9.3 for the phenotypic path analysis. Direct and indirect effects from this study were ranked similar to those of Lenka and Mishra (1973), as follows: 0.00 to 0.09 = negligible, 0.10 to 0.19 = low, 0.20 to 0.29 = moderate and > 0.30 = high path coefficients.
Results

Hybrid ranking

Grain yield for genotypes, environments and genotype x environment interaction were significant ($P < 0.05$) for hybrids evaluated under Tester 9, and DTAB32. Under Tester 9, hybrid number 79 (15XH121) and hybrid number 100 (BG5285) were the best in most environments and hybrid 79 was the most stable across low and high plant population density (Table 3). Under DTAB32, hybrids 179 (15XH214) and 180 (15XH215) outperformed the rest in most environments and were the most stable and high yielding across low and high plant population density (Table 4).

Stress tolerance index

Hybrids such as 15XH121 had a high stress tolerant index of 0.70, comparable to the check hybrid BG5285 (hybrid 100) that had a stress tolerance index of 0.78. It has also previously been reported that when STI is $\geq 1.0$, it indicates that a genotype is tolerant, while it is sensitive when STI is $\leq 1.0$ (Table 5).

Selection and realized breeding gains

Under low plant population density, the grain yield mean values ranged from 11.69 to 12.13 t ha$^{-1}$ among the top-yielding hybrids. The mean of top five selected hybrids (11.89 t ha$^{-1}$) out-yielded the mean of advanced check hybrids (9.78 t ha$^{-1}$). There was a 16.70% more grain yield gained over the population mean. Positive breeding gains were also obtained for most of the desired agronomic traits. There were significant genetic gains in grain yield, number of ears per plant, ear position, grain moisture content, ear and plant height, root lodging, stem lodging and total plant lodging for selected hybrids against mean of the checks (Table 6).

Under high plant population density, the mean grain yield values ranged from 11.44 to 12.04 t ha$^{-1}$ among the top-yielding hybrids (Table 7). All the selected experimental top five hybrids (11.62 t ha$^{-1}$) out-yielded the commercial check hybrids (10.68 t ha$^{-1}$) across sites. The top five selected experimental hybrids (11.62 t ha$^{-1}$) also out-yielded the advanced check hybrids (8.59 t ha$^{-1}$). There was a 22.70% grain yield gained over the population mean (Table 7). There were significant genetic gains of selected hybrids in all the traits except for number of tassel branches and number of leaves above the cob when assessed against the population mean and the mean of all the checks (Table 7). Root lodging, plant height, anthesis silking interval, number of tassel branched and number of leaves above the cob showed significant genetic loss against mean of the commercial checks, but grain yield, ear height, days to anthesis, ear position, ear prolificacy, grain moisture content, stem lodging, total plant lodging and days to 50% cob dryness exhibited significant gains (Table 7).

Correlation and path coefficient analysis between yield and yield related traits in maize hybrids

Under high plant population density, EPP and NTB did not contribute to grain yield across both testers and within each tester. Number of leaves above the cob (NLAC) had the largest direct effect (0.30) on grain yield under low and high plant population density across testers (Tables 8 and 9). Stem lodging had indirect effects on grain yield under high plant population density across testers. Root lodging had a huge direct effect (0.35) on grain yield under high plant population density across testers. The direct and indirect effects for EPP, DCD, TL, EH, EPO, PH, AD, ASI, NP and PopDen were inconsistent across different plant population densities and within testers. Across testers, under low plant population density NTB and MOI had direct effects -0.16 and 0.23 on grain yield, respectively, whereas RL had indirect effects on grain yield via NP. At high plant population density across all testers, DCD and RL had direct effects on grain yield while MOI and DCD had indirect effects on grain yield (Table 9).

Discussion

Hybrids evaluated performed differently thus raising an opportunity to perform selection of genotypes for advancement. The outstanding performance of the experimental hybrids over checks (Tables 3 and 4) is a good indication of significant genetic improvements, because these hybrids out-performed the check hybrid (BG5285) which is a widely grown hybrid in South
### Table 3
Mean values of the top 10 rated hybrids for grain yield in each site and across all the sites evaluated under Tester A

| Rank | Entry | Hybrid       | GY (t ha\(^{-1}\)) | Entry | Hybrid       | GY (t ha\(^{-1}\)) | Entry | Hybrid       | GY (t ha\(^{-1}\)) | Entry | Hybrid       | GY (t ha\(^{-1}\)) | Entry | Hybrid       | GY (t ha\(^{-1}\)) |
|------|-------|--------------|---------------------|-------|--------------|---------------------|-------|--------------|---------------------|-------|--------------|---------------------|-------|--------------|---------------------|-------|--------------|---------------------|
| 1    | 99    | **PAN 6Q-345** | 15.89               | 79    | 15XH121      | 12.91               | 83    | 15XH125      | 11.49               | 68    | 15XH110      | 7.90                | 79    | 15XH121      | 10.67               |
| 2    | 79    | 15XH121      | 14.37               | 100   | **BG5285**   | 12.00               | 79    | 15XH121      | 11.28               | 79    | 15XH121      | 7.05                | 68    | 15XH110      | 10.05               |
| 3    | 23    | 15XH65       | 14.31               | 3     | 15XH45       | 11.97               | 10    | 15XH52       | 11.12               | 100   | **BG5285**   | 6.74                | 100   | **BG5285**   | 9.75                |
| 4    | 68    | 15XH110      | 14.29               | 38    | 15XH80       | 11.81               | 77    | 15XH119      | 10.94               | 13    | 15XH55       | 6.63                | 99    | **PAN 6Q-345** | 9.55                |
| 5    | 93    | 15XH135      | 14.21               | 45    | 15XH87       | 11.68               | 28    | 15XH70       | 10.87               | 88    | 15XH130      | 6.18                | 51    | 15XH93       | 9.38                |
| 6    | 87    | 15XH129      | 14.09               | 39    | 15XH81       | 11.67               | 2     | 15XH44       | 10.76               | 64    | 15XH106      | 6.01                | 22    | 15XH64       | 9.28                |
| 7    | 22    | 15XH64       | 13.87               | 77    | 15XH119      | 11.67               | 97    | **11C1483** | 10.66               | 25    | 15XH67       | 5.62                | 88    | 15XH130      | 9.26                |
| 8    | 29    | 15XH71       | 13.83               | 80    | 15XH122      | 11.66               | 57    | 15XH99       | 10.53               | 40    | 15XH82       | 5.37                | 2     | 15XH44       | 9.23                |
| 9    | 81    | 15XH123      | 13.74               | 52    | 15XH94       | 11.60               | 93    | 15XH135      | 10.50               | 22    | 15XH64       | 5.29                | 93    | 15XH135      | 9.21                |
| 10   | 51    | 15XH93       | 13.65               | 82    | 15XH124      | 11.55               | 48    | 15XH90       | 10.47               | 2     | 15XH44       | 5.27                | 41    | 15XH83       | 9.20                |

Italic and bold values indicates check hybrids

Env-1 = Environment 1, Env-2 = Environment 2, Env-3 = Environment 3, Env-4 = Environment 4, and GY = Grain yield (t ha\(^{-1}\))
Table 4 Mean values of the top 10 rated hybrids for grain yield in each site and across all the sites evaluated under Tester B

| Rank | Ukulinga 1 Low density (Env-1) | Ukulinga 2 high density (Env-3) | CEDARA (Env-2) | Dundee (Env-4) | GY Across all sites |
|------|-------------------------------|---------------------------------|----------------|--------------|-------------------|
|      | Entry Hybrid                   | GY (t ha\(^{-1}\))               | Entry Hybrid   | GY (t ha\(^{-1}\)) | Entry Hybrid   | GY (t ha\(^{-1}\)) | Entry Hybrid   | GY (t ha\(^{-1}\)) | Entry Hybrid   | GY (t ha\(^{-1}\)) |
| 1    | 137 15XH172                    | 13.53                            | 180 15XH215    | 12.99         | 179 15XH214    | 11.35            | 180 15XH215    | 7.19           | 180 15XH215    | 10.61            |
| 2    | 180 15XH215                    | 13.26                            | 115 15XH150    | 12.25         | 120 15XH155    | 11.29            | 154 15XH189    | 6.96           | 179 15XH214    | 10.25            |
| 3    | 178 15XH213                    | 13.24                            | 140 15XH175    | 11.84         | 110 15XH145    | 11.29            | 163 15XH198    | 6.43           | 133 15XH168    | 10.02            |
| 4    | 152 15XH187                    | 13.23                            | 179 15XH214    | 11.80         | 133 15XH168    | 11.17            | 141 15XH176    | 6.14           | 177 15XH212    | 9.84             |
| 5    | 179 15XH214                    | 13.07                            | 182 15XH217    | 11.73         | 123 15XH158    | 11.00            | 130 15XH165    | 6.09           | 151 15XH186    | 9.84             |
| 6    | **200 BG5285B**                | 13.05                            | 141 15XH176    | 11.72         | 121 15XH156    | 10.80            | 151 15XH186    | 6.06           | 110 15XH145    | 9.80             |
| 7    | 177 15XH212                    | 12.68                            | 129 15XH164    | 11.66         | 151 15XH186    | 10.65            | 193 15XH228    | 6.00           | 122 15XH157    | 9.76             |
| 8    | 121 15XH156                    | 12.64                            | 122 15XH157    | 11.53         | 137 15XH172    | 10.48            | 191 15XH226    | 5.95           | 120 15XH155    | 9.64             |
| 9    | 139 15XH174                    | 12.64                            | 181 15XH216    | 11.35         | 180 15XH215    | 10.36            | **198 10HDTX11B** | 5.86      | 141 15XH176    | 9.60             |
| 10   | 103 15XH138                    | 12.59                            | 142 15XH177    | 11.16         | 177 15XH212    | 10.34            | 122 15XH157    | 5.85           | 126 15XH161    | 9.43             |

Italic and bold values indicates check hybrids

Env-1 = Environment 1, Env-2 = Environment 2, Env-3 = Environment 3, Env-4 = Environment 4, and GY = Grain yield (t ha\(^{-1}\))
| Entry | Hybrids         | UK 1   | UK 2   | STI   | UK 1   | UK 2   | UK 1   | UK 2   | UK 1   | UK 2   | UK 1   | UK 2   |
|-------|----------------|--------|--------|-------|--------|--------|--------|--------|--------|--------|--------|--------|
|       |                | Low plant population density | High plant population density |       |        |        |        |        |        |        |        |        |
|       |                | GY (t ha$^{-1}$) | PopDen (plants ha$^{-1}$) | GY (t ha$^{-1}$) | PopDen (plants ha$^{-1}$) |       |        |        |        |        |        |
| 79    | 15XH121        | 14.59  | 33,333 | 10.191 | 64,444 | 0.6985 | 17.19  | 1.889  | 4.52   | 43.314 | 21.71  | 45.2   |
| 8     | 15XH50         | 14.48  | 37,778 | 11.383 | 56,667 | 0.7856 | 40.26  | 0.245  | 0.182  | 17.65  | 40.44  | 17.4   |
| 52    | 15XH94         | 14.36  | 36,667 | 11.933 | 65,556 | 0.8309 | 79.63  | 10.11  | 0.305  | 5.019  | 79.93  | 15.13  |
| 27    | 15XH69         | 14.48  | 38,889 | 11.039 | 42,222 | 0.7693 | 11.55  | 0.976  | 0.059  | 6.315  | 11.61  | 7.29   |
| 46    | 15XH88         | 14.1   | 40,000 | 11.111 | 67,778 | 0.7880 | 14.27  | 21.4   | 2.877  | 25.96  | 17.15  | 47.36  |
| 57    | 15XH99         | 14.05  | 27,778 | 11.486 | 65,556 | 0.8175 | 40.04  | 8.502  | 1.288  | 5.019  | 41.33  | 16.91  |
| 10    | 15XH52         | 13.89  | 34,444 | 10.074 | 62,222 | 0.725  | 36.5   | 19.76  | 0.551  | 41.5   | 37.06  | 61.28  |
| 40    | 15XH82         | 13.85  | 37,778 | 11.345 | 64,444 | 0.8191 | 42.71  | 8.418  | 3.123  | 1.832  | 45.83  | 10.25  |
| 74    | 15XH116        | 13.84  | 41,111 | 10.997 | 60,000 | 0.7946 | 64.02  | 3.569  | 8      | 37.78  | 72.02  | 41.35  |
| 81    | 15XH123        | 13.76  | 42,222 | 9.611  | 68,889 | 0.6985 | 52.39  | 10.08  | 0.31   | 13.85  | 52.08  | 23.94  |

**Advanced and commercial hybrids**

| Entry | Hybrids         | UK 1   | UK 2   | STI   | UK 1   | UK 2   | UK 1   | UK 2   | UK 1   | UK 2   | UK 1   | UK 2   |
|-------|----------------|--------|--------|-------|--------|--------|--------|--------|--------|--------|--------|--------|
| 100   | BG5285A        | 15.86  | 41,111 | 12.411 | 73,333 | 0.7825 | 33.61  | 3.148  | 0.187  | 33.42  | 2.14   | 2.115  |
| 94    | 11C1774A       | 13.22  | 41,111 | 10.241 | 68,889 | 0.774  | 6.565  | 0.187  | 2.82   | 6.81   | 9.38   | 1.65   |
| 200   | BG5285B        | 13.15  | 42,222 | 10.577 | 74,444 | 0.8043 | 21.28  | 0.237  | 0.31   | 1.151  | 20.97  | 0.91   |
| 98    | 10HDTX11A      | 12.7   | 38,889 | 10.584 | 62,222 | 0.8334 | 40.72  | 8.752  | 0.059  | 5.458  | 40.78  | 14.21  |
| 97    | 11C1483A       | 11.75  | 42,222 | 9.135  | 60,000 | 0.7775 | 10.29  | 3.632  | 0.31   | 0.75   | 9.98   | 4.38   |
| 199   | PAN 6Q-345 CBB | 11.39  | 40,000 | 9.555  | 74,444 | 0.8389 | 3.27   | 3.463  | 0.064  | 12.24  | 3.21   | 15.71  |
| 95    | 11C1579A       | 11.14  | 36,667 | 8.958  | 60,000 | 0.8041 | 6.65   | 1.768  | 3.246  | 9.953  | 9.9    | 11.72  |
| 96    | 11C2245A       | 11.06  | 43,333 | 7.82   | 54,444 | 0.7071 | 10.84  | 0.306  | 0.433  | 4.113  | 10.41  | 3.81   |
| 99    | PAN 6Q-345 CBA | 10.65  | 42,222 | 11.784 | 76,667 | 1.1065 | 7.66   | 1.86   | 0.31   | 1.443  | 7.35   | 0.42   |

**Table 5** Average yields of maize hybrids for stress tolerance index (STI), standability and ear prolificacy evaluated under non-stress (Yp), low density (LD) and high density (HD) stress conditions at Ukulinga 1 and Ukulinga 2.
Africa. Results indicated a progress in breeding for high population density stress tolerance and high yield potential in the new maize hybrids 15XH215, 15XH214 and 15XH121. Temperate germplasm is resistant to abiotic stresses such root and stem lodging and has high grain yield potential under high population density. In South Africa, DAFF (2014) reported that there are farmers practising high, low and medium plant density culture. High plant population density can be achieved using various methods such as planting more than one plant per station (Aderemi and Olaitan 2020; Msuya 2021) as currently used in this study. However, other methods are reducing the distance either between plants or between rows. Planting more than one plant per station works well for smallholder farmers’ especially with conservation agriculture. On the other hand, reducing the distance between plants and rows would work well for highly mechanized commercial farms. In this regard, studies should focus on the relationships of the different methods and preference by commercial or subsistence farmers (Msuya 2021). The selected hybrids 15XH215 and 15XH214 under high plant population density stress can be recommended for farmers who wish to increase their plant population densities. These farmers should be able to provide suitable cultural practises such as fertilization and irrigation to reduce potential stresses common under plant population densities. However, hybrids 15XH121 and 15XH65 specifically performed well under low plant population density conditions, thus, these hybrids can be recommended for use in western part of South Africa where low plant population density cultural practise is applied.

The study revealed genetic gains of at least 26% for yield under high plant density through breeding from temperate × tropical germplasm populations. Positive genetic gains were observed for secondary traits that are associated with yield in the temperate × tropical germplasm populations. Genetic gains were also observed with respect to early physiological maturity of maize hybrids. The earliness of maize can be measured using physiological maturity where long-season hybrids reach maturity in 140–150 days, medium-season hybrids in 130–145 and short season hybrids in 115–130 days (Gasura et al. 2014) depending on the altitude. In the current study, hybrids which attained days to silking and anthesis earlier than those of PAN6Q-345 CB, between 70 and 71, under DTAB32 and 68 to 70 under Tester 9, had grain

| Table 5 continued | Entry | Hybrids | STI | GY (t ha⁻¹) | PopDen (plants ha⁻¹) | EPP | RL (%) | SL (%) | TL (%) | EPP |
|-------------------|-------|---------|-----|-------------|----------------------|-----|--------|--------|--------|-----|
| 196 | 11C2245B | 8.07 | 30,000 | 9.232 | 60,000 | 1.1439 | 4.72 | 5.845 | 5.209 | 2.474 | 0.49 | 8.32 | 1.313 | 0.994 |
| An EPP of below 1.0 indicates partial barrenness; an EPP of above 1.0 indicates ear prolificacy; GY = Grain yield (t ha⁻¹); STI = Stress tolerance index; EPP = Number of ear per plant; RL = Root lodging (%); SL = Stem lodging (%); TL = Total lodging (%) and PopDen = Plant population density (plants ha⁻¹).
### Table 6  Genetic gain for hybrids evaluated under low plant population density

| Entry | Hybrid | GY (t ha\(^{-1}\)) | PH (cm) | EH (cm) | AD (days) | EPO (ratio) | EPP | MOI (%) | RL (%) | SL (%) | TL (%) | NTB | NLAC | DCD |
|-------|--------|---------------------|--------|--------|-----------|-------------|-----|---------|-------|--------|-------|------|------|------|
| Top five hybrids (selected hybrids) | | | | | | | | | | | | | | |
| 79    | 15XH121| 12.13               | 248.70 | 134.80 | 78.00     | 0.54        | 1.24 | -0.50  | 16.68 | 7.31   | 10.99 | 18.30 | 12.33 | 6.67  | 126.70 |
| 23    | 15XH65 | 12.03               | 238.40 | 136.80 | 77.04     | 0.62        | 1.12 | -0.67  | 16.87 | 19.99  | 23.96 | 43.95 | 10.66 | 6.83  | 126.40 |
| 68    | 15XH110| 11.84               | 247.60 | 133.50 | 77.03     | 0.54        | 1.02 | -0.01  | 17.65 | 13.88  | 24.33 | 38.21 | 11.49 | 7.16  | 129.70 |
| 93    | 15XH135| 11.74               | 233.10 | 128.10 | 77.66     | 0.55        | 1.01 | 0.67   | 16.88 | 35.20  | 24.04 | 59.24 | 12.83 | 5.67  | 127.20 |
| 87    | 15XH129| 11.69               | 246.30 | 130.60 | 78.05     | 0.53        | 1.21 | -1.17  | 16.36 | 17.41  | 25.08 | 42.50 | 11.00 | 6.60  | 127.90 |
| Means | | | | | | | | | | | | | | |
| Mean of selected (S)        | 11.89 | 242.82             | 132.76 | 77.56   | 0.56      | 1.12 | -0.34  | 16.89 | 18.76  | 21.68 | 40.44 | 11.66 | 6.60  | 127.58 |
| Population mean (P)        | 10.18 | 242.57             | 128.71 | 77.26   | 0.53      | 1.08 | -0.61  | 16.61 | 15.41  | 20.28 | 35.68 | 11.98 | 6.60  | 127.21 |
| Mean of checks (C)         | 10.44 | 239.66             | 126.06 | 77.95   | 0.53      | 1.28 | -0.98  | 16.81 | 8.19   | 8.55  | 16.75 | 12.00 | 6.43  | 128.03 |
| Mean of set A checks (A)   | 9.78  | 239.80             | 126.64 | 78.03   | 0.53      | 1.23 | -1.17  | 16.75 | 7.14   | 7.04  | 14.17 | 11.57 | 6.30  | 127.96 |
| Mean of set B checks (B)   | 12.08 | 239.30             | 124.60 | 77.75   | 0.53      | 1.39 | -0.50  | 16.96 | 10.84  | 12.35 | 23.18 | 13.08 | 6.75  | 128.20 |
| Genetic gain (S–P)         | 1.70  | 0.25               | 4.05   | 0.30    | 0.02      | 0.04 | 0.27   | 0.28  | 3.35   | 1.40  | 4.76  | -0.32 | -0.01 | 0.37  |

**Percentage gain**

| S–P   | 16.70 | 0.10 | 3.15 | 0.39 | 4.69 | 3.63 | -44.53 | 1.67 | 21.73 | 6.93 | 13.33 | -2.65 | -0.10 | 0.29 |
| S–C   | 14.23 | 1.30 | 5.21 | -0.50 | 5.39 | -14.67 | -15.41 | 0.48 | 68.56 | 64.74 | 66.40 | -2.81 | 2.56 | -0.35 |
| S–A   | 20.68 | 1.24 | 4.75 | -0.61 | 5.47 | -10.45 | -16.67 | 0.83 | 75.41 | 72.23 | 73.61 | 0.80 | 4.49 | -0.30 |
| S–B   | -1.90 | 1.45 | 6.34 | -0.24 | 5.21 | -25.24 | -27.26 | -0.40 | 51.42 | 46.04 | 48.37 | -11.84 | 2.28 | -0.49 |

GY = Grain yield (t ha\(^{-1}\)); PH = plant height (cm); EH = Ear height (cm); AD = Days to anthesis; EPO = Ear position; EPP = Number of ear per plant; MOI = grain moisture content (%); ASI = Anthesis silking interval; RL = Root lodging (%); SL = Stem lodging (%); TL = Total lodging (%); NTB = Number of tassel branches; NLAC = Number of leaves above the cob and DCD = Number of day to 50% cob dryness, Set A checks = Advanced hybrids, and Set B checks = Commercial hybrids
### Table 7  Genetic gain for hybrids evaluated under high plant population density

| Entry | Hybrid | GY (t ha\(^{-1}\)) | PH (cm) | EH (cm) | AD | EPO | EPP | ASI | MOI (%) | RL (%) | SL (%) | TL (%) | NTB | NLAC | DCD |
|-------|--------|---------------------|--------|---------|----|-----|-----|-----|---------|-------|-------|-------|-----|------|-----|
|       |        | Top five hybrids (selected hybrids) |       |         |    |     |     |     |         |       |       |       |     |      |     |
| 179   | 15XH214| 12.04               | 263.20 | 150.20  | 80.86 | 0.57 | 1.64 | -1.47 | 15.37   | 5.40  | 21.88 | 27.28 | 14.46 | 5.48 | 131.80 |
| 180   | 15XH215| 11.68               | 240.10 | 127.70  | 80.19 | 0.53 | 1.80 | -0.69 | 17.17   | 0.04  | 11.64 | 11.64 | 11.53 | 6.18 | 130.50 |
| 115   | 15XH150| 11.49               | 240.80 | 130.40  | 77.50 | 0.54 | 1.60 | -1.00 | 16.21   | 0.23  | 3.28  | 11.51 | 13.16 | 5.83 | 128.70 |
| 122   | 15XH257| 11.45               | 246.80 | 129.20  | 78.95 | 0.52 | 1.61 | -1.19 | 17.03   | 4.56  | 27.14 | 31.70 | 12.21 | 5.52 | 133.00 |
| 141   | 15XH176| 11.44               | 48.10  | 127.60  | 78.66 | 0.51 | 1.73 | -1.18 | 16.47   | 2.62  | 13.92 | 16.54 | 11.68 | 6.01 | 127.70 |
|       |        | Means               |       |         |    |     |     |     |         |       |       |       |     |      |     |
|       |        | Mean of selected (S) | 11.62 | 247.80  | 133.02 | 78.83 | 0.54 | 1.68 | -1.11 | 16.45 | 4.16  | 15.57 | 19.73 | 12.61 | 5.80 | 130.34 |
|       |        | Population mean (P)  | 9.53  | 246.30  | 130.06 | 77.89 | 0.53 | 1.56 | -0.94 | 15.93 | 2.59  | 12.40 | 14.99 | 12.83 | 5.81 | 129.78 |
|       |        | Mean of checks (C)   | 9.19  | 246.99  | 129.61 | 78.49 | 0.53 | 1.44 | -0.86 | 16.00 | 3.33  | 10.17 | 13.51 | 12.65 | 5.85 | 130.07 |
|       |        | Mean of set A checks (A) | 8.59  | 245.26  | 129.98 | 78.58 | 0.53 | 1.38 | -0.73 | 16.13 | 2.99  | 8.19  | 11.18 | 12.39 | 5.74 | 130.46 |
|       |        | Mean of set B checks (B) | 10.68 | 251.30  | 128.70 | 78.27 | 0.50 | 1.58 | -1.19 | 15.70 | .18   | 15.14 | 19.33 | 13.30 | 6.10 | 129.10 |
|       |        | Genetic gain (S—P)   | 2.09  | 1.50    | 2.96   | 0.94 | 0.01 | 0.11 | -0.17 | 0.52   | 1.57  | 3.17  | 4.75  | -0.23 | -0.01 | 0.56 |
|       |        | Percentage gain      |       |         |       |     |     |     |       |       |       |       |       |       |       |     |
|       |        | S–P                 | 22.70 | 0.61    | 2.29   | 1.19 | 1.41 | 8.00 | 19.75  | 3.23   | 47.25 | 31.14 | 35.14 | -1.79 | -0.11 | 0.43 |
|       |        | S–C                 | 25.50 | 0.33    | 2.62   | 0.44 | 2.03 | 15.45 | 25.92  | 2.80   | 32.04 | 43.52 | 41.55 | -0.29 | -0.75 | 0.21 |
|       |        | S–A                 | 31.77 | 1.03    | 2.34   | 0.32 | 1.00 | 19.23 | 40.00  | 2.02   | 45.21 | 59.53 | 57.08 | 1.73  | 1.02  | -0.09 |
|       |        | S–B                 | 9.81  | -1.42   | 3.32   | 0.73 | 4.61 | 6.00 | -9.26  | 4.74   | -0.91 | 3.48  | 2.73  | -5.35 | -5.17 | 0.96 |

GY = Grain yield (t ha\(^{-1}\)); PH = plant height (cm); EH = Ear height (cm); AD = Days to anthesis; EPO = Ear position; EPP = Number of ear plant\(^{-1}\); MOI = grain moisture content (%); ASI = Anthesis silking interval; RL = Root lodging (%); SL = Stem lodging (%); TL = Total lodging (%); NTB = Number of tassel branches; NLAC = Number of leaves above the cob and DCD = Number of days to 50% cob dryness, Set A checks = Advanced hybrids, and Set B checks = Commercial hybrids.
The following is a table that describes phenotypic direct (diagonal in bold) and indirect effects and total path correlations coefficient analysis of grain yield component characters evaluated at Ukulinga 1 (Env-1) at low plant population density.

| Traits | PH (cm) | EH (cm) | AD | EPO | EPP | ASI (%) | MOI (%) | RL (%) | SL (%) | TL (%) | NTB | NLAC | DCD | PopDen (plants ha⁻¹) | NP | GY (t ha⁻¹) |
|--------|---------|---------|----|-----|-----|---------|---------|--------|--------|--------|-----|------|-----|---------------------|----|------------|
| PH     | 0.17    | 0.15    | 0.02 | 0.01 | 0.00 | 0.02    | -0.02   | 0.51   | -0.01  | -0.54  | -0.02 | 0.00  | 0.03 | 0.00                | 0.01 | 0.01       |
| EH     | -0.11   | 0.24    | 0.02 | -0.09 | 0.01 | 0.02    | -0.01   | 0.56   | 0.00   | -0.61  | -0.02 | -0.04 | 0.03  | 0.00                | 0.01 | 0.01       |
| AD     | -0.04   | 0.07    | 0.06 | -0.02 | 0.01 | 0.03    | 0.02    | 0.47   | 0.03   | -0.54  | -0.02 | -0.06 | 0.04  | 0.00                | 0.00 | 0.04       |
| EPO    | 0.01    | 0.16    | 0.01 | -0.13 | 0.00 | 0.01    | -0.01   | 0.31   | 0.00   | -0.34  | -0.02 | -0.05 | 0.01  | 0.00                | 0.01 | 0.01       |
| EPP    | -0.05   | 0.08    | 0.02 | -0.02 | 0.02 | 0.05    | -0.07   | 1.05   | 0.05   | -1.19  | -0.05 | -0.12 | 0.05  | -0.01               | 0.02 | -0.19*     |
| ASI    | 0.05    | -0.06   | -0.03 | 0.01 | -0.01 | -0.08   | 0.06    | -0.75  | -0.03  | 0.85   | 0.03  | 0.09  | -0.04 | 0.01                 | -0.02 | 0.09       |
| MOI    | 0.01    | -0.01   | 0.00 | 0.00 | 0.00 | 0.00    | -0.02   | 0.23   | 0.01   | 0.38   | 0.01  | 0.06  | 0.02  | 0.00                 | -0.01 | 0.34***   |
| RL     | 0.05    | -0.08   | -0.02 | 0.02 | -0.01 | -0.04   | 0.05    | -1.64  | 0.00   | 1.78   | 0.03  | 0.10  | -0.03 | 0.00                 | -0.01 | 0.22**    |
| SL     | 0.00    | 0.00    | -0.01 | 0.00 | 0.00 | 0.00    | -0.01   | -0.02  | -0.24  | 0.31  | 0.01  | 0.03  | -0.02 | 0.01                 | -0.01 | 0.04       |
| TL     | 0.05    | -0.08   | -0.02 | 0.02 | -0.01 | -0.04   | 0.05    | -1.62  | 0.04   | 1.81   | 0.03  | 0.10  | -0.04 | 0.00                 | -0.01 | 0.22**    |
| NTB    | -0.02   | 0.04    | 0.01 | -0.01 | 0.00 | 0.02    | -0.02   | 0.31   | 0.02   | -0.37  | -0.16 | -0.04 | 0.03  | 0.00                 | 0.00  | -0.18***  |
| NLAC   | 0.00    | -0.04   | -0.01 | 0.03 | -0.01 | 0.03    | 0.06    | -0.65  | -0.03  | 0.75   | 0.02  | 0.25  | -0.02 | 0.01                 | -0.01 | 0.30***   |
| DCD    | -0.04   | 0.06    | 0.02 | -0.01 | 0.01 | 0.03    | 0.04    | 0.42   | 0.04   | -0.51  | -0.04 | -0.05 | 0.13  | 0.00                 | 0.00  | 0.09       |
| PopDen | -0.01   | 0.02    | 0.00 | 0.00 | 0.00 | 0.00    | 0.00    | 0.16   | 0.03   | -0.21  | 0.00  | -0.04 | 0.00  | -0.04               | 0.09  | -0.02      |
| NP     | -0.01   | 0.02    | 0.00 | 0.00 | 0.00 | 0.02    | 0.00    | 0.16   | 0.03   | -0.21  | 0.00  | -0.04 | 0.00  | -0.04               | 0.09  | -0.02      |

Values in bold indicate direct effects.

GY = Grain yield (t ha⁻¹); PH = plant height (cm); EH = Ear height (cm); AD = Days to anthesis; EPO = Ear position; EPP = Number of ear plant⁻¹; MOI = grain moisture content (%); NP = Number of plants harvested; ASI = Anthesis silking interval; RL = Root lodging (%); SL = Stem lodging (%); TL = Total plant lodging (%); NTB = Number of tassel branches; NLAC = Number of leaves above the cob; DCD = Number of days to 50% cob dryness and PopDen = Plant population density (plants ha⁻¹).

*, **, *** significantly different at p ≤ 0.05, 0.01 and 0.001 probability levels, respectively.
Table 9 Phenotypic direct (in bold) and indirect effects and total path correlations coefficient analysis of grain yield component characters evaluated at Ukulinga 2 (Env-3) at high plant population density

| Traits | PH (cm) | EH (cm) | AD | EPO | EPP | ASI | MOI (%) | RL (%) |
|--------|---------|---------|----|-----|-----|-----|---------|-------|
| PH     | 0.052   | 0.030   | -0.002 | -0.036 | 0.007 | -1.9E-03 | -2.5E-04 | 0.022 |
| EH     | 0.017   | **0.095** | -0.002 | 0.056 | 0.003 | 4.5E-04 | 2.6E-05 | 0.028 |
| AD     | -0.001  | -0.001 | **0.101** | -0.001 | 0.010 | -3.6E-03 | 1.5E-03 | -0.022 |
| EPO    | -0.023  | 0.064  | -0.002 | **0.083** | -0.001 | 1.4E-03 | 1.8E-04 | 0.030 |
| EPP    | 0.004   | 0.003  | 0.010 | -0.001 | **0.099** | -1.3E-02 | -1.2E-03 | -0.101 |
| ASI    | -0.002  | 0.001  | -0.007 | 0.002 | -0.027 | **4.8E-02** | 5.4E-04 | 0.031 |
| MOI    | -0.003  | 0.001  | 0.031 | 0.003 | -0.024 | 5.3E-03 | **4.9E-03** | 0.051 |
| RL     | 0.000   | 0.008  | -0.007 | 0.007 | -0.029 | 4.4E-03 | 7.3E-04 | **0.345** |
| SL     | -0.002  | 0.011  | -0.010 | 0.008 | -0.024 | 1.2E-02 | -3.1E-04 | 0.077 |
| TL     | -0.002  | 0.012  | -0.011 | 0.010 | -0.030 | 1.2E-02 | -4.5E-05 | 0.175 |
| NTB    | 0.002   | -0.001 | -0.005 | -0.004 | 0.016 | -1.9E-03 | -4.6E-04 | -0.025 |
| NLAC   | -0.009  | 0.002  | -0.002 | 0.011 | -0.040 | 2.7E-03 | 1.3E-03 | 0.121 |
| DCD    | 0.013   | -0.006 | -0.001 | -0.019 | 0.041 | -6.7E-03 | -1.6E-03 | -0.128 |
| PopDen | 0.004   | -0.006 | 0.009  | -0.007 | 0.035 | -2.6E-03 | -7.2E-04 | -0.066 |
| NP     | 0.004   | -0.006 | 0.009  | -0.007 | 0.035 | -2.6E-03 | -7.2E-04 | -0.066 |

| Traits | SL (%) | TL (%) | NTB | NLAC | DCD | PopDen (plants ha⁻¹) | NP | GY (t ha⁻¹) |
|--------|--------|--------|-----|------|-----|-----------------------|----|-------------|
| PH     | -0.008 | 0.019  | 5.36E-04 | -0.050 | -0.030 | 8.5E-05 | 8.5E-05 | -0.018 |
| EH     | 0.022  | -0.066 | -1.32E-04 | 0.006  | 0.008  | -6.9E-05 | -6.9E-05 | 0.166 |
| AD     | -0.019 | 0.056  | -7.22E-04 | -0.007 | 0.002  | 1.0E-04 | 1.0E-04 | 0.114 |
| EPO    | 0.020  | -0.062 | -5.80E-04 | 0.038  | 0.028  | -1.0E-04 | -1.0E-04 | 0.176** |
| EPP    | -0.047 | 0.162  | 2.24E-03 | -0.121 | -0.050 | 4.0E-04 | 4.0E-04 | -0.052 |
| ASI    | 0.048  | -0.131 | -5.36E-04 | 0.017  | 0.017  | -6.0E-05 | -6.0E-05 | -0.003 |
| MOI    | -0.012 | 0.005  | -1.29E-03 | 0.079  | 0.040  | -1.7E-04 | -1.7E-04 | 0.179** |
| RL     | 0.043  | -0.270 | -9.83E-04 | 0.105  | 0.045  | -2.2E-04 | -2.2E-04 | 0.251*** |
| SL     | **0.194** | -0.507 | -2.54E-04 | 0.063  | 0.034  | -1.6E-04 | -1.6E-04 | -0.144* |
| TL     | 0.185  | **0.532** | -8.15E-05 | 0.088  | 0.044  | -2.1E-04 | -2.1E-04 | -0.049 |
| NTB    | 0.004  | 0.003  | **0.01** | -0.058 | -0.023 | 2.7E-04 | 2.7E-04 | -0.079 |
| NLAC   | 0.041  | -0.156 | -2.63E-03 | **0.300** | 0.087  | -4.5E-04 | -4.5E-04 | 0.355*** |
| DCD    | -0.055 | 0.195  | 2.53E-03 | -0.217 | **0.121** | 4.7E-04 | 4.7E-04 | -0.303*** |
moisture content below 12.5%, and were considered to be early maturing. These hybrids include 10HDTX11 and the rest which poorly performed in terms of grain yield. Unfortunately the earlier the hybrid, the low the grain yield potential. This proves to be the main challenge of breeding for early-maturing maize which is the negative correlation between yield and early physiological maturity (Gasura et al. 2014).

Differences in ranking of genotypes under high and low plant population density implied differential yield performance among the maize genotypes as a result of the significant cross over genotype by environment interaction (GxE) (Yan and Tinker 2006). The G x E may be managed by using specific cultivars for each environment or exploited by using cultivars with wide adaptability. In this study entries 79 (15XH121), 179 (15XH215) and 180 (15XH214) were the most ideal genotypes across stress levels in terms of high mean grain yield and stability. These hybrids could also have the greatest commercial success because they showed the high stability across stress levels (Abay et al. 2009). Grain yield stability is a highly heritable trait (Yan and Tinker 2006) and most genotypes that tolerate stress have been associated with high grain yield stability. Rossini et al. (2011) defined population density tolerance in plants as the extent to which the crop maintains high yield level when plant population density increases above average levels. The capacity of the new testcross hybrids to produce higher grain yield may be attributed to their ability to adapt to stress conditions (Carena et al. 2010). Yan et al. (2011) reported that future gains in yield can be made by improving maize for resistance to high plant population density stress through resistance to stem lodging. In line with this idea, Duvick (2005) and, Van Roekel and Coulter (2011) reported that maize grain yield had increased since the 1930s due to the adaptability to higher planting densities. Sangoi et al. (2002) observed that the highest plant population in their study resulted in the highest grain yield at three locations evaluated in Indiana. Similarly, the current study showed high yield among the stable varieties to be associated with increased plant density. This indicates that productivity of hybrids derived from the tropical × temperate germplasm genetic backgrounds can be enhanced by selecting for high yield under high density stress.

Some hybrids had high stress tolerance indices, a parameter which shows the relationship in

| Traits | SL (%) | TL (%) | NTB | PopDen (plants ha⁻¹) | GY (t ha⁻¹) | NP | GY = Grain yield (t ha⁻¹); PH = plant height (cm); EH = Ear height (cm); AD = Days to anthesis; EPO = Ear position; EPP = Number of ear plant⁻¹; MOI = grain moisture content; NP = Number of plants harvested; ASI = Anthesis silking interval; RL = Root lodging (%); SL = Stem lodging (%); TL = Total plant lodging (%); NTB = Number of tassel branches; NLAC = Number of leaves above the cob; DCD = Number of days to 50% cob dryness and PopDen = Plant population density (plants ha⁻¹). |
|--------|--------|--------|-----|----------------------|-------------|----| Values in bold indicates direct effects |
|        | 0.100  | 0.100  | 0.100 | 0.100                | 0.100       | NP | * ** *** significantly different at p ≤ 0.05, 0.01 and 0.001 probability levels, respectively |
| PopDen | 0.028  | 0.028  | 0.028 | 0.028                | 0.028       | NP | |
|        | 3.24E⁻³ | 3.24E⁻³ | 3.24E⁻³ | 3.24E⁻³              | 3.24E⁻³     | NTB| |
|        | 0.121  | 0.121  | 0.121 | 0.121                | 0.121       | DCD| |
|        | 1.1E⁻³ | 1.1E⁻³ | 1.1E⁻³ | 1.1E⁻³               | 1.1E⁻³      | GY | |
performance of yield under stress condition and non-stress. The yield gains observed among the selected hybrids could be attributed to their yield stability due to their high stress tolerance index due to resistance to stem lodging. These hybrids have several desirable attributes that give them high yield and stability better than the existing commercial hybrids. Indeed most of these hybrids were derived from the DTAB32 which is associated with a huge contribution to stress resistance including resistance to lodging. This agrees with reports in the literature with respect to temperate maize germplasm. Past genetic gains in modern hybrids were associated with tolerance to stress (Duvick 2005) and that include tolerance to high plant population density as reported by many researchers (Rossini et al. 2011; Yan et al. 2011; Ray et al. 2012). Genetic advance is the expected genetic progress resulting from selection of the best-performing genotypes for a given character. Currently, it can be concluded that the highest density (74 000 plants per ha) is still below the potential maximum yield densities because some plants could still produce more than one cob, an indicator of reduced stress. This indicated that the hybrids could still produce high yield at higher density levels. Future studies should test these hybrids at higher densities.

Relationships of grain yield and related traits under different plant densities and testers

Traits such as number of days to 50% cob dryness, total plant lodging, ear height, ear position, plant height, days to anthesis, anthesis-silking interval, number of plants per plot and plant population density were not associated with grain yield, suggesting that they are not ideal candidates to utilize during breeding for stress tolerance in this population of temperate × tropical germplasm lines. Directional selection from plant breeding overtime has resulted in the reduction of genetic variability for some important traits. Lee and Tollenaar (2007) noted that not all traits are useful in the current and future breeding of maize because of lack of enough variability.

Number of ears per plant and number of tassel branches were highly correlated with grain yield and had huge positive direct effects on grain yield under low plant population density. Number of ears per plant and number of tassel branches are parameters associated with high nutrition which is associated with low plant population density. This explains why number of ears per plant and number of tassel branches were high under low plant population density. However, in breeding for increased grain yield under stress it will be ideal to improve the number of ears per plant while reducing the number of tassel branches. Mostafavi et al (2013) noted ear prolificacy to be highly significant and to have a positive correlation with grain yield in maize. Grain yield is the key trait in maize-breeding programmes (Peng et al. 2011). However, for it to be improved to a greater extent, the contribution of other allied traits, such as the number of ears per plant and number of tassel branches must be considered. Tassels are normally strong sinks in maize nutrition due to their apical dominance and if the number of tassel branches increase they may also result in reduced grain yield. Normally only adequate (not excess) pollen grains are required in pollination. Sangoi (2002) asserted that genotypes with many tassel branches are likely to have reduced grain yield due to suppression of ear development and high assimilate expenditure for head maintenance.

Number of leaves above the cob is one of the most important traits in maize grain filling. Under both low and high plant population density, number of leaves above the cob was highly correlated with grain yield with a positive direct effect suggesting the importance of these trait under this conditions. In line with the study by Alvim et al (2011) which found that grain filling is only affected by the leaves above the cob and leaves located above the cob provide most of the photo-assimilates necessary for grain filling in the ear. Thus the more and the bigger the leaves above the cob the better the efficiency of grain filling (Gasura et al. 2014). Under stress conditions the leaves are reduced and genotypes that maintain relatively more and bigger leaves above the cob will be better in terms of the efficiency of grain filling. In breeding for maize with better yield under stress it will be logical to select genotypes with more and bigger leaves above the ear. Furthermore, selection of plants that have more of erectophile type of leaves is desirable since this can reduce mutual shading but rather increase light penetration into the canopy (Brekke et al. 2011; Edwards 2011). Hammer et al (2009), showed that erectophile leaves reduced canopy light extinction coefficient, increased light penetration to lower leaves, and enabled more uniform photosynthetic rates within the canopy. DTAB32 contributed more to number of
leaves above the cob, and this tester is well known for its wide adaptability across different production conditions.

In order to improve gains from selection, it is desirable to have positive significant correlations between yield and agronomic characteristics that contribute towards higher yield. Stem lodging and root lodging had indirect effects on grain yield because this trait reduces the number of plants per hectare and barrenness (reduced EPP) and thus grain yield. Tokatlidis and Koutroubas (2004 http://link.springer.com/article/10.1007/s13593-012-0108-7-CR50) observed the adverse effects of high plant population densities on maize grain yield stability because of high incidence of root and stem lodging and increased barrenness. Grain yield is mainly a function of the number of plants per hectare. The purpose of increasing plant population density is to improve the number of plants per hectare and thus grain yield. However, lodging has a negative effect on this approach because it reduces the number of plants per hectare. If lodging occurs before grain filling, the lodged plants suffer shading and may not produce grains at all. If lodging occurs after grain filling, the fallen plants may not be harvested by the combine harvester. In general, under high plant population density grain yield was low as compared to low plant population density for certain hybrids. Stem lodging had indirect effects on grain yield under high plant population density. Hashemi et al (2005) also stated that maize grain yield declines when plant density is increased beyond the optimum plant density primarily because of decline in the harvest index and increased stem lodging. In most cases, farmers in sub-Saharan Africa plant more plants per unit areas and they get less yield because the current hybrids on the market are not resistant to high plant population density stress. Thus promotion of the hybrids that are tolerant to stress, will result in increased grain yield per unit area.

Knowledge of associations among the yield components, can improve selection efficiency (Raghu et al. 2011) based on indirect selection using a trait that is easy to select but highly correlated with grain yield. In this study, the selection efficiency for grain yield based on number of leaves above the cob and stem lodging could be high because of high heritability of these traits and their high correlation with grain yield. The use of indirect traits in selection has improved selection of grain yield under stress and non-stress conditions (Gasura et al. 2014). There is great potential of increasing the plant density and hence grain yield above the levels reported in this study based on the careful use indirect selection traits such as higher number of leaves above the cob and resistance to stem lodging.

Conclusion

The study has shown that it is possible to improve maize grain yield in this breeding programme through increasing adaptation to high plant population density. Gains of at least 26% were observed by using tropical x temperate hybrids at high population density. The high yielding hybrids under high plant population density were associated with reduced stem lodging and increased number of leaves above the cob. Thus future improvement of maize yield in this germplasm set will primarily occur through tolerance to higher planting density by reducing stem lodging and increasing the number of leaves above the cob. Future studies should focus on evaluating the hybrids with potential for advancement at higher plant population densities by reducing the distance between plants.

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Data availability

Data and germplasm can be made available for research purposes.

Code availability

The codes used in the analysis are available in the public domain.

Declarations

Conflict of interest

There are no conflicts of interest.

References

Abay F, Bjørnstad A (2009) Specific adaptation of barley varieties in different locations in Ethiopia. Euphytica 167:181–195
Aderemi EO, Olatian OKQ (2020) Economic and yield assessment of maize varieties under recommended and double plant population densities. Am J Environ Sci 4(3):31
Ahmad A, Saleen M (2003) Path coefficient analysis in Zea mays. L Int J Agri Biol 5:245–248
Alvim KRT, Brito CH, Brandão AM, Gomes LS (2011) Redução de área foliar em plantas de milho na fase reprodutiva. Rev Ceres 58:413–418
Annor B, Badu-Apapru B, Nyadanu D, Akromah R, Fakorede MA (2020) Identifying heterotic groups and testers for hybrid development in early maturing yellow maize (Zea mays) for sub-Saharan Africa. Plant Breed 139(4):708–716
Awata LA, Ifie BE, Danquah E, Jumbo MB, Gowda M, Marchelo-Draggà PW, Olsen MS, Shorinola O, Yao NK, Boddupalli PM (2021) Introgresión de maíz letal necrosis resistance quantitative trait loci into susceptible maize populations and validation of the resistance under field conditions in Naivasha. Kenya Front Plant Sci 12:699
Bouslama M, Schapppa WT (1984) Stress tolerance in soybean. Part 1. Evaluation of three screening techniques for heat and drought tolerance. Crop Sci 24:933–937
Brekke B, Knapp A, Edwards J (2011) Selection and adaptation to high plant density in the Iowa stiff stalk synthetic maize population. Crop Sci 51(5):1965–1972
Cardwell VB (1982) Fifty years of Minnesota corn production: sources of yield increase. Agron J 74:984–990
Carena MJ, Bergman G, Riveland N, Eriksmoen E, Halvorson M (2010) Breeding maize for higher yield and quality under drought stress. Maydica 54:287–296
DAFF (2014) Demonstration of climate change adaptation and mitigation on-farm and food processor projects Australian government department of agriculture forestry and fisheries Australia. Available at http://www.daff.gov.au/. Accessed 28 Jan 2015
Dao A, Sanou J, Sanon RD, Zeba I, Coulibaly S, Lübberstedt T (2020) Exploring the potential usefulness of US maize expired plant variety protection act lines for maize breeding in sub-Saharan Africa. Crop Sci 60(5):2251–2265
Duvick DN (2005) The contribution of breeding to yield advances in maize. Agron J 86:84–145
Edwards JW (2011) Changes in plant morphology in response to recurrent selection in the Iowa Stiff Stalk synthetic maize population. Crop Sci 51(6):2352–2361
Gasura E, Setimela SP, Tarekegne A, Ichishahayo D, Edema R, Gibson PT, Okori P (2014) Variability of grain-filling traits in early maturing CIMMYT tropical maize inbred lines. Crop Sci 54:530–536
Hammer GL, Kroppf MJ, Sinclair TR, Porter JR (2009) Future contributions of crop modelling – from heuristics and supporting decision making to understanding genetic regulation and aiding crop improvement. Eur J Agron 18:15–31
Hashemi AM, Herbert SJ, Putnam DH (2005) Yield response of corn to crowding stress. Agron J 97:839–846
Koyejo, AO, Okpara, DA and Agugo, BAC, 2021 Effect of alley cropping on soil, maize and mungbean grown under different maize spatial arrangements and mungbean spacings in south east Nigeria. Agrofor Syst 1–10
Lee EA, Tollenaar M (2007) Physiological basis of successful breeding strategies for maize grain yield. Crop Sci 47:202–215
Lenka D, Mishra B (1973) Path coefficient analysis of yield in rice varieties. Indian J Agric Sci 43:376–379
Magorokosho C, Vivek B, MacRobert J (2009). Characterization of maize germplasm grown in eastern and southern Africa: results of the 2008 regional trials coordinated by CIMMYT. CIMMYT Reports, Harare, Zimbabwe.
Masuka B, Atlin GN, Olsen M, Magorokosho C, Labuschagne M, Crossa J, Bänziger M, Pixley KV, Vivek BS, von Biljon A, MacRobert J (2017) Gains in maize genetic improvement in Eastern and Southern Africa: I CIMMYT hybrid breeding pipeline. Crop Sci 57(1):168–179
Mostafavi K, Ghaemi M, Khorasani SK (2013) Using correlation and some genetics methods to study morphological traits in corn (Zea mays L) yield and yield components under drought stress conditions. Int Res J Appl Basic Sci 4:252–259
Msuya CP (2021) The important determinants of the adoption behavior: a case study of recommended maize production technologies in Tanzania. SAJAE 49(1):42–58
Musundire L, Derera J, Dari S, Tongoona P (2021) Assessment of genetic gains for grain yield and components from introgression of temperate donor inbred line into tropical elite maize inbred lines: II. Performance Inter Se. Euphytica 217(1):1–25
Mutimamaamba C, MacRobert J, Cairns JE, Magorokosho C, Ndhéla T, Mukungrutse C, Minnaar-Ontong A, Labuschagne M (2020) Line × tester analysis of maize grain yield under acid and non-acid soil conditions. Crop Sci 60(2):991
Olayiwola MO, Ajala SO, Ariyo OJ, Ojo DK, Gedil M (2021) Heterotic grouping of tropical maize inbred lines and their hybrid performance under stem borer infestation and low soil nitrogen condition in West and Central Africa. Euphytica 217(1):1–22
Osman AS, Badu-Apapru B, Ifie BE, Tongoona P, Obeng-Bio E, García-Oliveira AL (2020) Genetic diversity, population structure and inter-trait relationships of combined heat and drought tolerant early-maturing maize inbred lines from West and Central Africa. Agron J 109(9):1324
Peng B, Li Y, Wang Y, Liu C, Liu Z, Tan W, Zhang Y, Wang D, Shi Y, Sun B (2011) QTL analysis for yield components and kernel-related traits in maize across multi-environments. Theor Appl Genet 122:1305–1320
Raghu B, Suresh J, Kumar SS, Saaidiah P (2011) Character association and path analysis in Maize (Zea mays L). Madras Agric J 98:7–9
Ray DK, Ramankutty N, Mueller ND, WestPC, Foley JA (2012) Recent patterns of crop yield growth and stagnation. Nat Commun 3:1293
Rosie AA, Hamblin J (1981) Theoretical aspects of selection for yield in stress and non-stress environment. Crop Sci 21:943–946
Rossini MA, Maddonni GA, Otegui ME (2011) Interplant competition for resources in maize crops grown under contrasting nitrogen supply and density: variability in plant and ear growth. Field Crops Res 121:373–380
Sangoi L, Gracietti MA, Rampazzo C, Biachetti P (2002) Introgression of maize lethal necrosis resistance quantitative trait loci into susceptible maize populations and validation of the resistance under field conditions in Naivasha. Kenya Front Plant Sci 12:699
Sangoi L, Gracietti MA, Rampazzo C, Biachetti P (2002) Introgression of maize lethal necrosis resistance quantitative trait loci into susceptible maize populations and validation of the resistance under field conditions in Naivasha. Kenya Front Plant Sci 12:699
Siqueira AM, Tadei GM, Cárdenas CM, França VP (2001) Inheritance of resistance to stem borer in maize under low plant density. Maydica 47:202–215

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Singh RK, Chaudhary BD (2004) Biometrical methods in quantitative genetic analysis. Kalyani Publishers, New Delhi
Tokatlidis IS, Koutroubas SD (2004) A review study of the maize hybrids’ dependence on high plant populations and its implications on crop yield stability. Field Crops Res 88:103–114
Van Roekel RJ, Coulter JA (2011) Agronomic responses of corn to planting date and plant density. Agron J 103:1414–1422
Yan W, Tinker NA (2006) Biplot analysis of multi-environment trial data: principles and applications. Can J Plant Sci 86:623–645
Yan JB, Warburton ML, Crouch J (2011) Association mapping for enhancing maize (Zea mays L) genetic improvement. Crop Sci 51:433–449
Yusuf M (2010) Genetic variability and correlation in single cross hybrids of quality protein maize (Zea mays L). AJFAND 10:2166–2175

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