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Genetic Analysis for Seed Yield and Yield-Related Traits in Tepary Bean (*Phaseolus acutifolius* A. Gray) Under Drought-Stress and Non-stress Conditions

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ABSTRACT

Tepary bean (*Phaseolus acutifolius* A. Gray) is an under-utilized genetic resource with significant potential for food security and stress tolerance breeding. Expanding its cultivation in southern Africa requires high-yielding, locally adapted and drought-tolerant varieties. This study determined the combining ability and genetic components for seed yield and related traits in tepary bean genotypes under non-stress (NS) and drought-stress (DS) conditions. Seven parents were selected through rigorous phenotyping and crossed using a half-diallel design. The 7 parents and 21 F_2 progenies were evaluated in 2021/2022 season at Kasinthula and Bunda sites in Malawi under NS and DS conditions using a 4 × 7 lattice design with three replications. The specific combining ability (SCA) × location interaction effect was significant ($p < 0.05$) for DTF, NPP, and SY, suggesting that the genetic effects of crosses were influenced by the test locations. General combining ability (GCA) and SCA mean squares were significant for the number of seeds per pod (NSP) and SY under DS conditions, indicating both additive and non-additive gene effects. Baker's ratio (BR) > 0.50 for NPP and NSP under DS conditions suggested a preponderance of additive gene effects. G40145, G40148 and G40150 parental lines were good combiners for NPP and SY. The F_2 families from crosses such as Zimbabwe landrace/G40138, Zimbabwe landrace/G40150, G40059/G40145, G40059/G40148, G40138/G40150 and G40145/G40150 were identified as best specific combiners, with enhanced SY of 1.67 t/ha under DS conditions. The study recommends advancing high-performing early-generation families for selection across representative environments to facilitate variety release and commercialization.

1 | Introduction

Tepary bean (*Phaseolus acutifolius* A. Gray., 2n = 2x = 22) is a self-pollinating drought-tolerant legume crop. It is an alternative source of protein and essential nutrients for rural and resource-constrained farmers in sub-Saharan Africa (SSA) (Mwale et al. 2020). The crop is suitable for production in less fertile soils due to its ability to fix atmospheric nitrogen, thereby improving soil health in arid and semi-arid agroecologies (Mohrmann et al. 2017; Shisanya 2002). The crop is relatively highly tolerant to drought and heat stress, allowing cultivation in drought-stricken areas (Moghaddam et al. 2021; Polania et al. 2022; Porch et al. 2021). Tepary bean possesses unique genes conferring rust and common bacterial blight resistance (Barrera et al. 2020; Porch et al. 2021; Singh and Muñoz 1999; Urrea, Miklas, and Beaver 1999). These genes have been introgressed in closely related legume crops such as common bean (*Phaseolus vulgaris* L.) to develop varieties combining multiple resistance to abiotic and biotic stresses (Barrera et al. 2022; Mejía-Jiménez et al. 1994; Muñoz et al. 2004; Souter et al. 2017). Intraspecific hybrids of tepary bean were developed with high-yield potential and broad biotic and abiotic stress tolerance (Porch et al. 2021). Smallholder farmers predominantly cultivate tepary bean in SSA under unfavourable production conditions characterized by drought and heat stress and insect pests and disease pressure (Molosiwa et al. 2014). Moreover, farmers use unimproved tepary bean varieties that are low yielding due to the unavailability of improved and locally adapted genotypes (Mhlaba, Mashilo, et al. 2018; Molosiwa et al. 2014). Intermittent and terminal drought stress are reported in tepary bean production zones (Berny Miery Teran et al. 2019; White and Singh 1991). Yield losses ranging from 10% to 100% emanating from terminal drought (i.e., drought affecting the reproductive stages) have been reported in tepary bean and common bean (Polania et al. 2016a, 2016b; Rao et al. 2017), threatening sustainable production and food and nutritional security. Pre-breeding and breeding for enhanced drought tolerance in tepary beans is urgently required to deliver well-adapted and high-yielding genetic resources suited to rain-fed production environments.

Combining ability analysis is a useful quantitative genetic analysis procedure for identifying good parental genotypes and promising progenies for breeding and genetic advancement (Fasahat, Rajabi, and Derera 2015). Combining ability of genotypes is categorized into two types: general combining ability (GCA) and specific combining ability (SCA) (Sprague and Tatum 1942). The GCA refers to the parent's average performance in several hybrid combinations, whereas the SCA refers to a specific hybrid's performance that is relatively better or worse than expected based on the average performance of the parents involved (Sprague and Tatum 1942). High GCA and SCA mean squares indicate the dominance of both additive and non-additive genetic effects in parents and progenies, respectively (Fasahat, Rajabi, and Derera 2015). Previous studies assessed the combining ability effects for seed yield and related traits in soybean, cowpea, navy bean, common bean and pigeon pea (Chiipanthenga et al. 2021; Ezin et al. 2023; Mutari et al. 2022; Nkhata et al. 2021; Yohane et al. 2022). Through the combining ability analyses, the authors identified superior parents and crosses, which are valuable genetic stocks in the breeding programmes. In tepary bean, gene action conditioning the inheritance of common bean bacterial blight resistance (Drijfhout and Blok 1987; Dursun et al. 1995; Urrea, Miklas, and Beaver 1999) and rust resistance (Miklas and Stavely 1998) have been reported. Limited studies assessed the effects of combining ability on agronomic traits, including seed yield and yield-related traits under drought.

Tepary bean is re-emerging as an important food security crop in many parts of SSA, including Malawi, Botswana and South Africa. Presently, the cultivated varieties in the region are extremely low yielding, recording yields averaging approximately 0.57 t/ha (Konvalina 2016; Molosiwa, Baleseng, and Chirwa 2022). To develop new varieties with high yield potential and enhanced abiotic stress tolerance, tepary bean germplasm was acquired from the International Centre for Tropical Agriculture (CIAT) in Columbia. Preliminary studies by Mhlaba, Amelework, et al. (2018) and Mwale et al. (2023) identified parents for the improvement of agronomic traits and drought tolerance. Availability of high-yielding and locally adapted drought-tolerant varieties is a prerequisite for expanding the cultivation of tepary bean in Southern Africa and other African countries. Therefore, this study aimed to determine the combining ability effects and genetic components for seed yield and yield-related traits in parental and newly bred tepary bean genotypes under non-stress (NS) and drought-stress (DS) conditions in order to deploy superior and environmentally stable new-generation tepary beans. This will enhance the development of breeding populations and the selection of high-yielding and drought-tolerant progenies for genetic advancement, variety release and deployment in water-limited environments.

2 | Materials and Methods

2.1 | Plant Materials

Seven selected and genetically divergent tepary bean parental genotypes were used to develop the crosses in the current study. The parental genotypes were selected based on their high seed yield and variable drought tolerance (Mwale et al. 2023). The names, source of origin and levels of drought tolerance of the selected genotypes are shown in Table 1.

2.2 | Tepary Bean Population Development

The parental genotypes were grown in 10 L pots under room temperature conditions in a screen house at Chitedze Research

TABLE 1 | Names of the seven tepary bean genotypes used for drought assessment in the current study.

Code	Genotype	Origin	Description	Drought response	Reference
P1	Zimbabwe landrace	Zimbabwe	Landrace	Sensitive	Mwale et al. (2023)
P2	G40059	CIAT–Columbia	Breeding line	Moderately tolerant	Mwale et al. (2023)
P3	G40138	CIAT–Columbia	Breeding line	Very tolerant	Mwale et al. (2023)
P4	G40145	CIAT–Columbia	Breeding line	Moderately tolerant	Mwale et al. (2023)
P5	G40148	CIAT–Columbia	Breeding line	Very tolerant	Mwale et al. (2023)
P6	G40150	CIAT–Columbia	Breeding line	Very tolerant	Mwale et al. (2023)
P7	Uchokwane	South Africa	Landrace	Sensitive	Mwale et al. (2023)

Abbreviation: CIAT, International Center for Tropical Agriculture.

Station (13°85′ S and 33°38′ E; 1146 masl) in Lilongwe, Malawi, during the 2020/2021 growing season. The parents were planted at a 2-week interval for four times to synchronize flowering for hybridization. The flower bud of a female parent was gently opened using forceps; the stamens were removed, and the stigma was left exposed. The stigma on the open flower bud of a pollen plant, which was covered in pollen, was removed using forceps. The stigma covered in pollen was brushed onto the stigma of a female parent free of pollen. The pollen-bearing stigma was left attached to the stigma of a female parent. The pollinated flower was labelled using a small crossing tag. The self-pollinated flowers and pods near the pollinated flower were removed. Emasculation and hand pollination was done in the morning from 6 AM to 9 AM (Morales and Singh 1991). The parents were crossed following a 7 × 7 half-diallel mating design Method II (F_1's and parents without reciprocals) and Model I (fixed effects) to generate 21 F_1 progenies. Thereafter, the F_1 seeds were selfed to generate enough seeds for genetic analysis at the F_2 in replicated trials across two locations (Mutari et al. 2022; Nkhata et al. 2021). Genetic analysis at the F_2 generation in leguminous crops has been conducted by several breeders, including Nkhata et al. (2021) in common bean (*P. vulgaris* L.), Chiipanthenga et al. (2021) in soy bean (*Glycine max* (L.) Merrill), Mutari et al. (2022) in navy bean (*P. vulgaris* L.) and Ezin et al. (2023) in cowpea (*Vigna unguiculata* (L.) Walp). The F_2 generation constitutes considerable genetic diversity within a population, facilitating the assessment of representative number of segregating individuals with adequate generation variation. This enables more robust statistical analyses and comparisons for combining ability tests. The F_2 population represents a random sample of test genotypes with additive and non-additive genetic effects for the prediction of hybrid performance and the elucidation of the genetic architecture underlying traits.

2.3 | Experimental Design, Study Site and Trial Management

The 28 genotypes, inclusive of 7 parental lines and 21 F_2 progenies, were planted under two water regimes (NS and terminal DS) at two sites in Malawi during the 2021/2022 dry season from July to October. The study used an alpha lattice design with four incomplete blocks, each consisting of seven genotypes with three replications. The study sites were Kasinthula Agricultural Research Station (16°S and 34°5′ E; 60 masl) in Chikwawa District and the Lilongwe University of Agriculture and Natural Resources (LUANAR) Horticulture Research Farm (14°12′ S and 33°46′ E; 1200 masl) in Bunda, Lilongwe District. The average monthly temperature at LUANAR ranged from 26.8°C to 32.7°C, and it ranged from 31.71°C to 40°C at Kasinthula Agricultural Research Station. LUANAR's horticulture research farm has a loam, clay black soil type with a pH of 5.8, whereas Chikwawa's Kasinthula agricultural research station has a sandy loam soil type with a pH of 7.4. Genotypes were planted in a two-row plot measuring 3 m long and 0.75 m wide with an intra-row spacing of 0.15 m and a total plot area of 2.25 m^2. Furrow irrigation was used with approximately 35 mm of water per irrigation (80% field capacity [FC]) (Polania et al. 2017; Rao et al. 2013; Smith et al. 2019). An ML3 ThetaProbe (Delta T Devices, UK) and Chameleon soil moisture sensors (Figures S1 and S2) was used to monitor changes in soil moisture content, and the NS treatment was irrigated when the soil moisture dropped to 30% field capacity until physiological maturity. The DS treatment was imposed at the mid-pod filling stage by suspending irrigation until physiological maturity (Ambachew et al. 2015). A basal fertilizer was applied at a rate of 25 kg N/ha, 30 kg K_2O/ha and 60 kg P_2O_5/ha at both sites. Weeds, insect pests and diseases were controlled using both natural and chemical control methods following legume crop recommendations in Malawi.

2.4 | Data Collection

Data were collected for the following agronomic traits, namely, days to 50% flowering (DTF) calculated as the number of days from planting to when at least 50% of the plants in a plot had at least one flower opened; days to physiological maturity (DTM) calculated as the number of days from planting to when 90% of the pods in the plot changed colour from green to yellow or beige; and the number of pods per plant (NPP) recorded as the average count of the number of pods on 10 randomly selected and tagged plants in a plot at harvest (IBPGR [International Board for Plant Genetic Resources] 1985). The number of seeds per pod (NSP) were counted from 10 randomly selected pods from the 10 plants in a plot at harvest and expressed as an average. The crop was harvested per plot when it attained physiological maturity. The seed yield weight per plot was later adjusted for 14% moisture content and converted to kilograms per hectare, according to Parker and Namuth-Covert (2017).

2.5 | Statistical Analysis

2.5.1 | Analysis of Variance

The agronomic data collected from each location was subjected to an analysis of variance (ANOVA) using the Genstat software, 18th Edition (Payne, Murray, and Harding 2017). The homogeneity of variance was assessed through Bartlett's (1973) test prior to subjecting the agronomic data to a combined ANOVA. Trait entry means were compared through the least significant difference (LSD) at the 5% significance level (Cochran and Cox 1992). The linear model used for data analysis across locations for each water condition (i.e., NS and DS conditions) based on the restricted maximum likelihood (REML) procedure:

$$\mathrm{Yijkl} = \mu + \mathrm{Li} + \mathrm{rjLi} + \mathrm{BkrjLi} + \mathrm{gl} + \mathrm{gLli} + \mathrm{eijkl},$$

where Yijkl is the trait of focus; μ is the general population mean; Li, location effect; rjLi is replication nested in locations; BkrjLi is blocks nested in replication and locations; gl and gLli are genotype and genotype by location interaction effects, respectively; and eijkl is the lattice pooled error.

2.5.2 | Combining Ability and Gene Action

GCA of parents and SCA of crosses was estimated based on Griffing's method II (F1's and parents) and model I (fixed effects) (Dabholkar 1992; Griffing 1956) using AGD-R software Version 4.0 (Rodríguez et al. 2015) in line with the following statistical linear model:

$$\mathrm{Yijkpm} = \mu + \mathrm{gi} + \mathrm{gj} + \mathrm{sij} + \mathrm{giLk} + \mathrm{gjLk} + \mathrm{sijLk} + \mathrm{Lk} + \mathrm{rpLk} + \mathrm{BmLkrp} + \mathrm{eijkpm},$$

where Yijkpm is the observed value; μ is the general population mean; gi and gj is the GCA effects of ith and jth parents, respectively; sij is the SCA effect of the cross between parent i and parent j; gLik and gLjk is the interaction effect between GCA of ith and jth parents and the kth location, respectively; sLijk is the interaction effect between the SCA of the ith and jth parents and the kth location; Lk is the location effect; rkLi is replication nested in locations; BlLirk is blocks nested in replication and locations; and eijkpm is the pooled error. Combining ability analysis is undertaken after ANOVA reveals the significance of GCA and SCA effects, as well as the variance components. Genetic effects were estimated using the fixed effects model, given that a fixed number of desirable parents were purposively selected for the crosses. The test parents were selected for their superior agronomic performance and drought tolerance (Mwale et al. 2023).

A Student *t*-test was used to determine the statistical significance of parents' GCA effects and crosses' SCA effects. Baker's ratio (BR) was used to calculate the gene action for the trait as follows: $2\,\sigma^2$ GCA/($2\,\sigma^2$ GCA + σ^2 SCA) (Baker 1978). BR exemplifies the relative importance of additive or non-additive genetic effects in a trait, with a less than 50% value indicating the dominance of non-additive gene effects. BR values greater than 50% implies the preponderance of additive gene effects. Drought tolerance indices, including the drought intensity index (DII), percent seed yield reduction (%SYR), drought susceptibility index (DSI), geometric mean productivity (GMP) and drought tolerance index (DTI) for each tepary bean genotype, were computed as outlined by Mutari et al. (2022). Tepary bean genotypes exhibiting low values for %SYR and DSI and high values for DTI and GMP were classified as drought tolerant (Mutari et al. 2023). Pearson correlation analysis was used to elucidate the relationships between seed yield and drought tolerance indices. The correlations were visualized using a chord diagram, created with the corrplot and circlize packages (Gu et al. 2014; Wei et al. 2017). This chord diagram was constructed from a correlation matrix and employs colour to indicate the strength of the correlations. The colour gradient within the chord diagram represents the numerical values of the correlations, whereas the labels positioned outside the diagram denote the different indices.

3 | Results

3.1 | ANOVA

ANOVA revealed that the genotype × location interaction effect was significant ($p < 0.05$) for all the assessed traits under the NS condition except NSP (Table 2). Under the DS condition, the genotype × location interaction effect was significant ($p < 0.05$) for DTF, NPP and SY. The test location mean squares varied significantly ($p < 0.05$) for all the assessed traits under both NS and DS conditions except NPP under NS condition. The mean squares for genotypes varied significantly ($p < 0.05$) for all the evaluated traits under both NS and DS conditions.

3.2 | Combining Ability Analysis

The mean squares for combining ability analysis and BR for the assessed agronomic traits are presented in Table 3. The

TABLE 2 | Mean squares and significance tests for agronomic traits of seven tepary bean parents and 21 F_2 progenies evaluated under both non-stress (NS) and drought-stress (DS) conditions in two locations in Malawi.

		DTF		DTM		NPP		NSP		SY	
SOV	**DF**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**
Location (LOC)	1	12.05**	72.02***	3790.50***	4250.15***	0.45ns	1965.75***	4.67***	8.24***	824,578.90***	1,056,223.00***
REP (LOC)	4	0.89ns	3.54*	1.41ns	17.21ns	0.36ns	5.09ns	0.49*	0.06ns	289.90ns	657,95.00ns
BLOCK.REP.LOC	18	3.36***	3.39***	36.99***	16.63ns	72.65***	13.55***	0.60***	0.39ns	25,1126.10***	428,554.00***
Genotype	27	9.03***	6.03***	56.70***	31.88*	267.61***	64.21***	1.84***	1.26***	1,444,681.90***	1,085,094.00***
Genotype × LOC	27	3.93***	5.20***	54.66***	18.65ns	30.93***	18.86***	0.23ns	0.22ns	125,800.90***	114,966.00*
Error	90	1.16	1.39	3.00	17.80	1.58	2.37	0.19	0.28	327.30	57,327.00

Abbreviations: DF, degrees of freedom; DTF, days to 50% flowering; DTM, days to 90% physiological maturity; LOC, location; NPP, number of pods per plant; ns, non-significant; NSP, number of seeds per pod; REP, replication; SY, seed yield in kg ha^{-1}.
*$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$.

TABLE 3 | Mean squares of general combining ability (GCA) and specific combining ability (SCA) and significance tests for agronomic traits of seven tepary bean parents and 21 F_2 progenies evaluated under both non-stress (NS) and drought-stress (DS) conditions in two locations in Malawi.

		DTF		DTM		NPP		NSP		SY	
SOV	**DF**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**
Location	1	12.05**	64.93***	3790.50***	4250.15***	0.42ns	1491.16***	4.36***	8.24***	824,578.85***	884,450.27***
REP (Location)	4	0.89ns	3.19***	1.40ns	17.21ns	0.34***	3.87***	0.46***	0.06ns	289.95ns	55,094.88***
Cross	27	10.66*	7.19ns	67.87ns	34.73ns	310.10***	68.96**	2.11***	1.44***	1,600,487.07***	1,285,759.70***
GCA	6	15.70ns	9.52ns	19.92ns	33.45ns	785.32***	240.44***	2.07ns	5.29***	3,727,881.99**	2,754,407.55*
SCA	21	9.22ns	6.64ns	81.57ns	35.09ns	176.98**	22.30ns	2.14***	0.33***	992,659.95***	912,935.04***
Location × Cross	27	4.13***	5.07***	67.07***	19.83ns	33.48***	19.65***	0.19ns	0.20ns	137,275.15***	114,763.28*
GCA × Location	6	2.51ns	10.14*	92.89ns	6.83ns	13.26ns	30.92ns	0.12ns	0.22ns	84,926.91ns	159,747.59ns
SCA × Location	21	4.59***	3.66**	59.69***	23.54ns	39.43***	17.03***	0.21ns	0.20ns	152,231.80***	103,846.65*
Residual	90	1.07	1.41	2.78	16.60	1.55	2.31	0.20	0.26	307.23	57,466.67
GCA:SCA		0.20	0.17	0.02	0.10	0.50	1.32	0.11	7.37	0.42	0.35
Baker's ratio (BR)		0.29	0.26	0.05	0.17	0.50	0.73	0.18	0.94	0.45	0.41

Abbreviations: DF, degrees of freedom; DTF, days to 50% flowering; DTM, days to 90% physiological maturity; NPP, number of pods per plant; NSP, number of seeds per pod; ns, non-significant; NSH, narrow sense heritability; REP, replication; SOV, source of variation; SY, seed yield in kg ha^{-1}; V.GCA, variance general combining ability; V.SCA, variance specific combining ability.
*$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$.

GCA × Location interaction effect was statistically significant ($p < 0.05$) for DTF under DS condition. The SCA × Location interaction effect was significant ($p < 0.05$) for DTF, DTM, NPP and SY under NS condition. Under DS condition, SCA × Location effect was significant ($p < 0.05$) for D, NPP and SY. The GCA mean squares were significant ($p < 0.05$) for NPP and SY under NS condition. Under DS condition, the GCA mean squares were significant ($p < 0.05$) for NPP, NSP and SY. SCA mean squares varied significantly ($p < 0.05$) for NPP, NSP and SY under NS condition and NSP and SY under DS condition. The relative importance of additive and non-additive gene effects conditioning the agronomic traits was assessed through a BR. The BR was above 0.50 and high for NPP and NSP under DS condition. The BR was moderate for SY under both NS and DS conditions and at 0.50 for NPP under NS condition.

3.3 | Performance of Parents and F_2 Progenies for the Assessed Traits

The mean performances of parental genotypes and F_2 progenies for the evaluated traits under NS and DS conditions are presented in Table 4. The earliest flowering genotypes were G40059 (29 days), G40148 (30 days), G40145 and G40138 (31 days) under NS condition. Under NS condition, parental genotypes Uchokwane, Zimbabwe landrace and G40150 were late flowering, recording 32, 33 and 33 days. Genotype G40148 and G40145 were the earliest genotypes to mature in 75 and 76 days under NS condition, respectively. The highest NPP of 30 and 35 were recorded by G40138, G40145, and G40148 under NS condition. G40148 recorded the highest seed yield of 2126 kg ha^{-1} followed by G40159 (1773 kg ha^{-1}), G40138 and G40145 (1666 kg ha^{-1}).

DS reduced the maturity period of most genotypes under DS conditions, with the following being the earliest maturing genotypes: G40148 (67 days), Zimbabwe landrace, and G40138 (70 days). Under DS condition, the highest NPP was recorded for G40150 (18), G40059 (18), G40145 (19), and G40148 (20). Uchokwane landrace produced the highest NSP (6) followed by G40150, G40138 and G40059, each producing 5 seeds per pod under DS condition. For SY, the genotype G40150 recorded a value of 1452 kg ha^{-1} followed by G40148 (1351 kg ha^{-1}), G40059 (954 kg ha^{-1}), G40145 (846 kg ha^{-1}) and G40138 (781 kg ha^{-1}) under DS condition.

For the F_2 progenies, the earliest progenies to flower were G40148/G40150 (28 days), G40059/G40148 (29 days), G40138/G40145 (29 days), and G40145/G40148 (29 days) under NS condition. The following F_2 progenies were the earliest in attaining physiological maturity; Zimbabwe landrace/G40059 (68 days), G40138/G40150 (70 days), G40059/G40150 (71 days), and G40148/G40150 (71 days) under NS condition. The highest NPP in F_2 progenies was recorded by G40145/G40150 (31) and G40145/G40148 (34) under NS condition. The highest seed yield of 2211 kg ha^{-1} and 2468 kg ha^{-1} under NS condition in F_2 progenies was exhibited by G40145/G40150 and G40145/G40148.

The NPP under DS condition was highest for Zimbabwe landrace/G40150 (20) and Zimbabwe landrace/G40148 (21), and was lowest for Zimbabwe landrace/G40059 (9) and G40148/Uchokwane (9). Under DS condition SY exceeding 1700 kg ha^{-1} were recorded for G40138/G40150, G40145/G40150, Zimbabwe landrace/G40150, G40059/G40145, and G40059/G40138.

3.4 | DS Indices

The DS indices based on seed yield under NS and DS conditions are presented in Table 5. The DS severity effect on seed yield of the evaluated tepary bean genotypes across two locations, as represented by the DII, was moderate at 0.20. The genotypes G40150, Zimbabwe landrace/G40138, G40059/G40138 and G40059/G40145 were less sensitive to DS, as shown by their low DSI and %SYR, whereas tepary bean genotypes G40148, Zimbabwe landrace/G40138, Zimbabwe landrace/G40145, Zimbabwe landrace/G40148, Zimbabwe landrace/G40150, G40059/G40145, G40059/G40148, G40059/G40150, G40138/G40148, G40138/G40150, G40138/Uchokwane, G40145/G40148, G40145/G40150 and G40148/G40150 exhibited high DTI of > 1 and GMP values ranging from 1695 to 2054.

The correlation coefficients between seed yield under NS and DS conditions and drought tolerance indices are illustrated in Figure 1. Seed yield under non-stress (SYNS) conditions displayed a strong positive correlation ($r = 0.74$, $p < 0.001$) with seed yield under drought stress (SYDS). Both SYNS and SYDS exhibited significant positive correlations with GMP and DTI ($r = 0.92$, 0.89 and $r = 0.94$, 0.94, respectively; $p < 0.001$). Notably, GMP had a strong positive correlation with DTI ($r = 0.99$, $p < 0.001$), whereas %SYR showed a perfect and significant positive correlation with DSI ($r = 1.00$, $p < 0.001$). Conversely, SYDS was negatively and significantly correlated with DSI and %SYR ($r = -0.47$, $p < 0.05$).

3.5 | GCA Effects of Parents for Agronomic Traits

The estimates of GCA effects of 7 parents for the assessed agronomic traits are presented in Table 6. Parental genotypes G40059 (P2) and G40138 (P3) had high negative significant GCA effects for DTF and DTM, whereas G40150 (P6) had significant positive GCA effects for DTF and DTM under NS condition. The parental genotypes G40059 (P2), G40138 (P3), G40145 (P4), G40148 (P5) and G40150 (P6) exhibited desirable positive GCA effects for NPP and SY under NS condition. Under DS condition, parental genotype G40148 (P5) showed significant negative GCA effects for DTF and DTM, whereas parental genotype G40145 exhibited significant positive GCA effects for DTF and DTM. Parental genotypes G40145, G40148 and G40150 exhibited desirable significant positive GCA effects for NPP and SY.

3.6 | SCA Effects of Crosses for Agronomic Traits

Under NS condition, G40148/Uchokwane cross recorded positive and significant SCA effect for DTF, whereas crosses G40145/G40148, G40148/G40150 and Zimbabwe landrace/G40059 registered positive and significant SCA effects for DTM (Table 7). Crosses Zimbabwe landrace/Uchokwane, G40059/G40138, G40138/G40145 and G40138/G4015

TABLE 4 | Mean performance of seven parental tepary bean lines and 21 F_2 progenies for five agronomic traits evaluated under non-stress (NS) and drought-stress (DS) conditions in two locations.

	DTF		DTM		NPP		NSP		SY	
Genotypes	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**
Zimbabwe landrace	33	30	79	70	12	12	6	4	536	473
G40059	29	32	81	72	29	18	5	5	1773	954
G40138	31	31	80	70	30	15	5	5	1666	781
G40145	31	31	76	71	30	19	5	4	1666	846
G40148	30	32	75	67	35	20	4	5	2126	1351
G40150	33	29	83	71	25	18	6	5	1429	1452
Uchokwane	32	31	79	70	15	11	5	6	644	451
Zimbabwe landrace/G40059	30	30	68	75	24	9	5	5	1744	1239
Zimbabwe landrace/G40138	30	32	75	70	20	17	5	5	1613	1673
Zimbabwe landrace/G40145	32	33	72	71	25	19	5	5	1738	1669
Zimbabwe landrace/G40148	30	31	74	71	25	21	5	5	1691	1536
Zimbabwe landrace/G40150	30	30	76	72	29	20	4	4	2178	1927
Zimbabwe landrace/ Uchokwane	30	31	76	68	14	17	5	5	777	767
G40059/G40138	31	31	78	72	24	18	5	5	1569	2017
G40059/G40145	31	31	75	75	26	18	5	5	1850	1989
G40059/G40148	29	30	72	68	26	17	5	5	2053	1670
G40059/G40150	31	31	71	68	29	18	5	5	1946	1554
G40059/Uchokwane	32	33	76	72	14	13	5	6	1133	993
G40138/G40145	29	31	79	72	22	19	5	5	1741	1263
G40138/G40148	31	31	73	70	29	18	5	5	2097	1381
G40138/G40150	31	29	70	68	23	17	4	5	1795	1763
G40138/Uchokwane	34	31	74	69	13	11	6	6	1166	815
G40145/G40148	29	31	73	70	34	18	5	4	2468	1595
G40145/G40150	30	31	72	74	31	19	5	5	2203	1916
G40145/Uchokwane	32	34	77	75	14	12	6	5	1226	934
G40148/G40150	28	29	71	73	30	19	4	5	2211	1302
G40148/Uchokwane	30	32	76	68	14	9	6	6	871	680
G40150/Uchokwane	31	31	76	68	13	12	6	6	911	953
Grand mean	31	31	75	71	24	16	5	5	1601	1284
LSD $_{(5\%)}$	1.91	2.09	3.07	7.48	2.23	2.73	0.78	0.93	32.07	424.50
CV%	3.47	3.80	2.30	5.94	5.24	9.62	8.72	10.58	1.13	18.65

Abbreviations: CV%, coefficient of variation; DTF, days to 50% flowering; DTM, days to 90% physiological maturity; LSD, least square of the difference; NPP, number of pods per plant; NSP, number of seeds per pod; SY, seed yield in kilogram per hectare.

recorded negative and significant SCA effects for DTF and DTM under NS condition. Furthermore, crosses Zimbabwe landrace/G40145, Zimbabwe landrace/G40148, Zimbabwe landrace/G40150, G40059/G40138, G40059/G40145, G40059/G40150 and G40145/G40148 had positive and significant SCA effects for NPP. Additionally, crosses Zimbabwe landrace/G40138, Zimbabwe landrace/G40145, Zimbabwe landrace/G40148, Zimbabwe landrace/G40150, Zimbabwe landrace/Uchokwane, G40059/G40138, G40059/G40145, G40059/G40150, G40138/G40145, G40138/G40148 and G40138/

TABLE 5 | Drought tolerance indices derived from seed yield under non-stress (NS) and drought-stress (DS) conditions of seven parental tepary bean lines and 21 F_2 progenies evaluated in two locations in Malawi.

	Seed Yield		Drought Tolerance Indices			
Genotypes	**NS**	**DS**	**DSI**	**GMP**	**DTI**	**%SYR**
Zimbabwe landrace	536	473	0.59	503.52	0.10	11.75
G40059	1773	954	2.33	1300.55	0.66	46.19
G40138	1666	781	2.68	1140.68	0.51	53.12
G40145	1666	846	2.49	1187.20	0.55	49.22
G40148	2126	1351	1.84	1694.76	1.12	36.45
G40150	1429	1452	−0.08	1440.45	0.81	−1.61
Uchokwane	644	451	1.51	538.93	0.11	29.97
Zimbabwe landrace/G40059	1744	1239	1.46	1469.97	0.84	28.96
Zimbabwe landrace/G40138	1613	1673	−0.19	1642.73	1.05	−3.72
Zimbabwe landrace/G40145	1738	1669	0.20	1703.15	1.13	3.97
Zimbabwe landrace/G40148	1691	1536	0.46	1611.64	1.01	9.17
Zimbabwe landrace/G40150	2178	1927	0.58	2048.66	1.64	11.52
Zimbabwe landrace/Uchokwane	777	767	0.06	771.98	0.23	1.29
G40059/G40138	1569	2017	−1.44	1778.95	1.23	−28.55
G40059/G40145	1850	1989	−0.38	1918.24	1.44	−7.51
G40059/G40148	2053	1670	0.94	1851.62	1.34	18.66
G40059/G40150	1946	1554	1.02	1738.99	1.18	20.14
G40059/Uchokwane	1133	993	0.62	1060.69	0.44	12.36
G40138/G40145	1741	1263	1.39	1482.86	0.86	27.46
G40138/G40148	2097	1381	1.72	1701.75	1.13	34.14
G40138/G40150	1795	1763	0.09	1778.93	1.23	1.78
G40138/Uchokwane	1166	815	1.52	974.83	0.37	30.10
G40145/G40148	2468	1595	1.79	1984.05	1.54	35.37
G40145/G40150	2203	1916	0.66	2054.49	1.65	13.03
G40145/Uchokwane	1226	934	1.20	1070.09	0.45	23.82
G40148/G40150	2211	1302	2.08	1696.68	1.12	41.11
G40148/Uchokwane	871	680	1.11	769.60	0.23	21.93
G40150/Uchokwane	911	953	−0.23	931.76	0.34	−4.61
Grand mean	1601	1284				

Abbreviations: %SYR, percent seed yield reduction; DSI, drought susceptibility index; DTI, drought tolerance index; GMP, geometric mean productivity.

G40150 exhibited desirable positive and significant SCA effects for SY.

Under DS condition, crosses G40059/G40150 and G40059/Uchokwane had negative and significant SCA effects for DTM, whereas Zimbabwe landrace × Uchokwane and G40059/G40138 exhibited positive and significant SCA effects for DTM. Under DS condition, crosses Zimbabwe landrace/G40138, Zimbabwe landrace/G40145 and Zimbabwe landrace/G40148 showed desirable positive and significant SCA effects for NPP. Additionally, crosses Zimbabwe landrace/G40059, Zimbabwe landrace/G40138, Zimbabwe landrace/G40150, G40059/Uchokwane, G40059/G40145, G40059/G40148, G40138/G40145, G40138/G40150, G40148/G40150 and G40145/G40150 recorded desirable positive and significant SCA effects for seed yield.

4 | Discussion

The moderate DS level of 0.20, revealed by the DII, highlighted genotypic variations among the tested tepary bean genotypes, facilitating effective selection. Also, there were differential responses among the test genotypes for assessed traits. Previous studies by Mutari et al. (2023) and Darkwa et al. (2016) on common beans, as well as Rao et al. (2013) and Souter et al. (2017) on tepary beans, highlighted the use of moderate DS in genotype selection. The evaluated genotypes showed significant variation for days to 50% flowering, days to 90% physiological maturity, number of pods per plant, number of seeds per pod and seed yield. Trait differences indicate considerable genetic diversity among the parental lines and crosses, which is crucial for selection and accelerated genetic gains in breeding programmes (Varshney et al. 2018).

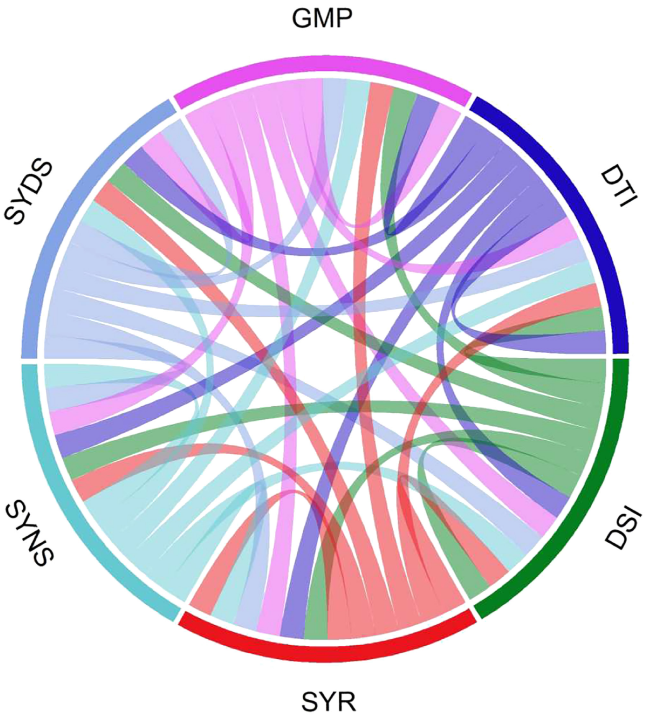

FIGURE 1 | Chord diagram based on correlation coefficients between seed yield under non-stress and drought-stress conditions and drought tolerance indices for 28 tepary bean genotypes evaluated across two locations in Malawi. % SYR, percent seed yield reduction; DSI, drought susceptibility index; DTI, drought tolerance index; GMP, geometric mean productivity; SYDS, seed yield under drought stress; SYNS, seed yield under non-stress.

Our study highlights that the tested genotypes are amenable to selection for early maturity, a higher number of pods and increased seed yield under drought stress. Due to their strong positive correlation, effective selection under both NS and DS conditions should focus on genotypes with high values for GMP and DTI. Genotypes exhibiting high GMP and DTI values exceeding 1 include G40145/G40150, Zimbabwe landrace/G40150, G40145/G40148, G40059/G40145, G40059/G40148, G40059/G40138, G40138/G40150, G40059/G40150, Zimbabwe landrace/G40145, G40138/G40148, G40148/G40150, G40148, Zimbabwe landrace/G40138 and Zimbabwe landrace/G40148.

Conversely, five genotypes demonstrated reduced sensitivity to DS, evidenced by negative values for DSI and %SYR. The superior performance of these genotypes under DS compared to NS conditions indicates that the genetic mechanisms responsible for achieving high seed yield under drought differ from those in NS environments (Mutari et al. 2023). This agrees with the findings of Hamabwe et al. (2023), who evaluated 155 derived recombinant inbred lines (RILs) and their parental lines in common beans. The authors identified four specific quantitative trait loci (QTL) associated with enhanced SYDS. These QTL were located on chromosomes 6, 7 and 10 and demonstrated consistent expression across various genotypes and environments. These findings underscore the conservation and expression of novel QTL under drought conditions, suggesting their potential utility in marker-assisted selection programmes. Darkwa et al. (2016) and Mutari et al. (2023) reported analogous findings in their assessments of drought

TABLE 6 | Estimates of general combining ability effects for agronomic traits of seven parental lines of tepary beans evaluated in two locations under non-stress (NS) and drought-stress (DS) conditions in Malawi.

	DTF		DTM		NPP		NSP		SY	
Parent	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
Zimbabwe landrace	0.31*	−0.24ns	−0.08ns	−0.08ns	−2.87***	−0.48*	−0.06ns	−0.30**	−221.43***	−51.01ns
G40059	−0.74***	−0.17ns	−0.39*	−0.03ns	1.07***	0.86**	−0.03ns	0.03ns	64.70***	95.62**
G40138	−0.57**	0.17ns	−0.39*	−0.68ns	2.99***	0.23ns	−0.10*	−0.14*	202.74***	−65.79*
G40145	−0.07ns	0.27*	−0.25ns	1.49*	2.66***	1.60***	−0.08ns	−0.20**	194.68***	93.24**
G40148	−0.13ns	−0.37*	−0.45*	−0.92*	2.18***	1.44***	−0.23**	−0.17*	167.76***	62.29*
G40150	0.50**	−0.41*	1.24***	−0.18ns	1.39***	0.86**	0.11*	0.14*	87.68***	299.14***
Uchokwane	0.70***	0.75***	0.33ns	0.40ns	−7.43***	−4.51***	0.38***	0.63***	−496.14***	−433.49***
SEM	0.09	0.11	0.15	0.36	0.11	0.14	0.04	0.05	1.56	21.36

Abbreviations: DTF, days to 50% flowering; DTM, days to 90% physiological maturity; NPP, number of pods per plant; ns, non-significant; NSP, number of seeds per pod; SEM; Standard error of the mean; SY, seed yield in kg ha^{-1}.
*$p<0.05$, **$p<0.01$, and ***$p<0.001$.

TABLE 7 | Estimates of specific combining ability effects for agronomic traits of 21 F_2 progenies of tepary beans evaluated in two locations under non-stress (NS) and drought-stress (DS) conditions in Malawi.

	DTF		DTM		NPP		NSP		SY	
F_2 families	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**
Zimbabwe landrace/G40059	−0.12ns	0.62ns	1.51*	−0.86ns	−8.36***	0.43ns	−0.18	0.12ns	−666.01***	294.30**
Zimbabwe landrace/G40138	−0.28ns	1.93***	0.51ns	1.29ns	−3.24***	3.02***	0.12	0.03ns	28.32***	420.65***
Zimbabwe landrace/G40145	1.22**	−0.14ns	−2.64***	−1.37ns	2.21***	2.81***	−0.37	0.26ns	166.51***	162.84ns
Zimbabwe landrace/G40148	−1.39**	−0.53ns	−0.77ns	2.87ns	2.30***	2.67***	0.08	0.06ns	142.54***	−305.75**
Zimbabwe landrace/G40150	−1.36**	0.36ns	0.05ns	−1.87ns	6.55***	0.22ns	−0.79	0.02ns	713.15***	430.71***
Uchokwane/Zimbabwe landrace	−1.39**	−1.62**	−7.05***	3.22*	11.18***	−2.33***	−0.82	−0.54*	866.14***	−30.68ns
G40059/G40138	−0.89*	−1.64**	−4.01***	3.40*	2.80***	1.19*	−0.58	−0.14ns	337.69***	−72.53ns
G40059/G40145	0.11ns	0.10ns	−2.49**	1.57ns	3.57***	0.25ns	−0.2	−0.14ns	346.02***	483.87***
G40059/G40148	0.50ns	−1.26*	−4.29***	−2.19ns	−3.86***	−1.13ns	−0.45	0.12ns	−37.46***	331.61**
G40059/G40150	0.20ns	0.30ns	−5.31***	−3.26*	3.49***	0.28ns	−0.05	0.05ns	195.66***	−75.34ns
G40059/Uchokwane	0.33ns	−0.54ns	1.27ns	−3.17*	−4.04***	−0.41ns	0.83	0.00ns	−263.13***	193.50*
G40138/G40145	−1.06*	−0.09ns	−1.49*	−0.45ns	5.18***	0.38ns	0.07	−0.04ns	466.57***	305.92**
G40138/G40148	0.66ns	−0.59ns	−1.45*	0.79ns	0.48ns	0.25ns	−0.05	−0.01ns	124.38***	46.06ns
G40138/G40150	−1.47**	−0.89ns	−3.81***	−1.95ns	−1.79**	0.05ns	−0.18	−0.31ns	165.51***	483.65***
G40138/Uchokwane	−0.50ns	0.60ns	0.94ns	−2.86ns	−5.39***	−2.34***	0.62	0.14ns	−437.49***	−120.28ns
G40145/G40148	−1.34**	0.62ns	3.73***	0.96ns	−5.89***	0.43ns	−0.04	0.02ns	−226.91***	−166.24ns
G40145/G40150	0.20ns	0.17ns	−1.12ns	2.72ns	−1.42*	−0.81ns	−0.01	−0.25ns	−31.48***	328.09**
G40145/Uchokwane	0.33ns	1.68*	1.95**	2.81ns	−5.66***	−1.55*	0.72	0.16ns	−71.27***	0.50ns
G40148/G40150	−0.41ns	0.00	1.92**	2.12ns	−2.54***	−0.76ns	−0.03	−0.38ns	−283.51***	395.09***
G40148/Uchokwane	2.88***	−0.18	−1.34*	−0.62ns	−5.02***	−2.21**	1.00	0.40*	−103.85***	−92.50ns
G40150/Uchokwane	−0.41ns	1.36	−0.53ns	1.14ns	−2.89***	0.77ns	−0.07	0.23ns	−60.02***	−380.69***
SEM	0.38	0.43	0.61	1.49	0.46	0.56	0.16	0.19	6.42	87.84

Abbreviations: DTF, days to 50% flowering; DTM, days to 90% physiological maturity; NPP, number of pods per plant; ns, non-significant; NSP, number of seeds per pod; SEM; standard error of the mean; SY, seed yield in kg ha^{-1}.
*$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$.

tolerance levels in common beans and navy beans, respectively. Genotypes with high seed yields ($>1400\,\mathrm{kg\,ha^{-1}}$) and minimal yield reductions ($<20\%$) under DS, include G40150, Zimbabwe landrace/G40148, Zimbabwe landrace/G40145, G40059/G40148, Zimbabwe landrace/G40138, G40138/G40150, G40145/G40150, Zimbabwe landrace/G40150, G40059/G40145 and G40059/G40138.

The phenotypic expression of a trait is determined by both genotypic and environmental factors (Acquaah 2007; Falconer and Mackay 1996). Conventionally, the influence of environmental factors is more dominant in quantitative traits such as seed yield (Falconer and Mackay 1996; Kayaga et al. 2017). The significant environmental effects observed for most of the assessed agronomic traits in the current study imply that the performance of the tested genotypes was different in the two environments. Significant mean squares for genotype-by-environment interaction were observed for most of the assessed traits, except for the number of seeds per pod under both NS and DS conditions, as well as days to 90% physiological maturity under DS condition (Table 2). This signified that the performance of the tested genotypes was not consistent across environments. More location and season testing is required to ably account for the magnitude of genotype-by-environment effects for these agronomic traits in the assessed genotypes.

Combining ability analysis is useful for selecting good parental genotypes for breeding and the genetic advancement of promising crosses (Sprague and Tatum 1942). The GCA is mostly associated with additive gene effects, whereas the SCA with non-additive gene effects (Sprague and Tatum 1942). The significant mean squares for GCA for number of seeds per pod under DS conditions and number of pods per plant and seed yield under both NS and DS conditions (Table 3) implied that additive gene effects contributed to the overall genetic control of these traits. The mean squares for SCA for number of pods per plant under NS condition and number of seeds per pod and seed yield under both NS and DS conditions were significant (Table 3), signifying that non-additive gene effects were involved in the genetic control of these traits. The SCA effects of the families were environment-specific, as revealed by significant SCA × Location interaction effects for days to 50% flowering, number of pods per plant and seed yield under both NS and DS conditions (Table 3). This suggests that the selection of crosses with SCA effects in the right direction would be useful and enhance genetic gains.

The high BR for number of pods per plant and number of seeds per pod under DS conditions suggests that additive gene action was more predominant in the expression of these traits. Thus, the performance of the crosses could be predicted from the parent's GCA effects. On the contrary, moderate to low BR for days to maturity and seed yield under the DS condition suggests the preponderance of non-additive gene effects, which are mostly due to dominance and epistatic genetic effects (Fasahat, Rajabi, and Derera 2015; Mwadzingeni, Shimelis, and Tsilo 2018). The implication of this in plant breeding programmes is that more crosses should be generated from divergent parental lines as the performance of these crosses cannot be readily determined from their parents' GCA effects.

The parental genotypes G40145, G40148 and G40150 were good general combiners for the number of pods per plant and seed yield under both NS and DS conditions. This implies that these parental genotypes are effective in passing useful genes for increasing the number of pods per plant and seed yield to their progenies (Table 6). These genotypes would be useful progenitors in tepary bean breeding programmes targeting improvements in the number of pods per plant and seed yield. G40059, G40138 and G40148 recorded negative GCA effects for days to 90% physiological maturity and are therefore useful progenitors for breeding programmes targeting early maturity. F_2 families Zimbabwe landrace/G40145, Zimbabwe landrace/G40148, G40059/G40138, G40059/G40145 and G40059/G40150 exhibited desirable positive SCA effects for number of pods per plant and SYNS condition. This implies that these cross combinations had a superior performance greater than what was predicted by their GCA effects of their parents (Ezin et al. 2023) and therefore are recommended for selection, genetic advancement and variety release for rainfall or irrigation dependent farming.

SCA results from dominance and/or gene interaction between additive and additive gene effects and is defined as the performance of a specific cross combination compared to what its parents' GCA effects predict (Sprague and Tatum 1942). Under water deficit conditions, F_2 families G40059/G40150 and G40059/Uchokwane had negative and significant SCA effects for days to 90% physiological maturity (Table 7). The significant SCA effects suggest that the segregating F_2 generation displays a dominant genetic effect needing continuous selfing to select homozygous and homogenous pure-line individuals with additive genetic effects. This suggests the occurrence of drought escape mechanisms in these crosses, which results in reduced net water requirements. Breeding for an increased number of pods per plant under water deficit conditions should target the following F_2 families: Zimbabwe landrace/G40138, Zimbabwe landrace/G40145 and Zimbabwe landrace/G40148, as they recorded desirable positive and significant SCA effects. Future genetic selection and genetic advancement to enhance SYDS conditions should prioritize the following crosses: Zimbabwe landrace/G40059, Zimbabwe landrace/G40138, Zimbabwe landrace/G40150, G40059/Uchokwane, G40059/G40145, G40059/G40148, G40138/G40145, G40138/G40150, G40148/G40150 and G40145/G40150.

The high SCA effect of these progenies for seed yield was possibly due to non-additive gene interactions, which are highly unpredictable and challenging for hybrid development in leguminous crops (Nkhata et al. 2021). But the large SCA effects can be thoroughly exploited through heterotic group breeding via the selection of good parental lines to be used for hybrid development (Napolitano et al. 2020; Nkhata et al. 2021: Mutari et al. 2022).

5 | Conclusions

This study determined the combining ability effects and gene action conditioning the inheritance of seed yield and yield-related traits among tepary bean genotypes. Parental genotypes designated as G40145, G40148 and G40150 were good general combiners for number of pods per plant and seed yield under both NS and DS conditions and would be useful parents in tepary bean breeding programmes. The F_2 families derived from Zimbabwe landrace/G40138, Zimbabwe landrace/G40150, G40059/G40145, G40059/G40148, G40138/G40150 and G40145/G40150 were good specific combiners for seed yield providing $>1600\,\text{kg}\,\text{ha}^{-1}$ under DS conditions. These F_2 families are recommended for further selection, genetic advancement and variety release.

Author Contributions

Conceptualization: S.E.M., H.S. and J.M. Methodology: S.E.M. Software: S.E.M. and W.N. Validation: S.E.M., H.S., W.N. and J.M. Formal analysis: S.E.M. and W.N. Investigation: S.E.M. Resources: S.E.M. and H.S. Writing – review and editing: S.E.M., H.S., W.N., A.S., I.F. and J.M. Supervision: H.S. All authors have read and agreed to the published content of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The dataset for the work is included in the article/Supporting Information; any further questions should be directed to the corresponding author.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.