Diallel analysis for seed yield and yield-related traits in tepary bean (Phaseolus acutifolius A. Gray) under non-stress and drought-stress conditions

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Abstract

Tepary bean (***Phaseolus acutifolius A. Gray***) cultivation is not expansive in Southern Africa due to the unavailability of high-yielding and locally adapted varieties. To deliver well-adapted and new-generation tepary beans in Africa, pre-breeding and breeding of drought tolerant and high-yielding varieties is a critical need. Therefore, the objective of this study was to determine the combining ability effects and genetic components for seed yield and yield-related traits in selected tepary bean genotypes under non-stressed (NS) and drought-stressed (DS) conditions. Seven parents and 21 F_2 progenies derived from a half-diallel design were evaluated at two sites in Malawi under NS and DS conditions using a 4 × 7 lattice design with three replications. The genotype × location interaction effect was significant ($p < 0.05$) for days to 50% flowering (DTF), number of pods per plant (NPP), and seed yield (SY) traits under both NS and DS conditions, implying a differential performance of genotypes across the two locations. The specific combining ability (SCA) × Location interaction effect was significant ($p < 0.05$) for DTF, NPP, and SY under both water regimes, implying the genetic effects of crosses were affected by test locations. General combining ability (GCA) and SCA mean squares were significant for number of seeds per pod (NSP) and SY under DS condition, indicating additive and non-additive gene effects controlled these traits. Baker's ratio (BR) > 0.50 for NPP and NSP under DS condition, suggested the preponderance of additive gene effects. The narrow-sense heritability estimates of > 0.60 for NSP under DS condition suggested relatively better trait transmissibility from parents to offspring. G40145, G40148, and G40150 were good general combiners for NPP and SY under both NS and DS conditions. F_2 families Zimbabwe landrace x G40138, Zimbabwe landrace × G40150, G40059 × G40145, G40059 × G40148, G40138 × G40150, and G40145 × G40150 were best-specific combiners with enhanced SY of 1.67 tons/ha under DS condition. The selected parents are valuable genetic resources for breeding programs to enhance the NPP and SY. High-performing early-generation families are recommended for genetic advancement and selection across representative growing environments for variety release and commercialization.

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) [30]. The crop is suitable for production in less fertile soils due to its ability to fix atmospheric nitrogen, thereby improving soil nutrition in arid and semi-arid agro-ecologies [24, 46]. The crop is relatively highly tolerant to drought and heat stress, allowing for cultivation in drought-stricken areas [23, 37, 41]. Tepary bean possesses unique genes conferring rust and common bacterial blight resistance [4, 41, 47, 51]. These genes have been introgressed in closely related legume crops such as common bean (*Phaseolus vulgaris*) to develop varieties combining multiple resistance to abiotic and biotic stresses [5, 19, 28, 49]. Intraspecific hybrids of tepary bean were developed with high-yield potential and broad biotic and abiotic stress tolerance [41].

Tepary bean production in SSA is predominantly carried out by smallholder farmers under unfavourable production conditions characterized by drought and heat stress, and pests and disease pressure [25]. Moreover, smallholder farmers in the SSA grow unimproved tepary bean varieties that are low-yielding due to unavailability of improved and locally adapted genotypes [20, 25]. Intermittent and terminal drought stress are reported in tepary bean production zones [7, 53]. 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 [38–39, 42], which threatens 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 varieties 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 [14]. Generally, combining ability effects are categorized into two types: general combining ability (GCA) effects and specific combining ability (SCA) effects [50]. The GCA effect 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 [50]. High GCA and SCA mean squares represent the predominance of both additive and non-additive genetic effects in the parents and progenies, respectively [14]. In tepary bean, gene action conditioning the inheritance of common bean bacterial blight resistance [10–11, 51] and rust resistance [22] have been reported. However, there are few studies assessing the combining ability effects for agronomic traits, including seed yield and yield-related traits.

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 tons/ha [18, 26]. To develop new varieties with high yield potential and enhanced abiotic stress tolerance, tepary bean germplasm was imported from the International Centre for Tropical Agriculture (CIAT) in Columbia. Preliminary studies by Mhlaba et al. [21] and Mwale et al. [31] identified parents for improvement of agronomic traits and drought tolerance. Developing tepary bean intraspecific crosses from the identified germplasm is essential to improving yield potential to combat food and nutritional challenges currently prevalent in SSA. Therefore, this study aimed to determine the combining ability and genetic components for seed yield and yield-related traits in selected tepary bean genotypes. 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.

Materials and methods

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 [31]. The names, source of origin and levels of drought tolerance of the selected genotypes are shown in Table 1.

Table 1
Names of the seven tepary bean genotypes and 21 F_2 families used for drought assessment in the current study.

Code	Genotype	Origin	Description	Drought
P1	Zimbabwe landrace	Zimbabwe	Landrace	Sensitive
P2	G40059	CIAT-Columbia	Breeding line	Moderately tolerant
P3	G40138	CIAT-Columbia	Breeding line	Very tolerant
P4	G40145	CIAT-Columbia	Breeding line	Moderately tolerant
P5	G40148	CIAT-Columbia	Breeding line	Very tolerant
P6	G40150	CIAT-Columbia	Breeding line	Very tolerant
P7	Uchokwane	South Africa	Landrace	Sensitive
P1 x P2	Zimbabwe landrace x G40059			
P1 x P3	Zimbabwe landrace x G40138			
P1 x P4	Zimbabwe landrace x G40145			
P1 x P5	Zimbabwe landrace x G40148			
P1 x P6	Zimbabwe landrace x G40150			
P1 x P7	Zimbabwe landrace x Uchokwane			
P2 x P3	G40059 x G40138			
P2 x P4	G40059 x G40145			
P2 x P5	G40059 x G40148			
P2 x P6	G40059 x G40150			
P2 x P7	G40059 x Uchokwane			
P3 x P4	G40138 x G40145			
P3 x P5	G40138 x G40148			
P3 x P6	G40138 x G40150			
P3 x P7	G40138 x Uchokwane			
P4 x P5	G40145 x G40148			
P4 x P6	G40145 x G40150			
P4 x P7	G40145 x Uchokwane			
P5 x P6	G40148 x G40150			
P5 x P7	G40148 x Uchokwane			
P6 x P7	G40150 x Uchokwane			

CIAT = the International Center for Tropical Agriculture.

Tepary bean population development

The parental genotypes were grown in 10 L pots under room temperature conditions in a screen house at Chitedze Research Station (13° 85´S and 33° 38´ E; 1146 m asl) in Lilongwe, Malawi during the 2020/2021 growing season. The parents were planted at a two-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 [27]. The parents were crossed following a 7 × 7 half-diallel mating design to generate 21 F_1 progenies and successful crosses were harvested at physiological maturity. Thereafter, the generated F_1 seeds were planted, self-pollinated and advanced to the F_2 generation.

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 (non-stressed, NS, and terminal drought stress, DS) at two sites in Malawi during the 2021/2022 dry season from July to October. The study used an alpha lattice design with 4 incomplete blocks, each consisting of 7 genotypes with three replications. The study sites were Kasinthula Agricultural Research Station (16° S and 34° 5' E; 60 m asl) in Chikwawa district and the Lilongwe University of Agriculture and Natural Resources (LUANAR) Horticulture Research Farm (14° 12’ S and 33° 46’ E; 1200 m asl) in Bunda,

Lilongwe district. The average monthly temperature at LUANAR ranged from 26.8 to 32.7 degrees Celsius, and it ranged from 31.71 to 40 degrees Celsius 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 total plot area of 2.25m^2. The intra-row spacing was 0.15 m, while the inter-row spacing was 0.75 m. Furrow irrigation was used to apply water, with approximately 35 mm of water per irrigation (80% field capacity, FC) [40, 43, 48]. An ML3 Theta Probe (Delta T Devices, UK) and Chameleon soil moisture sensors (Supplemental Figs. 1 and 2) 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 [2]. 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.

Data collection

Data was 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; 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 [16]. 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 [35].

Statistical analysis

Analysis of variance

The agronomic data collected from each location was subjected to an analysis of variance (ANOVA) using the Genstat software, 18th Edition [36]. Prior to subjecting the agronomic data to a combined analysis of variance, the homogeneity of variance was assessed through Bartlet's test [6]. Differences between entry means were compared through the Least Significant Difference (LSD) at the 5% significance level [9]. 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:

Yijkl = μ + Li + rjLi + BkrjLi + gl + gLli + 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; eijkl is the lattice pooled error.

Combining ability and gene action

General combining ability of parents and specific combining ability of crosses was estimated based on Griffing's method II (F1's and parents) and model I (fixed effects) [15] using AGD-R software version 4.0 [45] in line with the following statistical linear model:

Yijkpm = μ + gi + gj + sij + giLk + gjLk + sijLk + Lk + + rpLk + BmLkrp + + eijkpm, where, Yijk 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; eijkpm is the pooled error.

A student t-test was used to determine the statistical significance of parents' GCA effects and crosses' SCA effects. Baker's ratio was used to calculate the gene action for the trait as follows: 2 σ^2 GCA / (2 σ^2 GCA + σ^2 SCA) [3]. The Baker's ratio 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. Baker's ratio values greater than 50% implies the preponderance of additive gene effects. The narrow sense heritability estimated in AGD-R software version 4.0 [45] was categorized into low (< 30%), moderate (> 30% but < 60%) and high (> 60%) as outlined by Robinson et al. [44].

RESULTS

Analysis of variance

Analysis of variance 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.

Combining ability analysis and heritability

The mean squares for combining ability analysis, Baker's ratio, and narrow sense heritability estimates for the assessed agronomic traits are presented in Table 3. The 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. While under DS condition, SCA × Location effect was significant ($p < 0.05$) for DFL, NPP, and SY. The GCA mean squares as the main effect were significant ($p < 0.05$) for NPP and SY under NS condition. While under DS condition, the GCA mean squares were significant ($p < 0.05$) for NPP, NSP, and SY. SCA mean squares as the main effect 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 Baker's ratio (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.

The degree of trait transmissibility from parents to offspring was assessed through the computation of narrow-sense heritability (NSH) on a genotype-mean value basis. NSH was low for DTM, NPP, and SY; moderate for DTF; and high for NSP under the NS condition. Under DS condition, NSH was low for NPP; moderate for DTF, DTM, and SY; and high for NSP.

Table 2
Mean squares and significant tests for agronomic traits of seven tepary bean parents and 21 F_2 progenies evaluated under both non-stress (NS) and drought-s (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***	824578.90***	1056223.0
REP(LOC)	4	0.89ns	3.54*	1.41ns	17.21ns	0.36ns	5.09ns	0.49*	0.06ns	289.90ns	65795.00r
BLOCK.REP.LOC	18	3.36***	3.39***	36.99***	16.63ns	72.65***	13.55***	0.60***	0.39ns	251126.10***	428554.00
Genotype	27	9.03***	6.03***	56.70***	31.88*	267.61***	64.21***	1.84***	1.26***	1444681.90***	1085094.0
Genotype × LOC	27	3.93***	5.20***	54.66***	18.65ns	30.93***	18.86***	0.23ns	0.22ns	125800.90***	114966.00
Error	90	1.16	1.39	3.00	17.80	1.58	2.37	0.19	0.28	327.30	57327.00

* p < 0.05, ** p < 0.01, *** p < 0.001; SOV, source of variation; ns, non-significant; 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; SY, seed yield in kg/ha; Loc, location; REP, replication.

Table 3
Mean squares of general combining ability (GCA) and specific combining ability (SCA) and significant tests for agronomic traits of seven tepary bean parents 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***	824578.85***	884450.27*
REP(Location)	4	0.89ns	3.19***	1.40ns	17.21ns	0.34***	3.87***	0.46***	0.06ns	289.95ns	55094.88**
Cross	27	10.66*	7.19ns	67.87ns	34.73ns	310.10***	68.96**	2.11***	1.44***	1600487.07***	1285759.7(
GCA	6	15.70ns	9.52ns	19.92ns	33.45ns	785.32***	240.44***	2.07ns	5.29***	3727881.99**	2754407.5
SCA	21	9.22ns	6.64ns	81.57ns	35.09ns	176.98**	22.30ns	2.14***	0.33***	992659.95***	912935.04*
Location × Cross	27	4.13***	5.07***	67.07***	19.83ns	33.48***	19.65***	0.19ns	0.20ns	137275.15***	114763.28*
GCA × Location	6	2.51ns	10.14*	92.89ns	6.83ns	13.26ns	30.92ns	0.12ns	0.22ns	84926.91ns	159747.59r
SCA × Location	21	4.59***	3.66**	59.69***	23.54ns	39.43***	17.03***	0.21ns	0.20ns	152231.80***	103846.65*
Residual	90	1.07	1.41	2.78	16.60	1.55	2.31	0.20	0.26	307.23	57466.67
V.GCA		0.54	0.30	0.64	0.62	29.03	8.82	0.07	0.19	138058.32	99886.70
V.SCA		2.72	1.74	26.26	6.17	58.48	6.67	0.65	0.03	330784.24	285156.12
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
NSH		0.22	0.16	0.04	0.05	0.49	0.66	0.14	0.57	0.45	0.37

* p < 0.05, ** p < 0.01, *** p < 0.001; SOV, source of variation; ns, non-significant; 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; SY, seed yield in kg/ha; REP, replication; V.GCA, variance general combining ability; V.SCA, variance specific combining ability, NSH, narrow sense heritability.

Genotype mean performance for agronomic 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 followed by G40159 (1773 kg/ha), G40138 and G40145 (1666 kg/ha).

Drought stress 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 followed by G40148 (1351 kg/ha), G40059 (954 kg/ha), G40145 (846 kg/ha) and G40138 (781 kg/ha) under DS condition.

For the F_2 progenies, the earliest progenies to flower were G40148 x G40150 (28 days), G40059 x G40148 (29 days), G40138 x G40145 (29 days), and G40145 x 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 and 2468 kg/ha 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 were recorded for G40138 × G40150, G40145 × G40150, Zimbabwe landrace × G40150, G40059 × G40145, and G40059 × G40138.

Table 4
Mean performance of seven parental tepary bean lines and 21 F_2 progenies for five agronomic traits evaluated under NS and 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	424.5
CV%	2.51	3.78	2.3	5.96	5.35	9.44	8.7	10.79	1.13	18.65

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

GCA effects of parents for agronomic traits

The estimates of GCA effects of 7 parents for the assessed agronomic traits are presented in Table 5. Parental genotypes G40059 (P2) and G40138 (P3) had high negative significant GCA effects for DTF and DTM while G40150 (P6) had significant positive GCA effects for DTF and DTM under NS condition. The following 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 while 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.

SCA effects of crosses for agronomic traits

Under NS condition, G40148 × Uchokwane cross recorded positive and significant SCA effect for DTF while crosses G40145 × G40148, G40148 × G40150, and Zimbabwe landrace × G40059 registered positive and significant SCA effects for DTM (Table 6). Crosses Zimbabwe landrace × Uchokwane, G40059 × G40138, G40138 × G40145, and G40138 × G4015 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 × 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, while 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.

Table 5
Estimates of general combining ability effects for agronomic traits of seven parental lines of tepary beans evaluated in two locations under non-stressed (NS) and drought-stressed conditions (DS) 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

* $p < 0.05$, ** $p < 0.01$; ns: non-significant; DTF, days to 50% flowering; DTM, days to 90% physiological maturity; NPP, number of pods per plant; NSP, number of seeds per pod; SY, seed yield in kilogram per hectare, SEM; Standard error of the mean.

Table 6
Estimates of specific combining ability effects for agronomic traits of twenty-one F_2 progenies of tepary beans evaluated in two locations under non-stressed (NS) and drought-stressed conditions (DS) 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

* $p < 0.05$, ** $p < 0.01$; ns: non-significant; DTF, days to 50% flowering; DTM, days to 90% physiological maturity; NPP, number of pods per plant; NSP, number of seeds per pod; SY, seed yield in kilogram per hectare, SEM; Standard error of the mean.

Discussion

The evaluated genotypes exhibited significant differences in mean performance for days to 50% flowering, days to 90% physiological maturity, number of pods per plant, number of seeds per pod, and seed yield, signifying the presence of high genetic diversity in the parental lines and crosses. Genetic diversity is essential for selection and accelerated genetic gains in breeding programs [52]. The findings in the current study revealed that the tested genotypes were amenable to selection for early maturity, a higher number of pods and seed yield production under drought-stress conditions.

The phenotypic expression of a trait is determined by both genotypic and environmental factors [1]. Conventionally, the influence of environmental factors is more dominant in quantitative traits such as seed yield. 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 existed for genotype-by-environment interaction for most of the assessed traits except number of seeds per pod under both non-stress and drought stress conditions and days to 90% physiological maturity under drought-stress condition (Table 2) 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 [50]. The general combining ability is mostly associated with additive gene effects, while the specific combining ability with non-additive gene effects [50]. The significant mean squares for GCA for number of seeds per pod under drought-stress conditions and number of pods per plant and seed yield under both non-stress and drought-stress 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 non-stress condition and number of seeds per pod and seed yield under both non-stress and drought-stress 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 x Location interaction effects for days to 50% flowering, number of pods per plant, and seed yield under

both non-stress and drought-stress 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 Baker's ratio for number of pods per plant and number of seeds per pod under drought-stress 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 Baker's ratio for days to maturity, and seed yield under the drought-stressed condition suggests the preponderance of non-additive gene effects, which are mostly due to dominance and epistatic genetic effects [14, 29]. The implication of this in plant breeding programs is that more crosses should be generated from divergent parental lines since the performance of these crosses cannot be readily determined from their parents' GCA effects.

Heritability measures the extent to which genetic variances contribute to the total phenotypic variation of a trait, which is useful for selection programs. The high values for narrow-sense heritability indicated the high transmissibility of genetic effects from parents to offspring, especially for the number of pods per plant under drought-stressed conditions. This also indicated the dominance of additive genetic variance contributions to total phenotypic variance [1]. Thus, higher response to selection through mass selection and pedigree methods would be expected in early-generation selection for the newly developed crosses [13]. The moderate to low variation in transmissible genetic effects under drought-stressed conditions for the seed yield indicates that the trait is quantitative in nature and thus heavily influenced by the environment. As a result, selection should be delayed until later generations with more locations throughout multiple seasons of testing of these genotypes [8, 17, 32, 34].

Parental genotypes G40145, G40148, and G40150 were good general combiners for the number of pods per plant and seed yield under both non-stressed and drought-stressed 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 5). These genotypes would be useful progenitors in tepary bean breeding programs 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 programs 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 seed yield under non-stress condition. This implies that these cross combinations had a superior performance greater than what was predicted by their GCA effects of their parents [12] 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 [50]. Under water deficit conditions, F_2 families G40059 × G40150 and G40059 × Uchokwane had negative and significant SCA effects for days to 90% physiological maturity. 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 seed yield under drought stress 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 [34]. 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 [33].

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 non-stressed and drought-stressed conditions and would be useful parents in tepary bean breeding programs. 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 kg/ha under drought-stressed conditions. These F_2 families are recommended for further selection, genetic advancement, and variety release.

Declarations

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Author Contributions

SEM, HS, and JM conceived and designed the research. SEM performed the experiments. WN, AS, and IF assisted with designing the experiments. SEM and WN analyzed the data. SEM drafted the manuscript. HS, WN, AS, IF, and JM revised the manuscript. All authors read and approved the final manuscript.

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Data availability

The data set for the work is included in the article/Supplemental Material; any further questions should be directed to the corresponding author.

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