

Full Length Research Paper

Combining ability and effect of water stress on morphological and physiological traits of *Lablab purpureus* L. sweet

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Drought limits crop production worldwide, reducing yields by up to 70%. Lablab bean, suited for arid and semi-arid regions, shows notable drought tolerance, yet Kenya lacks improved drought-tolerant lablab varieties. This study aimed to (i) identify drought-tolerant lablab genotypes based on morphological and physiological traits and (ii) assess the combining ability of seven parental genotypes and 21 crosses to find promising combinations. In a controlled glasshouse experiment, ten genotypes were tested under well-watered, moderate, and severe water stress conditions using a split-plot design. Combining ability was studied using a 7×7 half-diallel design, creating 21 F2 crosses evaluated in a screen house in Uganda. Data on eight morphological and ten physiological traits showed significant genotypic differences, with severe stress reducing growth parameters and delaying flowering. Drought stress decreased fresh weight, dry weight, relative water content, photosystem II yield, and chlorophyll content, while increasing non-photochemical quenching. Genotypes D1, D3, and D7 performed best under stress. Additive gene action governed physiological traits, while non-additive action influenced morphological traits. Genotypes D3 and D8 were strong general combiners, and crosses D3×D8, D3×D5, and D5×D10 showed high yield potential, making them ideal candidates for breeding drought-tolerant lablab varieties.

Key words: Drought stress, *Lablab purpureus*, combining ability, morphology, physiology.

INTRODUCTION

Lablab purpureus (L.) sweet (2n = 22) is an important annual herbaceous forage legume and a member of the Fabaceae family, native to Africa (Seleiman et al., 2021). Its seeds contain approximately 20 to 28% protein, making it an essential protein source. Lablab is primarily grown in mixed cropping systems and utilized as a vegetable or

livestock forage (Pandey et al., 2021). This crop exhibits diversity and widespread distribution in arid and semi-arid tropical regions, where its yields are influenced by various abiotic factors, particularly water deficit (Singh and Abhilash, 2019). Drought stress can result in a reduction of crop yields by approximately 34%, leading to an overall

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loss of \$37 billion in the agricultural sector in least developed countries and low- to middle-income countries (Venkatappa et al., 2021). Water deficit during the reproductive stage greatly limits crop yield due to impairment of physiological, morphological, biochemical, and molecular processes (Chavan et al., 2021; Missanga et al., 2022). Reduced plant growth and productivity under drought are caused by altered plant water relations, decreased stomatal conductance resulting in low CO₂ utilization through photosynthesis, high cellular oxidative stress, tissue membrane damage, and inhibition of antioxidant enzyme activity (Seleiman et al., 2021). Prolonged water stress hastens flowering and decreases the length of grain filling, resulting in low grain set, size, and weight (Kuppler and Kotowska, 2021). Lablab varieties respond differently to drought stress depending on the intensity and severity of the drought, growth stage, and exposure period. However, progress in breeding lablab cultivars for dry environments has been slow, coupled with very little information on the actual drought tolerance mechanisms (Akello et al., 2023). A few studies have been conducted over the years to identify lablab adaptation strategies to water deficit (Missanga et al., 2022; Akello et al., 2023). However, reports addressing morpho-physiological processes in lablab are still limited, even though such changes can serve as reliable indicators for the early selection of genotypes with drought tolerance (Orek et al., 2020). In herbaceous annual legumes, desired genotypes that can be used to detect tolerance to drought stress can produce appreciable seed yields, including traits such as plant height, relative water content, chlorophyll content, photosynthetic efficiency, dry weight biomass, and flowering time (Wang et al., 2022). Such traits offer plant breeders various options for developing plants that can withstand drought through strategies such as drought escape, tolerance, avoidance, or a combination of these approaches (Naeem et al., 2023).

One strategy to address the recurrent drought problem is to identify genotypes with adequate levels of tolerance to water stress. To develop an effective breeding program aimed at enhancing drought tolerance, it is crucial to evaluate the existing lablab germplasm for agronomic, morphological, and physiological traits under drought stress conditions. This screening process helps identify genotypes that exhibit tolerance to drought and can serve as potential sources for developing drought-tolerant varieties, either directly or indirectly (Mesterházy et al., 2020). Lablab genotypes possess variable tolerance to drought due to a wide range of genetic diversity and could constitute a potential source of drought tolerance because of their adaptation to biotic and abiotic stress (Karimi et al., 2024). Robotham and Chapman (2017) reported significant genetic diversity in lablab lines from East Africa, which could contain favorable alleles for abiotic stress resistance and be used in lablab breeding for drought tolerance. The study of various yields and associated traits of the crop; therefore, it is crucial to evaluate the breeding potential of parents and select quality combiners (Begna, 2020). A

clear understanding of the mode of gene action, as well as the general and specific combining ability (GCA and SCA) of the parental lines concerning drought traits and yield components under water stress conditions, is vital for a lablab breeding program.

Crossing diverse local lablab genotypes with different levels of tolerance to water deficit could provide promising high-yielding and drought-tolerant F1 hybrids. Several research efforts on GCA and SCA have been conducted by previous authors, contributing to the understanding of the inheritance of grain yield and agronomic traits (González-Espíndola et al., 2024; Rony et al., 2019). However, there are few reports on the GCA and SCA effects for morphological and physiological traits under water stress conditions in lablab. This necessitates further inquiry to better understand the mode of gene action governing the inheritance of yield-associated traits under water stress conditions. Thus, the objective of this study was to assess the morphological and physiological responses of ten lablab genotypes to water stress and determine their combining ability under varying water stress conditions.

MATERIALS AND METHODS

Plant and experimental site

The plant material used for evaluating drought tolerance consisted of ten diverse and extensively grown lablab genotypes (Table 1) obtained from farmers in the eastern, coastal, and central regions of Kenya. The genotypes were selected based on their adaptation to and wide use in arid and semi-arid conditions. The screening of genotypes was conducted under glasshouse conditions at the Kabete Field Station, University of Nairobi, located at latitude 1°15' S and longitude 36°44' E, at an altitude of 1,850 m above sea level, with a mean temperature of 24.3°C during the day and 13.7°C at night, a 12/12 photoperiod, and 40 to 50% relative humidity. Two experiments were conducted from April to September 2021 and from October to February 2022.

Experimental design and layout

The experiments were laid out in a split-plot design with three replicates and two factors (water regimes and genotypes). The main plots consisted of well-watered (WW, 100% of field capacity), moderate stress (MS, 50% of field capacity), and severe stress (SS, 25% of field capacity) conditions, while the sub-plots comprised the ten lablab genotypes. Five seeds per genotype were planted in each 20 cm diameter plastic pot containing 5 kg of sterile sandy-loam soil, with four pots representing a plot. The plants were thinned to two plants per pot at the first fully expanded trifoliolate stage. Soil moisture was monitored using a tensiometer. Standard cultural practices were carried out, including spraying with 20 g/L Actara (Syngenta, USA) and 1.8 g/L Dynamec (Syngenta, USA) to protect the plants from pests.

Induction of water deficit and monitoring

Water stress treatment was imposed at the flowering stage and

Table 1. Lablab genotypes used in the study.

Collection	Genotype code	Site of collection	Region	Seed color	Drought tolerance
D2	11722	Mbeere	Eastern	Light brown	Tolerant
D4	21376	Mbeere	Eastern	Cream	Susceptible
D6	27002	Mbeere	Eastern	Black	Susceptible
D5	13129	Machakos	Eastern	Brown	Tolerant
D8	13083	Makueni	Eastern	Black	Tolerant
D9	12088	Meru	Eastern	Black	Susceptible
D10	11723	Limuru	Central	Black	Susceptible
D3	13758	Kilifi	Coastal	Black	Tolerant
D7	12187	Lamu	Coastal	Brown	Tolerant
D1	10706	Nakuru	Rift Valley	Brown	Tolerant

maintained at 50 and 25% field capacity for 21 days, by which time most genotypes showed symptoms of severe wilting, high senescence, or foliar abscission. After the treatment, data were recorded, and watering resumed to 100% field capacity until physiological maturity, as described by Plazas et al. (2019). The plants under well-watered conditions were watered three times a week throughout the growth period until harvest, and data were recorded.

Data collection and trait measurements

Data collection for the well-watered and water deficit conditions was conducted at the end of the drought period (21 days). All morphological, yield-related, and physiological traits were recorded from five randomly selected plants per plot, with all data expressed as means of triplicate readings. Eighteen traits were recorded, comprising eight morphological and ten physiological traits.

Evaluation of morphological and yield related traits

The morphological variables measured included days to 50% flowering (DTF), recorded as the number of days from planting to flower initiation in at least 50% of the plants in each genotype, days to pod formation (DTP), and days to maturity (DTM), as described by Keerthi et al. (2018). Pod length (PL), seed weight (SW) (in grams), and pods per plant (PPP) were recorded using the lablab descriptor sheet according to Byregowda et al. (2015). Pod lengths were measured from the base of the petiole to the tip of the pod. Plant height (PH) was measured at flowering for each accession in centimeters (cm), from the stem base at the soil surface to the topmost flower bud using a measuring tape. The seeds were harvested at their respective maturity stages.

Evaluation of physiological traits

The physiological measurements for all the genotypes and treatments were recorded at the end of the 21 days of water stress treatment. These parameters were measured between 9 AM and 12 noon on the middle, fully expanded upper leaf surface using a MultispeQ Beta device (v1.0 MI, USA) and submitted to the photosynQ platform (<http://www.photosynq.org>) (Kuhlgert et al., 2016). The measured parameters included photosystem II photochemical efficiency (Phi2), photo-protective non-photochemical quenching (PhiNPQ), basal dissipation of non-regulated light energy

(PhiNO), mean photochemical efficiency of photosystem II (Fv/Fm), relative chlorophyll content (SPAD), and total non-photochemical quenching (NPQt). Environmental parameters such as CO₂ concentration, light exposure, light absorbance, linear electron flow (LEF), ambient temperature, and relative humidity were captured using the MultispeQ device.

The plant relative water content (RWC) was determined as described by Sapes and Sala (2021). Detached shoots and roots were weighed separately to obtain the fresh weight (FW). The shoots and roots were then submerged in 1000 ml of distilled water in 30 cm wide basins in the dark for 6 hours at ambient room temperature to regain turgidity.

Afterward, the shoots and roots were removed, quickly blotted to remove excess water on the surfaces, and weighed to obtain the saturated turgid weight (TW). The shoots and roots were placed in an oven at 70°C for 48 h to obtain the dry weight (DW). The plant relative water content (RWC) in shoots and roots was computed for each genotype using the following formula:

$$\text{RWC (\%)} = \frac{\text{FW} - \text{DW}}{\text{TW} - \text{DW}} \times 100$$

Development of crosses, and evaluation of F₂ populations

Based on the findings from the evaluations of responses to water deficit, drought-tolerant genotypes (D1, D2, D3, D5, D7, and D8) and susceptible genotypes (D4, D6, D9, and D10) were selected as parents to generate new genetic combinations. The parents were crossed using the half diallel method II mating scheme to produce 21 F₁ hybrids. A crossing block was established in a screen house at the Department of Biochemistry, Faculty of Science and Technology, University of Nairobi, under controlled environmental conditions (24°C/17°C day/night temperatures, 12/12 h day/night photoperiod, and 70 to 80% relative humidity). Planting was staggered to ensure synchronization based on flowering dates. The female parents were hand emasculated, and pollinations were performed, followed by covering the stigma with emasculation bags to prevent extraneous pollen from contaminating the pollinated plants. The successful F₁ seeds were harvested separately per cross at maturity.

A total of seven parents (D1, D3, D5, D8, D4, D6, and D10) that produced more than 20 seeds per cross were selected, and the mating design was reduced to a 7 × 7 half diallel, which was then advanced to the F₂ population. The evaluation of the F₂ populations was conducted in a screen house at the Makerere University Agricultural Research Institute Kabanyolo (MUARIK), located at 0°28' N, 32°37' E, and 1200 m above sea level. The parental genotypes and F₂ populations were assessed under two watering

regimes: well-watered (WW, 100% field capacity) and severe stress (SS, 25% field capacity), using a split plot design with three replications. Water stress treatment was imposed at the flowering stage and maintained at 25% field capacity for 21 days, during which most genotypes showed symptoms of severe wilting, high senescence, and foliar abscission. Data were recorded on five morphological and five physiological traits.

Data analysis

Analysis of variance and correlation

The morphological and physiological data were subjected to analysis of variance to determine the effects of water stress on lablab genotypes using agricolae package R version 4.2.1 (R Core Team, 2021). The linear model representation was given by:

$$y_{ij} = \mu + g_i + t_j + gt_{ij} + \varepsilon_{ij}$$

where y_{ij} = observation of trait value of genotype i from treatment j (WW and SS), μ = overall mean effect, g_i = effects of genotypes i , t_j = effects of water treatment t , gt_{ij} = interaction effect of genotype i and treatment j , and ε_{ij} = experimental error. The genotypes were considered random effects whereas the water deficit considered fixed effects. The mean differences were separated by Fisher protected least significant differences (LSD) test at $P < 0.05$. Graphs were drawn using Microsoft Excel 2013. A two tailed Pearson's Correlations were calculated to determine the contributions of various traits to drought tolerance and their inter-relationship. A Principal component analyses (PCA) was done using R to understand the relationship between the morphological and physiological variables across the genotypes. PCs accounting for more than 15% of the variability and eigen values greater than 1 were retained.

Biplot analysis was done in the first and second principal components using the Factorextra package with RStudio in R statistical software to determine distribution of genotypes and variables measured. Two biplot views were used to visually assess genotype performance across the treatments for morphological and physiological traits.

Combining ability estimates

The coefficient of genetic determination (CGD) was calculated to estimate inheritance of physiological and morphological traits. The Analysis of Genetic Designs- (AGD-R) for Windows Version 5.0 was used to analyze the data). The Griffing's (1956) method I and model I was used to obtain the estimates of the general combining ability (GCA) and specific combining ability (SCA) effects following the statistical model:

$$y_{ijkl} = \mu + g_i + g_j + s_{ij} + t_k + l_{gm} + ls_{ijk} + + e_{ijkl}$$

Where, y_{ijk} is the mean value of the hybrid combination (i, j) or the parent ($i = j$); μ = overall mean; g_i and g_j = GCA effect of the i th and j th genotype, s_{ij} = SCA effect for the crosses among the i th and j th parent, t_k = effect of k th treatment, l_{gm} is the effect of m th interaction between treatment and genotype, ls_{ijk} = effect of the interaction between k th treatment and SCA of the ij th genotype, and e_{ijkl} is the experimental error. The Baker's ratio was estimated as GCA over SCA (Baker, 1978).

$$Y = \frac{2\sigma_g^2}{2\sigma_g^2 + \sigma_s^2}$$

Where $2\sigma_g^2$ is the GCA variance and σ_s^2 is SCA variance. The variance ratios were used to calculate the broad-sense coefficient of genetic determination (BSCGD) and narrow-sense coefficient of genetic determination (NSCGD) as follows:

$$\text{BSCGD } (H^2) = \frac{2\sigma_g^2 + \sigma_s^2}{2\sigma_g^2 + \sigma_s^2 + \sigma_e^2}$$

$$\text{NSCGD } (h^2) = \frac{2\sigma_g^2}{2\sigma_g^2 + \sigma_s^2 + \sigma_e^2}$$

RESULTS

Morphological and yield related traits evaluated under water stress at Kabetet Field Station

The variation among the genotypes and the influence of water stress on the evaluated traits of the ten lablab genotypes are presented in Table 2. The combined ANOVA revealed significant ($P < 0.001$ and $P < 0.05$) genotypic variation for all morphological and yield-related traits, except for plant height, pods per plant, and seed weight in response to water stress. Significant ($P < 0.001$ and $P < 0.05$) differences were observed in the mean squares of all the traits evaluated under water stress.

Days to flowering (DTF)

Increasing water stress caused a significant ($p < 0.01$) delay in flowering time. The average DTF under well-watered conditions was 82 days, which delayed to 84 days under severe water stress. The average DTF in moderately stressed plants remained the same as in the well-watered plants. Genotype D2 and D7 took the longest DTF (105 and 95 days, respectively), whereas genotypes D1 and D9 recorded the shortest DTF (62 and 65 days, respectively). The significant interaction between genotypes and water stress indicated a differential change in DTF in well-watered and severely stressed plants.

Days to podding (DTP)

The average DTP was significantly ($p < 0.05$) affected by increasing water stress, slightly delaying from 89 days under well-watered conditions to 90 and 91 days under moderate and severe stress conditions, respectively.

The longest and shortest DTP were recorded in genotypes D2 (118 days) and D1 (70 days) under severe water stress. The significant interaction between the genotypes and water stress indicated a differential change in DTP with increasing water stress.

Days to maturity (DTM)

The DTM was significantly ($p < 0.05$) affected by water

Table 2. Mean performance and analysis of variance of ten lablab genotypes for morphological traits evaluated under well-watered, moderate and severe water stress conditions at Kabete Field Station.

Genotype	Days to flowering			Days to podding			Days to maturity			Plant height (cm)			Pod length (cm)			Pod width (cm)			Pods per plant			Seed weight (g)			
	WW	MS	SS	WW	MS	SS	WW	MS	SS	WW	MS	SS	WW	MS	SS	WW	MS	SS	WW	MS	SS	WW	MS	SS	
D1	60	59	62	65	61	70	79	75	82	257	208	198	5.3	4.8	3	1.0	1	0.6	25	17	4.5	18	13	2	
D2	108	104	105	125	119	118	138	133	132	235	153	188	4.3	4.1	2.9	0.9	0.8	0.6	21	14	5	17	15	4	
D3	94	94	94	99	99	99	113	113	113	217	201	165	4.2	4.2	3.5	0.8	0.8	0.7	24	17	4	18	14	2	
D4	80	74	84	84	83	88	98	97	102	22	245	205	4.7	4.9	3	0.9	1	0.6	23	14	3	18	10	1	
D5	70	77	71	75	83	86	88	97	90	242	250	170	3.8	4.6	3.4	0.7	2	0.6	18	20	5	10	12	5	
D6	92	92	92	98	98	97	111	112	111	292	229	163	4	4.3	2.9	0.8	0.9	0.6	23	18	5	16	13	4	
D7	88	86	95	101	96	105	115	110	118	240	242	183	5.6	5.2	3.9	1	1	0.8	25	23	6	17	18	6	
D8	90	90	90	95	96	95	109	109	109	282	237	217	4.5	4 b	3.8	0.9	0.8	0.8	20	21	5	18	14	4	
D9	60	61	65	71	71	74	85	84	90	224	211	205	4.3	4.7	3.1	0.9	1	0.6	20	26	5	19	14	2	
D10	86	83	84	92	93	82	106	107	110	243	255	163	6 a	4.4	4 c	1.2	0.9	0.7	26	26	4	20	19	3	
Means	Days to flowering			Days to podding			Days to maturity			Plant height (cm)			Pod length (cm)			Pod width (cm)			Pods per plant			Seed weight (g)			
Control	82.8 ^a			90 ^a			104 ^a			245.6 ^a			4.59 ^a			0.918 ^a			22.45 ^a			17.15 ^a			
Moderate	82 ^a			89 ^a			104 ^a			223.3 ^b			4.51 ^a			0.902 ^a			19.68 ^a			13.95 ^b			
Severe	84.3 ^b			91.4 ^b			106 ^b			185.5 ^c			3.27 ^b			0.654 ^b			4.58 ^b			3.30 ^c			
LSD	3.14			2.4			4.3			37.89			0.6			0.13			5.17			3.9			
%CV	4			5.4			4.7			21.7			20.7			20.7			42.7			30			
ANOVA	Df	Days to flowering			Days to podding			Days to maturity			Plant height (cm)			Pod length (cm)			Pod width (cm)			Pods per plant			Seed weight (g)		
R	2	31.6			65			65.1			9777			1.5			0.06			2.6			42.9		
G	9	2536.2 ^{***}			3145.7 ^{***}			3145.7 ^{***}			2898 ^{ns}			1.4 [*]			0.05 [*]			39.3 ^{ns}			26.8 ^{ns}		
T	2	52.2 [*]			5.4 [*]			5.9 [*]			36938 ^{***}			21.9 ^{***}			0.87 ^{***}			3701.5 ^{***}			2483.9 ^{***}		
G × T	18	30.5 ^{**}			25.2 [*]			26.3 [*]			2497 ^{ns}			0.7 ^{ns}			0.02 ^{ns}			32.6 ^{ns}			19.3 ^{ns}		
Residual	87	11			24.1			24.2			2251			0.7			0.02			44.1			11.9		

WW well-watered, MS moderate stress, SS severe stress, LSD least significant difference, % CV percentage coefficient of variation, R replications, G genotype, T treatment, Df degrees of freedom. ^{****} 0.001 ^{***} 0.01 ^{**} 0.05 ^{ns} not significant at 5 % confidence level.

stress. Under well-watered conditions, the DTM was 104 days, which delayed to 106 days under severe stress conditions. The average DTM in moderately stressed plants remained the same as in the well-watered plants. Genotypes D1, D5, and D9 took the shortest DTM, recording 82 and 90

days, respectively, whereas genotypes D2 and D7 took the longest, with 132 and 118 days, respectively. The significant interaction of genotypes and water stress treatment indicated a variable response of genotypes for DTM with the imposition of water stress.

Plant height (PH)

Water stress caused a significant ($p < 0.05$) decline in PH. Compared to the well-watered plants, the average PH was 246 cm, which declined to 223 cm (9%) and 185 cm (25%) under moderate and

severe stress, respectively. Genotype D8 had the longest PH at 2.17 m under severe stress, while D2 had the shortest PH of 1.53 m under moderate stress. The reduction in PH was differentially influenced due to the significant ($p < 0.05$) interaction between genotypes and water stress.

Pod length (PL)

A significant ($p < 0.01$) decline in PL of the lablab beans due to increased water stress was observed. The average PL in well-watered plants was 5 cm, which significantly reduced to 3 cm (29%) under severe water stress conditions. Genotype D7 recorded the longest PL (3.85 cm), while D6 recorded the shortest PL (2.85 cm) under severe stress. The significant interaction of genotypes and water stress treatment indicated a variable response of PL with the imposition of water stress.

Pod width (PW)

The pod width was significantly ($p < 0.05$) lower in water-stressed plants compared to well-watered plants. The average PW in well-watered plants was 0.9 cm, which declined to 0.7 cm (29%) under severe stress. The longest and shortest PW were recorded in genotype D10 (0.73 cm) and D6 (0.57 cm), respectively, under severe stress.

Pods per plant (PPP)

A significant decline in PPP was observed in the lablab genotypes due to water stress. The average PPP in well-watered plants was 22, which drastically declined to 19 under moderate stress and to 4 (79%) among severely stressed plants. Among the genotypes, the decline was more pronounced in D4, which had only three pods per plant.

Seed weight (SW)

Water stress caused a significant ($p < 0.001$) reduction in SW of the lablab genotypes. The SW under well-watered conditions was 17 g, which declined to 14 g (19%) and to 3 g (80%) under moderate and severe water stress, respectively. Genotype D7 recorded the highest SW at 5.6 g, while D4 recorded the lowest at 1.3 g under severe water stress.

Evaluation of physiological traits of ten lablab genotypes under severe water stress at Kabete field station

The effects of water stress on the physiological traits are

presented in Table 3.

Phi2 efficiency

Increasing water stress had a significant ($p < 0.001$) negative effect on Phi2 efficiency. The mean Phi2 efficiency in well-watered plants was 0.54, which declined to 0.41 (24%) under moderate stress and to 0.27 (50%) under severe water stress conditions. Genotype D4 had the highest Phi2 efficiency (0.44), while D9 had the lowest (0.19) under severe water stress. The interaction between genotypes and water stress treatments was significant ($p < 0.05$), indicating a differential change in Phi2 efficiency in well-watered and water-stressed plants.

PhiNPQ

Water stress significantly ($p < 0.001$) affected the PhiNPQ of the lablab genotypes. In control plants, the average PhiNPQ was 0.24, which increased to 0.41 (35.9%) under moderate stress and to 0.64 (62.5%) under severe water stress. The genotypes differed significantly ($p < 0.05$), with D9 exhibiting the highest PhiNPQ (0.72) while D6 recorded the lowest PhiNPQ (0.17) under severe stress.

PhiNO

The average PhiNO increased significantly ($p < 0.001$) with increasing water stress. The average PhiNO in control plants was 0.09, which increased to 0.18 (14%) under moderate stress and to 0.21 (57%) under severe stress. Significant ($p < 0.05$) genotypic differences were observed for PhiNO, with D4 having the highest PhiNO (0.18) while D1 recorded the lowest. The increase in PhiNO rate was differentially influenced in well-watered and water-stressed plants, as indicated by a significant interaction between genotypes and water stress treatments.

LEF

Water stress resulted in significant ($p < 0.001$) reductions in LEF rate. Compared to the average LEF rate of 110.7 under well-watered conditions, it drastically declined to 72.7 (34%) under moderate stress and to 22.8 (79%) under severe stress conditions. Genotype D3 had the highest LEF rate (39), whereas D6 had the lowest (15) under severe water stress. The interaction between genotypes and water stress treatments was significant ($p < 0.05$), indicating a differential change in LEF rate in well-watered and water-stressed plants.

NPQt

Increasing water stress had a significant ($p < 0.01$)

Table 3. Mean performance of ten lablab genotypes for physiological traits evaluated under severe water stress at Kabete Field Station.

Genotype	Phi2	PhiNPQ	PhiNO	LEF	NPQt	Fv_Fm	SPAD	SFW	SDW	RFW	RDW	SWC	RWC
D1	0.22	0.7	0.08	24.33	17.79	0.31	21.41	11.75	7.45	1.47	0.95	35.98	34.12
D2	0.33	0.58	0.09	17.78	16.37	0.39	32.65	16.25	8.63	1.98	0.61	59.95	70.35
D3	0.28	0.63	0.11	29.69	35.57	0.36	36.35	11.25	8.28	1.70	0.39	69.15	77.91
D4	0.44	0.38	0.18	76.28	2.51	0.61	46.82	12.25	4.45	1.65	0.54	35.35	55.25
D5	0.33	0.56	0.11	25.92	26.43	0.43	33.72	10.21	6.73	1.13	0.49	37.63	57.13
D6	0.26	0.66	0.08	15.93	63.64	0.31	29.63	14.25	8.52	1.43	0.47	42.23	61.72
D7	0.28	0.61	0.11	25.25	11.52	0.41	28.87	10.42	6.56	1.26	0.33	46.65	68.28
D8	0.29	0.61	0.1	21.36	14.32	0.38	30.03	15.25	5.24	1.98	0.87	26.22	48.98
D9	0.19	0.72	0.08	21.88	24.98	0.29	20.25	12.25	8.38	1.53	0.68	29.85	55.56
D10	0.31	0.59	0.11	28.55	12.06	0.4	28.18	14.51	7.68	2.12	0.85	22.75	45.85
Means	Phi2	PhiNPQ	PhiNO	LEF	NPQt	Fv/Fm	SPAD	SFW	SDW	RFW	RDW	SWC	RWC
Well-watered	0.54 ^a	0.24 ^a	0.09 ^a	110.66 ^a	3.3 ^a	0.58 ^a	49.26 ^a	100.5 ^a	25.2 ^a	8.2 ^a	2.1 ^a	60.9 ^a	65.2 ^a
Moderate stress	0.41 ^b	0.41 ^b	0.18 ^b	72.7 ^b	1.12 ^b	0.58 ^a	48.5 ^a	28.7 ^b	11.4 ^b	3.2 ^b	0.97 ^b	48.7 ^b	60.9 ^a
Severe stress	0.27 ^c	0.64 ^c	0.21 ^c	22.8 ^b	24.8 ^c	0.36 ^b	28.8 ^b	12.8 ^b	7.2 ^c	1.6 ^b	0.62 ^c	40.6 ^b	57.5 ^a
LSD	0.08	0.1	0.02	20.61	14.33	0.33	5.76	20.94	3.87	1.6	0.34	10.8	9.9
% CV	30.87	36.87	34.3	2.93	22.33	9.41	20.7	94.1	53.6	78.9	60.5	38.7	30.2
ANOVA	Phi2	PhiNPQ	PhiNO	LEF	NPQT	Fv/Fm	SPAD	SFW	SDW	RFW	RDW	SWC	RWC
Replication	0.03	0.02	0	133.9	657	0.23	3	198	127.62	63.23	0.95	502.33	3046.41
Genotype	0.01*	0.02*	0.01*	203*	484*	0.28 ^{ns}	178*	3600*	123.21*	12.81*	0.84*	621.6*	528.14*
Water stress	1.11***	2.43***	0.22***	1165***	10185**	1.05*	8072***	8748***	355.2***	479.3***	22.9***	4187.1**	593*
Genotype × Treatment	0.01*	0.02*	0.01*	1997*	494*	0.22 ^{ns}	61**	3560*	123.11*	7.93 ^{ns}	0.32 ^{ns}	478.78 ^{ns}	346.61*
Residual	0.02	0.03	0.01	3248	471	0.25	76	1984	61.34	11.72	0.51	374.92	341.44

Phi2 photosystem II efficiency, PhiNPQ photo-protective non-photochemical quenching, PhiNO basal dissipation of light energy, LEF Linear Electron Flow, NPQt total non-photochemical quenching, Fv/Fm mean photochemical efficiency of photosystem II, SPAD relative chlorophyll content, SFW shoot fresh weight (g), SDW shoot dry weight (g), RFW root fresh weight (g), RDW root dry weight (g), SWC shoot water content, RWC root water content, LSD least significant difference, %CV coefficient of variation. Means with the same letter are not significantly different. '***' 0.001 '**' 0.01 '*' 0.05 ns not significant at 5% confidence level.

influence on NPQt. In the leaves of control plants, the average NPQt rate was 1.12, which increased to 3.3 (14.3%) under moderate stress and to 24.8 (57%) under severe water stress. Genotype D6 had the highest NPQt (2.8), while D4 had the lowest NPQt rate (0.8) under severe water stress. A significant ($p < 0.05$) interaction between genotypes and water stress indicated that the

reduction in NPQt in water-stressed plants was higher than in control plants.

Fv/Fm

The average Fv/Fm ratio significantly ($p < 0.05$) declined with increasing water stress, from 0.58 to

0.36 (37.9%). The average Fv/Fm ratio in moderately stressed plants remained the same as in control plants. Genotype D5 exhibited the highest Fv/Fm ratio (0.43), while D4 recorded the lowest (0.28) under severe stress. The interaction between genotypes and water stress was not significant for the Fv/Fm ratio, indicating a similar response in well-watered plants to increasing water

stress.

SPAD

Water stress had a significant ($p < 0.001$) impact on the total chlorophyll content of the lablab genotypes. Compared to the average SPAD in well-watered plants, which was 49.26 mg/g fresh weight, a slight decline was observed to 48.5 mg/g (1.5%) and to 28.8 mg/g (42%) under moderate and severe stress, respectively. The interaction between genotypes and water stress was significant, indicating a differential response of well-watered and water-stressed plants. Significant ($p < 0.01$) genotypic differences were recorded in SPAD content among the lablab genotypes, with D3 and D7 recording the highest values, while D1 and D9 recorded the lowest under severe water stress.

Shoot fresh weight (SFW)

Water stress significantly ($p < 0.001$) decreased the SFW of the lablab seedlings. The average SFW in well-watered plants was 100 g, which declined to 28 g under moderate stress and to 13 g under severe water stress. Genotype D2 recorded the highest SFW (16.25 g), whereas genotype D7 recorded the lowest SFW (10 g) among the genotypes under severe water stress conditions.

Shoot dry weight (SDW)

Increasing water stress resulted in a significant ($p < 0.001$) decline in SDW. The average SDW decreased from 25 g under well-watered conditions to 11 g under moderate water stress and to 7 g under severe water stress. Among the genotypes, D2 recorded the highest SDW at 8.6 g, while D4 recorded the lowest SDW at 4.5 g under severe water stress.

Root fresh weight (RFW)

A significant ($p < 0.001$) decline in RFW was observed among the lablab genotypes due to increasing water stress. The average RFW of the plants under well-watered conditions was 8.2 g, which drastically declined to 3.2 g under moderate stress and to 1.6 g under severe water stress. Among the genotypes, D10 recorded the highest RFW at 2.11 g, while D5 recorded the lowest RFW at 1.1 g under severe water stress conditions.

Root dry weight (RDW)

RDW was significantly ($p < 0.001$) affected by water stress. In well-watered plants, the average RDW was 2.1 g, which decreased by 57% under moderate stress and by 71%

under severe water stress. Genotype D1 recorded the highest RDW at 0.96 g, while D7 recorded the lowest RDW at 0.33 g under severe water stress.

Shoot water content (SWC)

A significant ($p < 0.05$) reduction in SWC was observed among the lablab genotypes due to increasing water stress. The average SWC in control plants was 60.9%, which declined to 20% under moderate stress and showed a 33% decline under severe stress. Genotype D3 recorded the highest SWC at 69.2%, while D10 recorded the lowest shoot water content at 22.8% under severe water stress.

Root water content (RWC)

Water stress caused a significant ($p < 0.05$) reduction in the RWC of the lablab genotypes. The average RWC in well-watered plants was 65.3%, which declined by 7% and 12% under moderate and severe water stress, respectively. Genotype D3 recorded the highest RWC at 77.9%, while D1 recorded the lowest RWC at 34.1% under severe water stress.

Pearson's correlation analysis

A Pearson's correlation among well-watered and severe water stressed plants is presented in Figure 1A and B, respectively.

Under well-watered conditions, significant ($p < 0.001$) and positive correlations were recorded between days to podding and days to flowering ($r = 0.97$), days to maturity and days to flowering ($r = 0.97$), days to maturity and days to podding ($r = 1$), shoot fresh weight and shoot water content ($r = 0.65$) at ($p < 0.05$), pod length and pods per plant ($r = 0.77$) at ($p < 0.01$), pod width and pods per plant ($r = 0.77$) at ($p < 0.01$), pod width and pod length ($r = 1$) at ($p < 0.001$), root dry weight and pod length ($r = 0.66$) at ($p < 0.05$), and root fresh weight and root dry weight ($r = 0.77$) at ($p < 0.01$).

The correlation analysis among severely stressed plants revealed significant ($p < 0.01$) and positive correlations between root fresh weight and shoot fresh weight ($r = 0.81$), seed weight and pods per plant ($r = 0.83$) at ($p < 0.01$), days to podding and days to flowering ($r = 0.99$) at ($p < 0.001$), and pod width and pod length ($r = 1$) at ($p < 0.001$). Additionally, significant negative correlations were observed, including shoot dry weight and shoot water content ($r = -0.72$) at ($p < 0.05$), and root dry weight and root water content ($r = -0.85$) at ($p < 0.01$).

Principal component analysis of morphological and physiological variables

The PCA of the all the studied traits of ten lablab

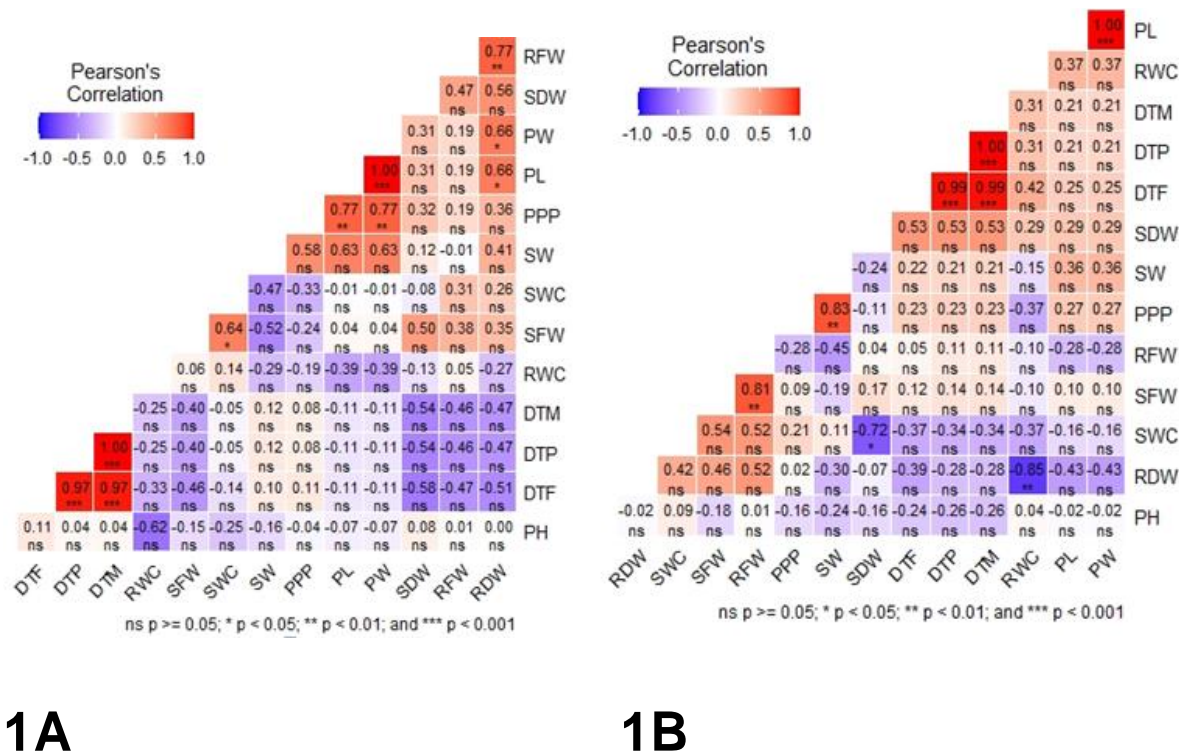


Figure 1. A Pearson's correlation for traits under well-watered conditions, B Pearson's correlation for traits under severe water stress. PH plant height (cm), DTF days to flowering, DTP days to podding, DTM days to maturity, RWC root water content, SFW shoot fresh weight, SWC shoot water content, SW seed weight, PPP pods per plant, PL pod length, PW pod weight, SDW shoot dry weight, RFW root fresh weight, RDW root dry weight. Dark purple color on the scale indicates strong negative correlation while red indicates strong positive correlation, ns no significant correlation.

2d1 genotypes under well-watered and severe water stress are presented in Table 4.

The variables were divided into two components, with each component having eigenvalues that exceeded 1, explaining 50.11 and 59.99% of the cumulative variability among the variables in the control and severe water stress conditions, respectively. Among the well-watered plants, the first component accounted for 28.23% of the variability and was largely associated with days to flowering (DTF), shoot fresh weight (SFW), shoot dry weight (SDW), root dry weight (RDW), and Phi2 as the most dominant variables with high eigenvalues. The second component accounted for 21.87% of the variability and was largely dominated by pods per plant (PPP), Fv/Fm, PhiNPQ, pod length (PL), and pod width (PW), which recorded the highest eigenvalues.

Among the severely stressed plants, the first component accounted for 40.88% of the variability and was largely dominated by Phi2, PhiNPQ, Fv/Fm, NPQt, and SPAD, recording the highest eigenvalues. The second component accounted for 19.11% of the variability and was dominated by days to podding (DTP), days to maturity (DTM), days to flowering (DTF), pods per plant (PPP), and PhiNO, which recorded the highest eigenvalues.

PCA Biplot analysis

Biplot of the first two components showing distribution of genotypes and variables across well-watered and severe water stress treatments is presented in Figure 2.

Under well-watered conditions (Figure 2A), genotypes D9, D1, and D2 were positioned farthest from the biplot origin, indicating better performance. In contrast, genotypes D4 and D3 were closer to the biplot origin, suggesting the least variability for the studied traits under well-watered conditions. Under severe water stress (Figure 2B), genotypes D4, D2, and D1 were most distinct from the biplot origin, indicating the greatest variability compared to the other genotypes. Genotypes D10 and D5 were located nearest to the biplot origin, implying the least variability under severe water stress conditions.

Analysis of variance and heritability effects of parental genotypes and F₂ crosses under severe water stress

The results of analysis of variance and the GCA and SCA mean squares for various morphological and physiological traits of lablab genotypes under well-watered and severe

Table 4. Eigen values and percentage of total variability explained for two PCs for traits evaluated at Kabete Field Station.

Variable	Well-watered		Severe water stress	
	PC1	PC2	PC1	PC2
Phi2	-0.63	-0.50	0.94	-0.20
PhiNPQ	0.18	0.60	-0.92	0.34
PhiNO	-0.30	-0.51	0.76	-0.52
LEF	0.23	-0.15	0.81	0.19
NPQt	0.45	-0.45	-0.87	0.34
Fv_Fm	0.13	-0.74	0.90	-0.39
SPAD	-0.35	-0.47	0.85	-0.35
DTF	0.77	-0.54	0.52	0.77
DTP	0.79	-0.50	0.44	0.82
DTM	0.79	-0.50	0.44	0.82
PH	0.19	-0.03	-0.46	-0.34
PL	-0.57	-0.59	-0.68	-0.47
PW	-0.57	-0.59	-0.68	-0.47
PPP	-0.48	-0.78	0.10	-0.52
SW	-0.30	-0.24	0.35	-0.11
SFW	-0.75	-0.16	0.56	-0.35
SDW	-0.72	-0.02	0.80	-0.15
SWC	-0.32	-0.21	-0.04	-0.31
RFW	-0.50	0.51	0.42	0.02
RDW	-0.68	0.45	-0.16	-0.35
RWC	0.51	0.12	0.48	0.18
Eigen value	5.93	4.59	8.58	4.01
Proportion of variance	28.23	21.87	40.88	19.11
Cumulative variance	28.83	50.11	40.88	59.99

water stress conditions evaluated at MUARIK are presented in Table 5.

ANOVA revealed significant ($p < 0.001$, $p < 0.01$, $p < 0.05$) genotypic mean squares for all morphological and physiological traits, except for leaf area efficiency (LEF) and SPAD. The effect of water stress was significant for all morphological traits ($p < 0.01$, $p < 0.001$) but non-significant for all physiological traits, except for SPAD ($p < 0.1$). The interaction between the parental genotypes, F_2 crosses, and water stress was non-significant for all studied traits, except for the mean squares of NPQt and days to flowering (DTF) ($p < 0.05$). Variance components under severe water stress revealed significantly different ($p < 0.001$, $p < 0.01$, $p < 0.05$) cross mean squares for all studied traits, except for pods per plant, plant height, and LEF.

General combining ability (GCA) mean squares were significant ($p < 0.001$, $p < 0.01$) for all studied traits, except for seed weight, pods per plant, plant height, LEF, and SPAD. Specific combining ability (SCA) mean squares were significant ($p < 0.01$, $p < 0.05$) for all traits except for pods per plant, plant height, Phi2, LEF, and NPQt. The Baker's ratio varied from 0.369 to 0.99 for morphological traits and from 0.4 to 0.99 for physiological traits. The

Baker's ratio was above 50% for all traits except for pods per plant (0.369) and SPAD (0.4). The non-specific combining genetic distance (NSCGD) was above 0.5 for most studied traits, except for pod length (PL) (0.07), pods per plant (PPP) (0.01), LEF (0.38), and SPAD (0.4). The broad-sense combining genetic distance (BSCGD) was above 0.5 for most traits, except for PL (0.10), PPP (0.03), and Phi2 (0.315).

Non-significant variation was recorded among the mean squares of the crosses under well-watered conditions. The GCA and SCA mean squares were non-significant for all traits, except for LEF ($p < 0.01$) and NPQt ($p < 0.05$). The Baker's ratio varied from 0.76 to 0.99 for morphological traits and from 0.39 to 0.99 for physiological traits. The NSCGD ranged from 0.21 to 0.99 for morphological traits and from 0.02 to 0.34 for physiological traits. The BSCGD mean squares ranged from 0.19 to 0.99 for morphological traits and from 0.03 to 0.88 for physiological traits.

General combining ability estimates of lablab parental genotypes under water stress

The results of GCA effects for morphological and

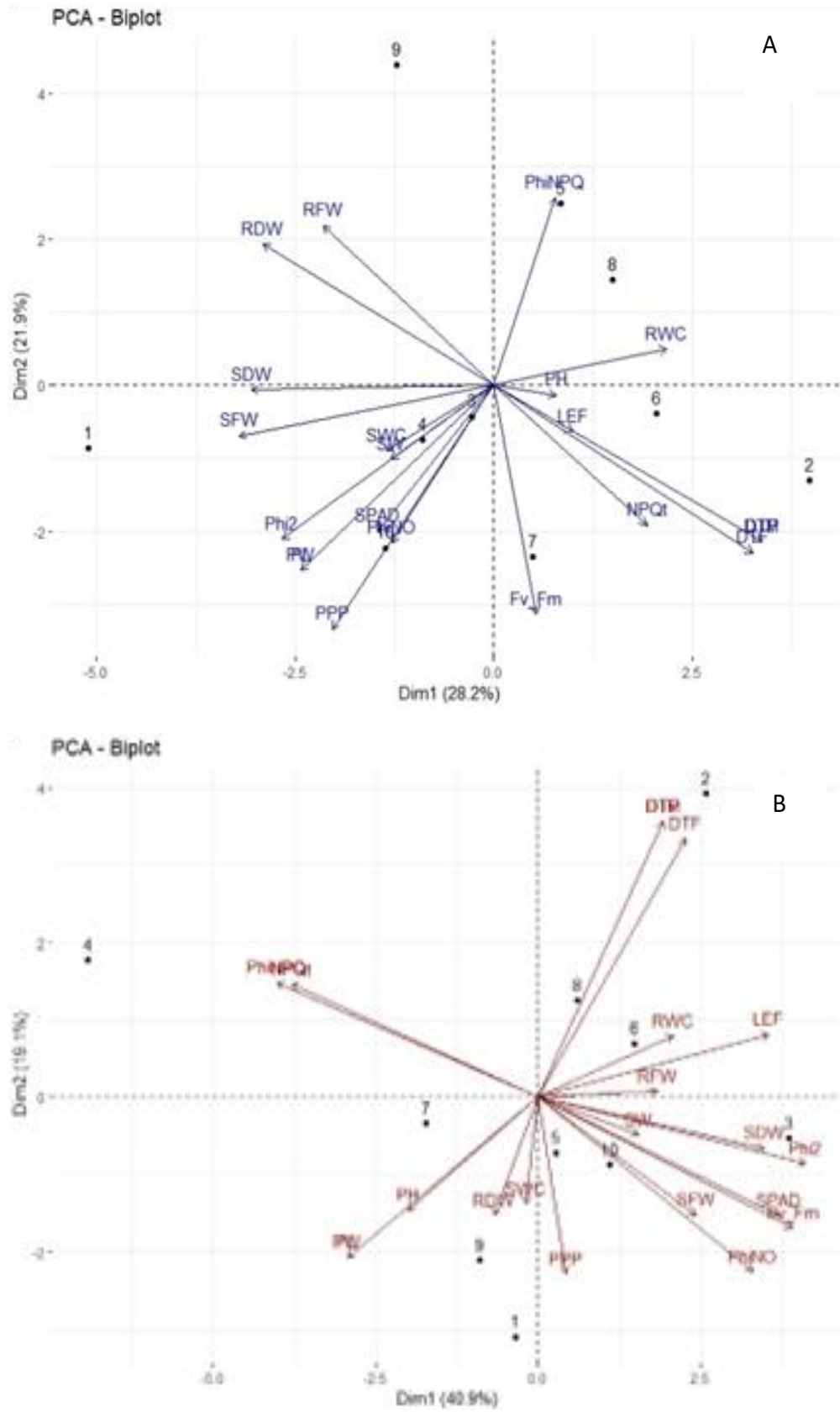


Figure 2. PCA biplots of lablab genotypes D1-1D10 plotted against first two components with variable eigen values. (2A) PCA for well-watered plants. (2B) PCA for severe water stressed plants.

Table 5. Analysis of variance and variance components of morphological and physiological traits of lablab parental genotypes and F₂ crosses under severe water stress.

ANOVA	Df	DTF	SW (g)	PL (cm)	PPP	PH (cm)	Phi2	PhiNPQ	LEF	NPQt	SPAD
Replication	2	3.15	41.8	6.129	1229	4251	0.001	0.169	31736	971.1	6178
Genotype	27	21.09**	55.10*	0.852*	33***	3238*	0.013***	0.025*	2579 ^{ns}	13.9*	82 ^{ns}
Water stress	1	84.86**	2431.9***	18.40***	4239***	47232***	0.0028 ^{ns}	0.0013 ^{ns}	76 ^{ns}	0.0053 ^{ns}	216*
Genotype × treatment	27	16.82*	21.1 ^{ns}	1.01 ^{ns}	58 ^{ns}	1564 ^{ns}	0.002 ^{ns}	0.014 ^{ns}	2822 ^{ns}	5.7*	68 ^{ns}
Water stress variance components											
Crosses	20	22.8**	14.58*	0.62*	41 ^{ns}	3125 ^{ns}	0.002*	0.004***	3205.6 ^{ns}	10.14*	106.2*
GCA	6	39.7***	11.42 ^{ns}	0.48*	18 ^{ns}	1805.5 ^{ns}	0.004**	0.006***	2250.6 ^{ns}	17.63**	49.30 ^{ns}
SCA	20	18**	15.49*	0.66*	48 ^{ns}	3502 ^{ns}	0.002 ^{ns}	0.003**	3478.3 ^{ns}	8.00 ^{ns}	122.4*
Residual	54	7.54	7.921	0.90	49	3641.3	0.001	0.001	3058.79	4.67	53.26
Baker's ratio		0.98	0.99	0.73	0.37	0.516	0.98	0.99	0.65	0.98	0.40
NSCGD (h ²)		0.99	0.48	0.07	0.01	0.488	0.703	0.98	0.38	0.99	0.40
BSCGD (H)		0.84	0.65	0.10	0.03	0.947	0.315	0.485	0.60	0.96	1.00
Well-watered variance components											
Crosses	20	8.74 ^{ns}	62.40 ^{ns}	1.25 ^{ns}	49.65 ^{ns}	1676.47 ^{ns}	0.00 ^{ns}	0.02 ^{ns}	2724.9 ^{ns}	12.03 ^{ns}	91.75 ^{ns}
GCA	6	8.63 ^{ns}	70.20 ^{ns}	2.15 ^{ns}	40.03 ^{ns}	2461.17 ^{ns}	0.00 ^{ns}	0.01 ^{ns}	3635**	7.54 ^{ns}	72.6 ^{ns}
SCA	20	8.77 ^{ns}	60.27 ^{ns}	0.99 ^{ns}	52.39 ^{ns}	1452.30 ^{ns}	0.00 ^{ns}	0.03 ^{ns}	2464.7 ^{ns}	13.31*	97.2 ^{ns}
Residual	54	7.99	48.43	0.99	73.89	1788.50	0.00	0.02	1843.20	6.86	68.14
Baker's ratio		0.98	0.98	0.99	0.76	0.98	0.39	0.42	0.99	0.57	0.75
NSCGD (h ²)		0.98	0.95	0.99	0.21	0.33	0.34	0.09	0.13	0.02	0.03
BSCGD (H)		0.99	0.81	0.46	0.27	0.19	0.88	0.20	0.09	0.03	0.05

DTF days to flowering, SW seed weight, PL pod length, PPP pods per plant, PH plant height, Phi2 photosystem II efficiency, PhiNPQ photo-protective non-photochemical quenching, LEF Linear Electron Flow, NPQt total non-photochemical quenching, SPAD relative chlorophyll content, GCA general combining ability, SCA specific combining ability, NSCGD narrow sense coefficient of genetic determination, BSCGD broad sense coefficient of genetic determination. **** 0.001 *** 0.01 ** 0.05, ns not significant.

physiological traits of seven parental genotypes evaluated under well-watered and severe water stress are presented in Table 6. Parental genotype D3 exhibited the highest significant ($p < 0.05$) negative GCA effect for days to flowering, while parental genotype D1 recorded the highest positive GCA effect for days to flowering (DTF). Genotypes D5, D8, and D3 showed the highest positive GCA effects for seed weight, pod length, and pods per plant, respectively.

Positive and significant ($p < 0.05$) GCA effects for

plant height and Phi2 were recorded in genotype D8. Genotype D6 recorded the highest significant ($p < 0.05$) and positive GCA effects for PhiNPQ, whereas genotype D10 exhibited positive GCA effects for leaf area efficiency (LEF) and NPQt. The highest GCA effects for SPAD content were recorded in genotype D1.

Overall, among all the parental genotypes, D3 and D8 exhibited desirable GCA effects for most traits related to grain yield, while parental genotype D10 recorded the highest number of physiological

traits with desirable GCA effects. Negative GCA effects were recorded in genotype D6 for seed weight and pod length, D4 for pods per plant, D5 for plant height, D4 and D6 for Phi2, D4 for PhiNPQ and NPQt, D5 for LEF, and D6 for SPAD under severe water stress.

Specific combining ability estimates

The specific combining ability (SCA) effects for

Table 6. GCA estimates for morphological and physiological traits of seven lablab parental genotypes evaluated at MUARIK under well-watered and severe water stress.

Parent	DTF		SW		PL		PPP		PH		Phi2		PhiNPQ		LEF		NPQt		SPAD	
	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS
D1	0.17	0.69	1.76	0.04	-0.1	-0.08	0.48	0.15	17.11*	4.44	-0.01	0	0.02	0.02	-7.19*	5.72	0.03	0.38	3.13**	2.9
D3	-0.11	-2.09*	-1.35	-0.49*	0.18	0.12	-1.09*	0.29	2.89	-0.2	0.01	0.01*	-0.01	-0.01	10.22	6.84*	-0.46	-0.89	-2.76**	-1.23
D4	-1	-1.09*	-1.02	1.04*	-0.09	-0.05	-1.52	-1.13*	-2.22	-1.8	-0.01	-0.01*	-0.04	-0.04*	5.86	-4.02	-0.15	-1.08**	1.29	0.6
D5	-0.17	1.52**	-1.29	1.07*	-0.15	-0.02	1.20**	-0.02	-15.72	-11.8**	0.01	0	0.01	0.01	-14.42**	-7.04	0.01	0.41	-1.71	-0.97
D6	1.33	0.58	-1.96	-1.07	-1.25	-0.53	-1.13	-1.02	-8.5*	-5.11	-0.02	-0.01*	0.04	0.04*	-6.57	-5.26	0.64*	0.96	2.51	-1.86*
D8	1.69**	-0.17	0.43	-0.18	-0.25	0.15*	3.1	0.2	21.83	9.0*	0.03	0.02**	-0.01	-0.014	22.81	5.89	-0.31	-0.7	-1.55	1.53*
D10	-0.06	-1.31*	3.43	-0.4	0.73	0.08	-0.29	-0.8	-6.11	-3.8	-0.01	-0.01	-0.01	-0.01	-21.11	8.28**	0.38	0.76*	-1.52	-1.01

WW well-watered, SS severe stress, DTF days to flowering, SW seed weight, PL pod length, PPP pods per plant, PH plant height, Phi2 photosystem II efficiency, PhiNPQ photo-protective non-photochemical quenching, LEF Linear Electron Flow, NPQt total non-photochemical quenching, SPAD relative chlorophyll content, **** 0.001 *** 0.01 ** 0.05.

morphological and physiological traits of 21 F₂ crosses evaluated under well-watered and severe water stress are presented in Table 7. The highest negative SCA effects of -5.39, -5.00, and -4.89 for days to flowering were recorded in the crosses (D3 × D8), (D5 × D10), and (D4 × D10), respectively, under severe water stress.

Significantly ($p < 0.01$) positive SCA effects were observed in the crosses D1 × D10 (4.17), D4 × D5 (3.69), and D5 × D10 (3.63) for seed weight under severe water stress. The highest positive SCA effects for pod length were recorded in the crosses D4 × D10 (0.75), D4 × D8 (0.45), and D3 × D6 (0.30), respectively, under severe water stress. The highest positive SCA effects for pods per plant of 7.5, 6.6, and 6.1 were recorded in the crosses (D3 × D5), (D4 × D8), and (D6 × D8), respectively.

Significant ($p < 0.05$) and positive SCA effects of 34.4, 34.1, and 24.21 were observed for plant height in the crosses (D3 × D4), (D3 × D5), and (D3 × D6), respectively, under severe water stress. Cross D5 × D10 recorded the highest positive SCA estimate of 0.3 for Phi2 under severe water stress. Positive SCA effects of 0.7 for PhiNPQ were

recorded in the crosses (D5 × D8), (D5 × D10), and (D8 × D10).

The highest positive SCA effects for leaf area efficiency (LEF) under severe water stress were recorded in the crosses D3 × D6 (46.72), D4 × D8 (18.5), and D4 × D5 (15.82). Three crosses had significant and positive SCA effects for NPQt, including D1 × D5 (6.06), D3 × D4 (3.83), and D6 × D8 (3.93) under severe water stress. The crosses (D6 × D8), (D3 × D6), and (D1 × D3) exhibited the highest significant and positive SCA effects of 8.32, 8.03, and 7.74, respectively, for SPAD under severe water stress.

Mean performance

The mean effect of water stress on the studied traits of seven lablab parental genotypes and crosses evaluated in MUARIK is given in Figure 3. The mean effects of water stress on the studied traits are shown in Figure 3. The mean performances of the lablab parental genotypes and F₂ crosses for the traits studied under well-watered

and severe water stress conditions are presented in Table 8.

Days to flowering

Increasing water stress significantly ($p < 0.05$) reduced the number of days to flowering from 54 under control conditions to 42 days among severely stressed plants. A reduction in the number of days to flowering was recorded in parental genotypes D3 (5 days), D4 (2 days), D6 (5 days), and D8 (6 days) due to water stress; however, parental genotype D10 exhibited delayed flowering time, increasing from 53 days to 57 days. Cross D4 × D5 recorded the longest number of days to flowering at 56 days, while D4 × D10 took the shortest at 46 days.

Seed weight

Water stress significantly ($p < 0.05$) affected seed weight, which was 13.7 g under well-watered

Table 7. SCA estimates for morphological and physiological traits of 21 F₂ crosses evaluated under well-watered and severe water stress at MUARIK.

Parent	DTF		SW		PL		PPP		PH		Phi2		PhiNPQ		LEF		NPQt		SPAD	
	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS
D1×D3	-1.56	2.61*	-6.06	-2.67*	0.31	0.12	-1.63	-1.5	-19	14.54	-0.04**	-0.04	-0.02	-0.05	41.32	4.65	-0.14	-2.14	10.51***	7.74
D1×D4	2.83	1.11	-2.39	-1.78	0.18	0.09	1.7	-0.4	-55.35	-22.3	-0.06**	-0.02	0.12**	0.12	-49.3	-44.2	0.32	2.34*	-4.08	0.83
D1×D5	0.11	-3**	-2.28	0.19	0.37	0.26	-5.96	3.1	-25.1	8.71	0.12***	-0.02	-0.11*	0.13	-32.74	8.8	1.29	6.06	-4.67	-1.51
D1×D6	0	-0.06	1.39	1.24	0.25	-0.01	6.1	0.4	-27.3	-11.85	-0.03	0.01	0.02	-0.1	30.94	3.13	1.17	-0.08	7.04**	0.18
D1×D8	-0.22	-2.17	-6	2.94*	-0.35	-0.09	-3.46	0.3	89.9**	8.21	-0.03	0.01	0.02	0.03	-33.6	-15.36	0.49	-0.04	-10.35**	0.55
D1×D10	-0.83	1.83	4.66	4.17**	0.26	0.13	-5.0	3.26*	29.82	-13.4	0.05**	0.02	0.03	-0.047*	21.13	-9.64	-2.23*	-0.97	5.49*	-0.45
D3×D4	-4	1.89	-3.44	1.83	0.74*	-0.16	5.6*	0.21	-37.46	34.4*	-0.02	0	0.02	0.12	20.77	13.71	4.66***	3.83	-2.92	-0.48
D3×D5	-1.22	-1.22	4.67	-3.21**	0.94**	-0.14	7.5**	-0.85	46.6**	34.1	0.01	0.01	0	-0.016	-56.7*	-9.17	-0.78	-0.53	-0.84	-0.55
D3×D6	0.17	-0.28	3.85**	-1.17	1.38	0.3	-2.3	0.54	-26.7	24.21	0.05	0.02	-0.05*	-0.1	-46.94	46.72	-1.49	-3.7	-1.11	8.03
D3×D8	-0.67	-5.39***	-5.39	0.55	-0.82**	-0.2	2.9	0.88	13.3	2.71	0.04*	0.01	-0.03	-0.12*	64.31**	-2.87	-0.51*	-0.44	-12.1***	-8.77
D3×D10	0.5	-2.39*	13.17	-1.23	-6.01	-0.76	-2.1	-0.21	16.9	10.6	0.02	0.01	0.04	0.05*	50.4*	-18.28	-0.21	0.54	-2.65	1.73
D4×D5	-1.72	2.78**	1.28	3.69**	4-2.07	-0.09	5.8*	0.1	-45.9**	-7.85	-0.07	0.02	0.021	-0.14	39.03	15.82	-1.3	-3.62	-13.7	-0.32
D4×D6	0.67	-0.28	-2.56	-0.26	6.15	0.2	3.5	-0.66	25.8	4.76	0.10***	0	-0.05	-0.08*	35.15	-26.32	-1.48	-2.8	4.05	1.73
D4×D8	-3.67	-2.39*	-0.28	0.94	-2.35	0.45	6.6**	0.83	-54.24	-44.2**	-0.07	-0.02	0.01	-0.06*	-39.21	18.5	-0.34*	2.36	2.99	1.6
D4×D10	2.83	-4.89***	-2.11	-4.8***	-1.04***	0.75	-4.6	2.26	37.4*	-15.85	0.06**	-0.03	-0.04*	0.06	72.71**	-40.63	2.40**	3.7	-12.9***	-1.69
D5×D6	-0.11	1.11	5.67	-5.0***	-1.44	0.25	-2.13	1.9	-30.3*	3.54	0.021	0	-0.036*	-0.04	54.3*	11.73	-1.73	-2.06	-2.6	1
D5×D8	1.17	-1	7.28	-1.59	-0.32	-0.25	3.8	-3.32	-19.9	-3.12	-0.023	0.01	0.03	0.07	-21.33	-19.21	0.55	1.32	7.83**	3.39
D5×D10	-3.94	-5***	-8.56	3.63**	-1.03	0.41	6.5**	1.04	8.54	-4.79	-0.027	0.03	-0.41*	0.07	-83.17	8.24	1.46	-3.94	-17.25	2.79
D6×D8	-0.28	0.44	3.22	-1.03	-0.43	0.14	-13.96	6.6*	28.5	18.71	-0.04*	-0.04	0.06**	0.1	-25.5	-8.69	1.43	3.93**	-3.82	8.32
D6×D10	-0.78	-1.06	1.89	0.69	-0.73	-0.17	-5.1*	2.15	45.2**	18.1	-0.02	0	0.02*	0.04	-34.6	0.2	-0.18	-1.48	1.87	-4.87
D8×D10	1.72	2.83**	-5.5	-0.12	0.73	0.17*	7.93	-1.4	40.2**	-3.85	-0.02	0.01	0.03**	0.07	-33.83	-30.51	0.23	-1.1	5.39*	-4.96

WW well-watered, SS severe stress, DTF days to flowering, SW seed weight, PL pod length, PPP pods per plant, PH plant height, Phi2 photosystem II efficiency, PhiNPQ photo-protective non-photochemical quenching, LEF Linear Electron Flow, NPQt total non-photochemical quenching, SPAD relative chlorophyll content, '****' 0.001 '***' 0.01 '**' 0.05.

conditions but reduced to 5.4 g under severe water stress. Parental genotypes D3 and D10 recorded the highest seed weight of 10 g, while D4 recorded the least weight of 3 g under severe water stress. Crosses D4 × D5 and D1 × D10 recorded the highest seed weights of 11 and 9.5 g, respectively, while cross D4 × D10 showed the greatest reduction in seed weight, decreasing by 85.7% under severe water stress.

Pod length

A significant ($p < 0.05$) reduction in pod length was observed with increasing water stress. Compared to the average pod length of 4.4 cm in control plants, it declined to 3.59 cm under water stress. Parental genotype D8 recorded the longest pod length at 4.2 cm, while D6 recorded the shortest at 3 cm under severe water stress. Cross D5 × D8

had the longest pods (4.55 cm), while cross D6 × D8 had the shortest pod length (2.55 cm) compared to other crosses under severe water stress.

Pods per plant

The average number of pods per plant showed no

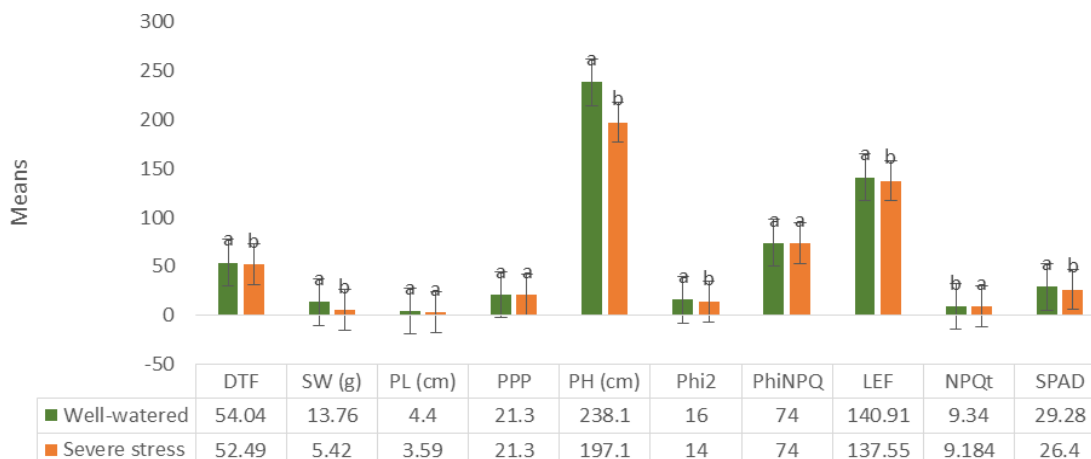


Figure 3. Mean effect of water stress on the morphological and physiological traits of 7 lablab parental genotypes and crosses. DTF days to flowering, SW seed weight, PL pod length, PPP pods per plant, PH plant height, Phi2 photosystem II efficiency, PhiNPQ non-photochemical quenching, LEF Linear Electron Flow, NPQt total non-photochemical quenching, SPAD relative chlorophyll content, %CV coefficient of variation, LSD least significant difference, means with the same letter are not significantly different.

significant differences between control and water-stressed plants. Parental genotype D1 recorded the greatest number of pods per plant (7), while D4 recorded the least (3) under severe water stress. The highest and lowest number of pods per plant under severe water stress were recorded in crosses D3 × D6 (16.5) and D4 × D5 (4), respectively.

Plant height

Water stress had a significant ($p < 0.05$) effect on plant height. Compared to the average plant height (PH) in control plants, which was 238.1 cm, it declined to 197.1 cm under severe water stress. The highest and lowest plant heights of 255 cm and 105 cm were recorded in parental genotypes D1 and D6, respectively. Cross D1 × D8 had the longest plant height at 250 cm, while D5 × D8 recorded the shortest at 150 cm under severe water stress.

Phi2

Increasing water stress significantly ($p < 0.05$) decreased the Phi2 efficiency from 0.16 to 0.14 under severe water stress. The highest and lowest Phi2 values of 0.14 and 0.06 were recorded in parental genotypes D8 and D5, respectively, under severe water stress. Cross D3 × D8 recorded the highest Phi2 at 0.24, while D1 × D4 recorded the lowest at 0.07 under severe water stress.

PhiNPQ

The average PhiNPQ remained unchanged under severe

water stress. Parental genotypes D5 (0.86) and D8 (0.67) recorded the highest and lowest PhiNPQ values, respectively, under severe water stress. The highest and lowest PhiNPQ values were recorded in crosses D1 × D4 (0.84) and D4 × D10 (0.28), respectively, under severe water stress.

LEF

Water stress had a non-significant effect on LEF. The parental genotypes with the highest and lowest LEF under severe water stress were D1 (134.74) and D5 (74.6), respectively. Cross D3 × D8 recorded the highest LEF at 189.04, while cross D1 × D5 recorded the lowest LEF at 97.11 under severe water stress.

NPQt

The effect of water stress on NPQt was non-significant, with genotypes D5 (12.41) and D8 (9.35) recording the highest and lowest NPQt values under severe water stress. Crosses with the highest and lowest NPQt were D1 × D6 (14.51) and D3 × D8 (4.52), respectively, under severe water stress.

SPAD

Water stress caused a significant ($p < 0.05$) reduction in SPAD values, which declined from 29.28 under control conditions to 26.40 under severe stress. Genotype D3 recorded the highest SPAD value of 31.98, while D10 recorded the lowest SPAD of 22.27 under severe water

Table 8. Mean performance of lablab parental genotypes and crosses for morphological and physiological traits evaluated at MUARIK under well-watered and water stress conditions.

Parent	DTF		SW (g)		PL (cm)		PPP		PH (cm)		Phi2		PhiNPQ		LEF		NPQt		SPAD	
	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS	WW	SS
D1	56	56	12.5	11	5.2	2.95	23.5	7	285	255	0.15	0.13	0.72	0.78	159.41	134.74	7.04	9.9	28.89	26.12
D3	59	54	12	12	4.6	3.35	26	5.5	225	175	0.16	0.09	0.76	0.83	206.94	123.67	10.06	10.57	35.73	31.98
D4	55.5	54	18	3	4.4	3.05	15.5	3	230	220	0.15	0.11	0.76	0.83	214.22	82	7.91	12.37	32.81	30.55
D5	51	51.5	3.5	7.5	4.25	3.4	26	5.5	210	150	0.15	0.06	0.86	0.78	141	74.63	10.11	12.41	34.05	24.6
D6	59	54	8.5	4.5	3.8	3	16	5	215	105	0.13	0.12	0.77	0.8	135.34	119.01	9.97	11.59	29	27.35
D8	60	54.5	4	3	3.75	4.2	24.5	5.5	315	200	0.18	0.14	0.67	0.73	188.87	111.18	8.82	9.35	29.22	26.25
D10	53	57	17.5	12	7.75	3.2	21.5	5	220	145	0.14	0.12	0.76	0.8	108.85	94.65	9.24	11.56	30.76	22.27
D1xD3	53	54	7.5	1.5	4.7	3.75	19.5	9	260	195	0.18	0.1	0.7	0.83	198.18	125.5	6.69	12.1	35.8	32.66
D1xD4	56.5	53.5	11.5	4.5	4.35	3.25	19.5	10	185	190	0.16	0.07	0.75	0.84	127.15	98.41	8.9	9.9	30.74	29.93
D1xD5	54.5	52	15	6.5	4.15	3.75	27.5	11	215	175	0.25	0.15	0.67	0.78	170.54	97.11	9.66	11.8	27.77	23.66
D1xD6	52	54	9.5	6	4	3.8	20.5	14	240	200	0.13	0.11	0.79	0.82	153.78	139.37	10.6	14.51	35.95	31.33
D1xD8	55	53	28.5	8	3.55	3.4	18.5	7.5	275	250	0.18	0.12	0.7	0.8	151.16	144.02	7.23	9.56	25.11	20.79
D1xD10	54.5	54	24	9.5	3.85	3.6	19	10.5	240	180	0.18	0.13	0.71	0.77	137.25	116.54	8.05	9.06	28.78	27.86
D3xD4	53.5	51.5	8.5	7	4.7	4	13.5	12	247.5	170	0.12	0.12	0.82	0.82	186.24	114.37	12.67	14.36	24.27	23.48
D3xD5	54	51	4.5	2	4.25	3.35	17.5	11.5	275	235	0.18	0.13	0.73	0.77	128.73	108.93	8.42	8.57	33.77	24.01
D3xD6	54.5	51	14.5	7.5	4	4.4	19	16.5	270	235	0.18	0.11	0.77	0.7	135.39	116.48	7.95	8.87	34.96	26.84
D3xD8	52.5	47	13.5	4.5	4.25	4.1	22	16	255	160	0.25	0.24	0.59	0.62	212.96	189.04	4.13	4.52	20.54	9.92
D3xD10	55.5	47	22.5	2.5	4.9	3.55	24	5.5	215	190	0.15	0.13	0.76	0.79	203.69	110.81	8.69	10.16	27.04	22.72
D4xD5	52.5	56	15	11	4.2	3.75	23	4	250	170	0.22	0.13	0.64	0.79	150.97	132.73	8.24	8.34	25.97	24.85
D4xD6	55	52	9	5.5	4.3	3.8	20	4.5	255	160	0.23	0.17	0.64	0.71	177.31	143.45	6.45	7.9	37.54	21.6
D4xD8	54	51	10	7	4.4	3.1	29	11.5	262.5	230	0.14	0.13	0.64	0.74	133.38	101.61	5.7	7.21	31.62	29.51
D4xD10	49.5	45.5	7	1	4.05	4	20.5	13.5	225	200	0.18	0.13	0.8	0.28	198.95	152.98	5.64	10.55	28.69	8.24
D5xD6	55	56	4.5	0.75	3.7	2.5	21	12	220	190	0.21	0.15	0.65	0.77	211.89	124.43	6.58	9.87	26.7	18.44
D5xD8	50.5	55	12	4.5	4.65	4.55	22	17	190	150	0.15	0.13	0.76	0.79	195.89	101.89	9.01	10.08	41.12	24.75
D5xD10	54	48	18.5	9.5	4.55	3.8	7	16	235	210	0.12	0.08	0.85	0.8	104.07	117.25	11.16	10.97	36.02	31.49
D6xD8	58.5	55.5	9.5	3.5	4.65	2.55	25.5	3.5	239	235	0.14	0.1	0.77	0.83	141.65	116.52	10.6	12.01	28.84	25.68
D6xD10	55	51	16.5	5	4.05	3.25	22	2	245	230	0.13	0.12	0.77	0.79	125.81	113.44	8.63	10.5	32.67	22.53
D8xD10	56	56	11.5	4.5	5.15	4.65	32	7	250	242.5	0.2	0.16	0.69	0.75	131.77	108.78	7.93	8.09	34.38	18.38
% CV	6.03		56.78		24.26		53.96		23.9		32.48		15.05		34.73		28.32		30.5	
LSD	1.08		7.681		1.376		16.3		73.7		0.07		0.16		68.51		5.206		3.217	

WW indicates well-watered, and SS indicates severe stress. DTF refers to days to flowering, SW to seed weight, PL to pod length, PPP to pods per plant, PH to plant height, Phi2 to photosystem II efficiency, PhiNPQ to photo-protective non-photochemical quenching, LEF to linear electron flow, NPQt to total non-photochemical quenching, and SPAD to relative chlorophyll content. Significant results are indicated at $P < 0.05$.

stress. Cross D1 × D3 recorded the highest SPAD at 32.66, while cross D3 × D8 recorded the lowest SPAD at 9.92 under severe water stress.

DISCUSSION

Effect of water stress on morphological traits

Significant genotypic differences for all morphological traits indicated the presence of adequate genetic variability among the evaluated lablab genotypes. This variability is highly relevant in breeding programs aiming for drought tolerance, as it can be exploited to develop drought-adapted lablab cultivars. Flowering time plays a crucial role in determining grain yield, especially when crops are subjected to prolonged or severe drought stress conditions (Wang et al., 2022). Increasing water stress during the reproductive stage of flowering was highly detrimental to grain yield. In this study, water stress delayed the average flowering time, which occurred two days later than in control plants. Late flowering under limited water availability is associated with a delayed floral transition between panicle initiation and pollen meiosis, adversely affecting pollination, leading to flower loss, grain shedding, and a higher proportion of undeveloped grains (Patra et al., 2024).

Genotypes D2 and D7 took the longest time to flower under water stress conditions, negatively impacting their yield. Similar findings have been reported in rice subjected to water stress (Pappula-Reddy et al., 2024; Kang and Futakuchi, 2019). Early flowering time is often associated with early maturity, which enables reproductive growth to occur before terminal stress (Helmsorig et al., 2024). Genotypes D1, D5, and D9 exhibited the shortest flowering times under severe water stress, indicating early flowering, which is a partial escape response to ensure survival by completing their life cycle before drought. Early flowering times under drought stress have also been reported in rice, pearl millet, and sorghum (Ishimaru et al., 2022; Choudhury et al., 2022; Frantová et al., 2024).

Drought stress was associated with delays in the days to podding and maturity in genotypes D2 and D7, indicating sensitivity of these genotypes to water stress during the reproductive stage. This sensitivity is attributable to reduced translocation of assimilates toward the developing reproductive parts, resulting in flower abscission and reduced pod setting (Jarín et al., 2024). However, genotype D1 exhibited the shortest time to podding and maturity, indicating early maturity, which is desirable for drought escape.

Significant variations were observed in plant growth traits among lablab genotypes subjected to water stress. Such differences in plant growth among genotypes may be attributed to diversity in root depth and genetic potential for water uptake from the rhizosphere (Mamnabi et al., 2020). In this study, water stress caused dramatic reductions in

plant height, pod length, pod width, number of pods per plant, and seed weight by 25%, 29%, 79%, and 80%, respectively. The reduction in plant height under water stress could be attributed to dehydration of the protoplasm and loss of turgidity, leading to diminished cell expansion and division (Nyaupane et al., 2024). Similar findings have been previously reported in soybean, wheat, and Arabidopsis (Poudel et al., 2023; Nyaupane et al., 2024; Yang et al., 2021). Grain yield is generally associated with pod length, pod width, number of pods per plant, and seed weight. A remarkable reduction in mean seed weight of up to 80% was observed under severe water stress compared to the control. This reduction in seed weight may be attributed to disturbed photosynthetic translocation and nutrient uptake due to moisture shortage, which lowered the rate of metabolic processes needed to accumulate starch and dry matter, thereby affecting growth and development (Du et al., 2024). Under drought stress conditions, the availability of assimilate required for seed filling typically declines. In such cases, genotypes can preserve carbohydrates in the stem to maintain better seed filling or partition more photosynthates to the grain relative to the shoot, leading to an increase in grain yield (Semahegn et al., 2020). In this study, genotypes D7, D8, and D10 recorded the highest seed weights, suggesting better adaptation to nutrient resource partitioning. A positive correlation between seed weight and pods per plant confirmed the relationship between lablab yield and pod number, indicating that increased seed weight was associated with a higher proportion of filled pods per plant.

Effects of water stress on physiological traits

Significant variations across genotypes for physiological traits were observed, indicating the presence of genetic diversity that may be utilized in breeding lablab for drought tolerance. In this study, the decline in water availability reduced the fresh and dry weights of the shoots and roots of the lablab genotypes, indicating susceptibility to water stress. The decline in biomass could be attributed to decreased plant growth, leaf senescence, and defoliation, leading to a reduction in photosynthesis due to changes in water and nutrient uptake (Brown et al., 2021). This finding aligns with reports on wheat subjected to water stress (Zhao et al., 2020). However, genotype D7 showed higher dry weight compared to the other genotypes, indicating better drought stress tolerance.

The plant relative water content (RWC) is one of the most important physiological traits for assessing cell hydration and is arguably the most meaningful measure of plant water status under water deficit. Plant RWC indicates the ability of plants to maintain adequate water status during water stress. RWC in leaves responds to drought stress and correlates with drought tolerance, making it a better indicator of drought stress than other plant indices. Some studies have suggested that high RWC is closely

related to drought resistance, as observed in cowpea landraces (Zegaoui et al., 2017) and wheat (Makebe et al., 2024), and it has been successfully used as a screening tool for selecting drought-tolerant barley (Langan et al., 2024).

A significant reduction in average shoot and root relative water content was observed due to water stress, with genotypes D10 and D1 recording the lowest shoot and root relative water content under severe water stress. Insufficient soil moisture content could have limited the ability of the lablab genotypes to compensate for water loss through transpiration, resulting in an inability to accumulate and adjust osmotically to maintain tissue turgor and physiological activities. This research is consistent with findings in soybean and cotton genotypes subjected to water stress (Bukan et al., 2024; Guo et al., 2024). A lesser reduction in RWC in response to drought stress has been associated with drought-tolerant genotypes (Forghani and Aghaie, 2024). Similarly, in our study, genotypes D3, D2, and D7 maintained a greater amount of water in the shoots and roots under water stress than the other genotypes, suggesting a better adaptive response to drought.

Chlorophyll fluorescence is a non-destructive measurement of photosynthetic efficiency and photochemical and non-photochemical quenching activities in plants under biotic and abiotic stresses (Moustakas et al., 2022). Higher Phi2 efficiency serves as a protective mechanism to enhance water retention through turgor adjustment under water stress, accumulating energy to promote the dark reactions for carbon assimilation and the accumulation of organic matter (Khan et al., 2018). In this study, water stress resulted in photoinhibition of Phi2 efficiency, a decline in photochemical quenching activities, and an increase in the non-photochemical quenching among lablab genotypes. Genotypes D4 and D9 recorded the lowest Phi2 activity under severe water stress, indicating sensitivity to water deficit. Our results are consistent with previous reports by Akello et al. (2023) and Zheng et al. (2019).

The disruption of Phi2 efficiency is attributable to either non-stomatal or stomatal conductance effects. Under severe water stress, Phi2 efficiency may be inhibited by inadequate transfer of energy absorbed by chlorophyll within the light-harvesting complex, which hinders electron transport processes and ATP synthase formation (Ghasemi and Shafiee, 2020). Additionally, water stress leads to stomatal closure, limiting the diffusion of CO₂ for Rubisco, which restricts the electrons required for photochemical quenching, resulting in Phi2 photodamage (Guidi et al., 2019). Genotypes D2, D3, and D5 exhibited the greatest photosynthetic efficiency under severe water stress, implying they would be more suited to drought conditions.

The Fv/Fm ratio represents the maximum quantum yield of Phi2 in an unstressed plant after sufficient dark adaptation and is used to measure stress in leaves (Wu et

al., 2023). In our study, the mean Fv/Fm ratio in moderately stressed plants remained the same as in the control plants, but it declined under severe water stress, with genotype D4 recording the lowest Fv/Fm ratio, confirming photoinhibition of Phi2 under severe stress. Water stress led to the closure of the Phi2 reaction center, resulting in restricted electron transfer and a decrease in the amount of light energy available for the photochemical reactions within the Phi2 reaction center. These findings are similar to those in a study by Epaku et al. (2021). Genotypes D7 and D3 exhibited a higher Fv/Fm ratio under severe stress, reflecting greater Phi2 efficiency as a drought tolerance mechanism.

LEF involves the transfer of excited electrons from photosystem II to photosystem I, leading to the production of ATP and NADPH, which are vital for the subsequent light-independent reactions of photosynthesis (Shimakawa and Miyake, 2021). In this study, LEF remarkably declined in genotypes D4 and D6, indicating susceptibility to water stress. Our findings are consistent with reports by Shin et al. (2021) and Wang et al. (2022). A decline in LEF is associated with a decrease in leaf water content due to drought stress, which affects photosynthesis through stomatal closure, causing a shortage of CO₂ supply that leads to a decline in LEF (Wang et al., 2018).

Non-photochemical quenching parameters (PhiNPQ and NPQ) estimate the rate of heat loss from Phi2 by removing excess excitation energy to prevent the formation of free radicals that could damage the photosynthetic apparatus (Murakami et al., 2024). This result showed that the PhiNPQ and NPQt parameters of lablab genotypes increased significantly under moderate stress, indicating a high involvement of non-photochemical quenching mechanisms. Under moderate stress, lablab genotypes dissipated excess excitation energy as heat to prevent photooxidation and photoinhibition caused by excessive energy absorbed by the Phi2 reaction center. However, the PhiNPQ and NPQ values significantly declined under severe water stress, signifying limited heat dissipation capacity and destruction of the Phi2 apparatus, probably due to reduced electron transport and quantum efficiency, as indicated by the reduced LEF and Fv/Fm ratio. Similar findings have been reported by Madumane et al. (2024).

PhiNO, a parameter that represents the non-regulated fraction of light energy dissipated as heat or fluorescence (Gitau et al., 2022), also declined under severe water stress, indicating that the photo-protective mechanisms of lablab genotypes were impaired. This aligns with findings by Huang et al. (2019) on maize seedlings under drought stress. SPAD, an index for measuring chlorophyll content, can be used to assess plant responses to drought stress (Pallavolu et al., 2023). In this study, SPAD values declined due to water stress, with genotypes D1 and D9 showing the highest SPAD reduction, implying susceptibility to water stress. This decline was likely due to an insufficient supply of the necessary factors for

chlorophyll synthesis, resulting from the degradation of photosynthetic pigments and leading to the destruction of their structure under stress conditions (Thakur and Shinde, 2020). However, genotypes D3 and D7 maintained a higher SPAD value, suggesting that they could sustain a high photosynthetic rate, thereby increasing biomass production and demonstrating better endurance to drought stress. Wei et al. (2024) reported a significant positive correlation between SPAD content and photosynthetic rate in tomatoes.

Analysis of variation of the parental genotypes and crosses

Significant variations among the parental genotypes and crosses in morphological and physiological traits indicated considerable genetic variability among the lablab parental genotypes, which could be exploited for the genetic improvement of lablab yield under drought stress conditions. The significant GCA mean squares for days to flowering, pod length, Phi2, PhiNPQ, and NPQt indicated that additive gene action was involved in the expression of these traits, implying that they are fixed and that genetic gain could be achieved through early-stage selection of the progenies to produce pure lines (Xu et al., 2019). Rony et al. (2019) reported the involvement of additive gene action in the expression of days to flowering in lablab beans. The SCA mean squares were highly significant for days to flowering, seed weight, pod length, PhiNPQ, and SPAD, highlighting the involvement of non-additive gene action, which could be useful for hybrid production where dominance is important at early stages of selection. Nayak et al. (2018) reported that non-additive gene action predominated for pod length, days to flowering, and seed weight in lablab. Both types of gene action contributed significantly to traits such as days to flowering, pod length, and PhiNPQ, indicating the importance of both additive and non-additive effects in the genetic control of these traits. This implies that both gene effects should be considered for the selection of superior lines when developing breeding schemes (Arruda et al., 2019). Similar findings were reported in cowpeas (Olajide and Olawale, 2021).

Both the GCA and SCA mean effects were not significant for LEF, number of pods per plant, and plant height, implying that epistatic gene effects may play a substantial role in the genetic control of these traits. The Baker's ratio was high (above 50%) for all the studied traits except for SPAD and the number of pods per plant, indicating the preponderance of additive gene effects in the expression of specific traits over non-additive gene action. Similar results regarding days to flowering, pod length, and pod weight exhibiting a predominance of additive gene effects have been reported in maize (Lima et al., 2019). This gene effect could facilitate breeding programs for drought tolerance through genetic gain by

fixing the traits over successive generations of self-fertilization. The estimated SCA variance ratio was higher than the GCA variance ratio for SPAD and the number of pods per plant, suggesting the predominance of non-additive gene action, which implies that these two traits are governed by dominance or epistatic gene effects (Yang et al., 2018). This result is similar to findings by Al-Mamun et al. (2022) on hibiscus.

The broad-sense coefficient of genetic determination was high for most traits under water stress, except for pod length, pods per plant, and Phi2, indicating a high heritability of these traits due to the substantial role played by genetic variation over the observed phenotypic variation among the lablab genotypes. This information is valuable for breeding programs aimed at enhancing drought tolerance. The narrow-sense coefficient of genetic determination was low for pod length, pods per plant, LEF, and SPAD, indicating the involvement of non-additive gene effects, which have little genetic influence on the expression of these traits. Thus, focus could be placed on improving environmental conditions or other non-genetic factors to enhance these traits.

General combining ability

The combining ability was investigated to identify genotypes with high genetic potential for creating cross combinations with desirable traits and to examine the action of genes involved in trait expression. Parental genotype D3 was the highest negative general combiner for days to flowering, indicating early flowering, which leads to early maturity. Early flowering before upcoming drought stress conditions is an important trait that can be used to reduce days to flowering among progenies, helping them escape terminal drought (Seleiman et al., 2021). In addition, genotype D3 was the highest positive general combiner for pods per plant, making it a desirable parent for improving these traits in a breeding program. Parental genotype D8 had favorable GCA effects for pod length, plant height, and Phi2 efficiency, and exhibited the longest pod length under severe water stress; it could therefore be recommended as a parent for enhancing yield-related traits in a breeding program. Genotype D5 showed a positive and significant GCA effect on seed weight, which is desirable for increasing crop yields under drought stress conditions. In this study, genotypes D6, D10, and D1 were the most desirable general combiners for PhiNPQ, LEF, NPQt, and SPAD, thus they could be considered for breeding drought-tolerant lablab. Parental genotype D4 did not exhibit any beneficial traits and showed no significant contribution to the traits of interest; therefore, it is not considered a desirable candidate for the breeding program. A positive relationship between mean performance and GCA effects was observed among the lablab genotypes. For instance, parental genotype D3 was early flowering and showed significant negative GCA

effects for this trait. Genotype D3 also demonstrated high mean performance and positive GCA effects for seed weight and SPAD. A similar pattern of correlation was observed for genotype D8 concerning pod length and Phi2 efficiency, suggesting that genotypes D3 and D8 were excellent general combiners contributing the greatest number of desirable traits under severe water stress conditions. Thus, selecting these parental genotypes based on their high general combining ability could be essential for a successful breeding program aimed at enhancing drought tolerance.

Specific combining ability

SCA elucidates the deviation of hybrid or cross performance from that of the parental genotypes utilized and allows for the estimation of non-additive gene effects. Hybrids with significant SCA effects are excellent choices for the selection of segregates (Sakran et al., 2022). The cross (D3×D8) exhibited the highest significantly negative SCA effect for early flowering, followed by (D5×D10) and (D4×D10). The cross combinations with significant positive SCA effects, which were desirable for the improvement of morphological traits, included D1×D10, D4×D5, and D5×D10 for seed weight; D4×D10, D4×D8, and D3×D6 for pod length; D3×D5, D4×D8, and D6×D8 for pods per plant; and D3×D4, D3×D5, and D3×D6 for plant height. Conversely, the best cross combinations for improving physiological traits were D5×D10 for Phi2; D5×D8, D5×D10, and D8×D10 for PhiNPQ; D3×D6, D4×D8, and D4×D5 for LEF; D1×D5, D3×D4, and D6×D8 for NPQ; and crosses D6×D8, D3×D6, and D1×D3 for SPAD, indicating that the parental genotypes were genetically diverse.

The cross combinations exhibiting significant SCA effects comprised parental genotypes with both low and high GCA effects, such as D4×D8 for seed weight, D4×D10 for pod length, and D3×D4 for plant height. These findings indicate the involvement of both additive and non-additive gene actions, acting in a complementary fashion to maximize the effects of the two gene actions in the expression of lablab bean traits, which could be exploited to develop high-yielding varieties under drought stress (Díaz-Valenzuela et al., 2023). Significant SCA effects observed from crosses between parental genotypes that were both good general combiners, such as D3×D8, D3×D5, and D5×D10 for early flowering, pods per plant, seed weight, and Phi2 efficiency, imply additive gene activity. This suggests that the best progeny might be derived from crosses involving genotypes with the highest GCA. Such crosses would be desirable segregants to be fixed early in an advanced generation, as reported by Ginkel and Ortiz (2018). A comparison between the mean performance and SCA effects of the crosses revealed a positive relationship, where some crosses, such as D4×D10, D4×D5, and D1×D3, demonstrated high mean performance and positive SCA effects for early flowering, seed weight, and SPAD, indicating their desirable specific

combining ability in a breeding program. However, the mean performance and SCA effects of most crosses were dissimilar under water stress, implying that both parameters should be considered in a breeding program for the selection of hybrids.

Conclusion

Lablab genotypes exhibited considerable genotypic variation in morphological and physiological changes, which could be exploited for genetic improvement aimed at enhancing drought tolerance. Severe water stress during the reproductive stage led to a significant decline in the morphological and physiological traits of the lablab genotypes. However, the more drought-tolerant genotypes D1, D3, and D7 were primarily associated with a greater ability to escape drought, accumulate more starch, exhibit high photosynthetic efficiency, and enhance water and nutrient uptake. These genotypes could be leveraged for higher yields under water stress conditions. Both additive and non-additive gene actions were important in the expression of the morphological and physiological traits; additive gene action was more predominant in controlling physiological traits, whereas non-additive gene action played a greater role in morphological traits. Parental genotypes D3 and D8 emerged as the most promising general combiners, possessing the highest number of desirable traits for improving lablab yield. The crosses D3×D8, D3×D5, and D5×D10 showed the most promise, with high mean performance and significant SCA effects for yield per plant, making them suitable candidates for breeding for drought tolerance.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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