

## ORIGINAL ARTICLE

## Plant Genetic Resources

# Identification of drought and heat tolerant tepary beans in a multi-environment trial study

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## Abstract

Abiotic constraints, such as drought and heat driven by climate change, negatively impact the production of the common bean (*Phaseolus vulgaris* L.), an essential grain legume worldwide. The ability to tolerate drought and heat stress in common bean can be improved by introducing genetic variation from related species, such as tepary bean (*Phaseolus acutifolius* A. Gray), which has recently gained attention because of its adaptation to drought and heat stresses and potential use as a genetic resource and alternative crop. To better understand the phenotypic response of tepary bean to drought and heat stress in multiple environments and trials and to select highly adapted tepary beans, we conducted two field experiments. In Experiment 1, we compared the adaptation to drought stress of tepary bean ( $n = 10$ ), common bean ( $n = 10$ ), and Lima bean (*Phaseolus lunatus* L.;  $n = 9$ ) by assessing the reduction in grain yield under terminal drought compared to well-irrigated conditions in two California locations with arid summer conditions. Of the three species, tepary bean showed the statistically strongest adaptation to terminal drought, followed by Lima bean and common bean. In Experiment 2, we evaluated a set of 22 tepary beans from contrasting origins for drought and heat stresses across multi-environment trials

**Abbreviations:** ALV, Alvarado, Colombia; ANOVA, analysis of variance; BLUE, best linear unbiased estimator; BLUP, best linear unbiased predictor; CAR, Caribia, Colombia; CIAT, International Center for Tropical Agriculture; DREC, University of California Desert Research and Extension Center; Dr, drought stress; FA1, factor analytic order 1; FA2, factor analytic order 2; GH, growth habit;  $G \times E$ , Genotype  $\times$  Environment; Ht, heat stress; Irr, well-irrigated; MET, multi-environment trials; PAL, Palmira; PSC, primary seed color; SSC, secondary seed color; SCP, seed color pattern; SCBR, seed brilliance; SSZ, seed size; TARS, Tropical Agriculture Research Station; UCD, University of California, Davis; UNL, University of Nebraska Lincoln; USDA, United States Department of Agriculture; WRPIS, USDA-National Plant Germplasm System-Western Regional Plant Introduction Station; WSREC, University of California West Side Research and Extension Center.

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(METs) in California, Nebraska, and Colombia, with common bean as a control. We found a considerable variation in the tepary bean phenotypic response to these MET conditions, as a result of a strong genotype  $\times$  environment interaction. Also, we identified tepary bean accessions adapted to drought, heat, and well-irrigated conditions across multiple climate zones. Understanding the performance of tepary bean across multiple environments and identifying tepary beans with broad and target-specific adaptation will maximize the potential use of the species.

### Plain Language Summary

The effect of global warming on agricultural productivity can be potentially mitigated by the choice of crops that are more drought and heat tolerant. Currently, the common bean (*Phaseolus vulgaris*) is the most widely consumed grain legume, as a dry grain or a snap bean, despite its drought and heat susceptibility. We examined whether alternative domesticated relatives, the tepary bean (*P. acutifolius*) and the Lima bean (*P. lunatus*), would be more tolerant to drought by comparing them in side-by-side field trials in two locations of California's Central Valley under irrigated conditions, simulating terminal drought conditions. Results show that tepary bean and, to a lesser extent, Lima bean are more tolerant of this type of drought conditions than common bean. A further, in-depth study of tepary bean confirmed the superiority of tepary bean. Nevertheless, it also showed intraspecific diversity for drought tolerance and the merit of breeding to achieve further drought tolerance improvement.

## 1 | INTRODUCTION

It has become abundantly clear that humanity is faced with a rapid change in the global climate (IPCC, 2023). This change is anthropogenic as it results in the sharply increased emission of greenhouse gases, mainly carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), and nitrous oxides (N<sub>2</sub>O), mainly since the Industrial Revolution in the 19th century. Consequently, global surface temperature has increased by 1.1°C since the 19th century. Global greenhouse gas emissions have continued to grow from 2010 to 2019, arising from various processes such as fossil fuel energy use, land use and land-use changes, lifestyles, and production and consumption patterns (IPCC, 2023). The goal of limiting global warming to 1.5 or 2.0°C seems increasingly unattainable. In addition, observed changes in extreme weather events such as heatwaves, excessive precipitations, and droughts are becoming increasingly frequent and contrast with the relative climate stability that characterized the Holocene since the origins of agriculture (Bettinger et al., 2009; Richerson et al., 2001).

The current episode of rapid climate change is reducing food and water security. Among the various agricultural adaptation tactics to these conditions is adopting improved cultivars and alternative crops, the two approaches being long-term mainstays of crop improvement and being not mutually

exclusive (Araújo et al., 2015; Dwivedi et al., 2023; IPCC, 2023; Pathak et al., 2018). Global warming and drought stress, two of the most critical constraints caused by climate change, negatively impact the production of the common bean (*Phaseolus vulgaris* L.) (Beebe et al., 2013), the main *Phaseolus* domesticated species and one of the most widely consumed legumes (Parker & Gepts, 2021; Parker et al., 2023). Prolonged environmental temperatures that surpass 20°C at night and 30°C during the day disrupt the physiology of the common bean plant, leading to a significant yield reduction (Shonnard & Gepts, 1994; Suárez et al., 2020). Similarly, drought stress affects around 70% of the global regions where the common bean is produced (Beebe, 2012). By 2050, the suitable areas to grow common bean will be reduced by 50% due to the dramatic increase in global warming and drought stress (Beebe et al., 2011).

Although there have been efforts to improve the common bean's ability to tolerate high temperatures, these efforts have mainly been focused on selecting genetic variability within the same species under high temperatures in lowland tropical areas (Rosas et al., 2000; Suárez et al., 2020) and selecting lines during seasonal heat stress in temperate climates (Shonnard & Gepts, 1994). Similarly, the improvement of the common bean's ability to tolerate drought stress has primarily focused on the selection of variability within the races

Durango and Mesoamerica under semi-arid conditions in North and Central America, as well as low seasonal precipitation in the tropics (Beebe et al., 2013). However, these efforts have still been insufficient to overcome the coming climate-change-induced drought and heat stresses in common bean and other crops (Parker et al., 2023; Yuan et al., 2023; Zabel et al., 2021).

We posit here that the feasibility of choosing alternative crops to mitigate the deleterious effects of global climate change is facilitated when a phylogenetically closely related, heat- and drought-tolerant crop can be chosen whether to improve individual cultivars of the target crop or to introduce a complementary, alternative crop. We seek to illustrate this approach in the genus *Phaseolus* by comparing the heat and drought tolerance of common bean (*P. vulgaris* L.) with those of tepary bean (*P. acutifolius*; Federici et al., 1990; Mwale et al., 2020; Pratt & Nabhan, 1988; Schinkel & Gepts, 1988, 1989) and Lima bean (*P. lunatus* L.; Garcia et al., 2021; Martínez-Castillo et al., 2023). This is the first study to our knowledge that compares the productivity of three domesticated *Phaseolus* species under well-watered and drought-stressed conditions.

The tepary bean species in the tertiary gene pool of the common bean has recently gained special attention due to its drought and heat tolerance. Because of its inherent adaptation to desert climates (Debouck et al., 2023; Nabhan & Felger, 1978), the tepary bean has unique traits that confer high drought and heat tolerance (Porch et al., 2022). Some tepary beans tolerate very high temperatures in the greenhouse (Rainey & Griffiths, 2005) and field evaluations (Burbano-Erazo et al., 2021). Similarly, the tepary bean has shown high levels of drought stress tolerance under controlled conditions (Markhart, 1985) and field evaluations (Rao et al., 2013). Therefore, the tepary bean is considered a vital genetic resource to improve the common bean's ability to tolerate warmer and drier climates (Barrera et al., 2022; Beebe et al., 2013; Burbano-Erazo et al., 2021; Cruz et al., 2023; Moghaddam et al., 2021; Muñoz et al., 2004). Tepary bean is also considered an attractive alternative crop that could mitigate climate change stresses (Moghaddam et al., 2021). However, the low production and consumption of tepary beans worldwide have delayed breeding efforts to develop improved cultivars with tolerance to biotic and abiotic stresses until recently (e.g., Bornowski et al., 2023; Porch et al., 2022, 2023). Lima bean belongs to the quaternary gene pool of common bean as it cannot be crossed to the latter species (Parker & Gepts, 2021). Nevertheless, it is a species of interest because of its broad adaptation to tropical regions, including humid areas in the rainy tropics (e.g., the Yucatán Peninsula and Central Africa) and arid subtropical areas (in Brazil and Colombia) (Baudoin & Mergeai, 2001; Delgado & Gama-López, 2015).

### Core Ideas

- Tepary bean is better adapted to heat and terminal drought stresses than Lima bean and common bean.
- The environment (location) influences the yield response of tepary beans more than the stress condition.
- Improved tepary beans performed better across multiple environments than tepary landraces or wild accessions.
- Tepary bean with broad adaptation is an essential source to improve common bean or as an alternative grain legume.

We hypothesized that the original arid or hot environments in which tepary and Lima beans originated would confer adaptation across a broad swath of climates, especially in comparison with common bean. To test this hypothesis, we first conducted a terminal-drought evaluation of genotypes of common beans, tepary beans, and Lima beans in two locations in California with different climates, namely the University of California, Davis (UC Davis), and the University of California, Agricultural and Natural Resources, West Side Research and Extension Center (WSREC) during the summer of 2016 (Experiment 1: Figure 1, Table 1). We define terminal drought as drought stress affecting plants in the latter part of the growth cycle, especially from flowering (R6 stage) to physiological maturity (R9; Fernández et al., 1983), either because plants are growing solely under residual soil moisture or because irrigation is limited or eliminated during that period. This type of drought stress is most likely to affect tepary and Lima beans in their respective natural habitats. This evaluation aimed to compare the terminal drought responses of the three *Phaseolus* species and identify potential inter- and intraspecific genetic variation for drought tolerance.

Then, we evaluated 22 tepary genotypes at six locations in Colombia and the United States (Experiment 2: Figures 1 and 2, Table 2) in a multi-environment trial study (MET). This MET study aimed to broaden the understanding of the tepary bean performance across multiple temperate and tropical environments and stress conditions. These conditions involved drought stress and well-watered treatments in climates ranging from humid tropical (Colombia) to arid, hot environments (California's inland valleys and Nebraska's Panhandle). We concluded this study by identifying tepary beans that were broadly adapted across multiple locations as well as drought and heat stress conditions.

TABLE 1 Environmental and weather conditions for well-irrigated (Irr), drought (Dr), and heat (Ht) stress trials.

Trial locations <sup>a</sup>	Year	Decimal coordinates (N: latitude, W: longitude)	Altitude (masl)	Soil order	Köppen–Geiger climate <sup>b</sup>	Average minimum temperature (°C) <sup>c</sup>	Average maximum temperature (°C) <sup>c</sup>	Relative humidity (%) <sup>c</sup>	Trial type <sup>d</sup>	Precipitation during trial (mm)	Irrigation supplied (mm)	Average yield (kg/ha)	Yield reduction (%)
<b>Experiment 1: Comparison of terminal drought tolerance in common, Lima, and tepary beans</b>													
Westside, CA	2016	36.34, –120.11	68	Aridisol	BSk	10.0	25	48.3	Irr	0	204	2261	49
									Dr	0	52	1154	
Davis, CA	2016	38.53, –121.78	16	Entisol	Csa	13.3	32.7	49.6	Irr	0	204	1847	53
									Dr	0	27	876	
<b>Experiment 2: Analysis of genetic diversity for drought and heat stress tolerance within tepary bean</b>													
Drought stress trials													
Palmira, Colombia	2017	3.50, –76.35	956	Mollisol	Af	19.0	30.6	55.5	Irr	228	177	1798	56
									Dr	169	122	783	
Davis, CA	2018	38.53, –121.78	16	Entisol	Csa	13.9	32.7	53.2	Irr	3.2	205	2166	16
									Dr	3.2	50	1816	
Scottsbluff, NE	2018	41.95, –103.70	1317	Mollisol	BSk	13.7	29.5	61.9	Irr	108	344	794	0.3
									Dr	108	0	792	
High heat trials													
Alvarado, Colombia	2017	4.54 6, –74.96	460	Andisol	Af	22.4	33.7	70.3	Ht	344	175	934	48 <sup>c</sup>
Caribia, Colombia	2018	10.76, –74.14	18	Entisol	Af	23.5	33.4	65.0	Ht	215	0	736	59 <sup>c</sup>
Holtville, CA	2018	32.8, –115.44	–22	Entisol	Af	24.3	39.7	37.6	Ht	13.3	965	353	84 <sup>d</sup>
									Dr + Ht	13.3	508	184	91 <sup>e</sup>

<sup>a</sup>Trial locations: Alvarado, Tolima, Colombia; Caribia, Magdalena, Colombia; Holtville, CA, USA; University of California Desert Research & Extension Center, DREC; Palmira, Colombia; CIAT, Palmira, Valle del Cauca; UCD, University of California Davis; Scottsbluff, NE, USA; University of Nebraska, Panhandle Research and Extension Center; Westside, CA, USA; University of California West Side Research & Extension Center, WSREC.

<sup>b</sup>According to Beck et al. (2018); Peel et al. (2007); Rubel and Kottek (2010). See also text and Figure 1.

<sup>c</sup>The climatic conditions are averaged over the duration of the trials from planting to harvest.

<sup>d</sup>The yield reduction was assessed by comparing it to a well-irrigated trial in Palmira in year 2017.

<sup>e</sup>The yield reduction was assessed by comparing it to a well-irrigated trial in Davis in year 2018.

TABLE 2 Tepary bean (*Phaseolus acutifolius*) genotypes used in this multi-environment trial (MET) study.

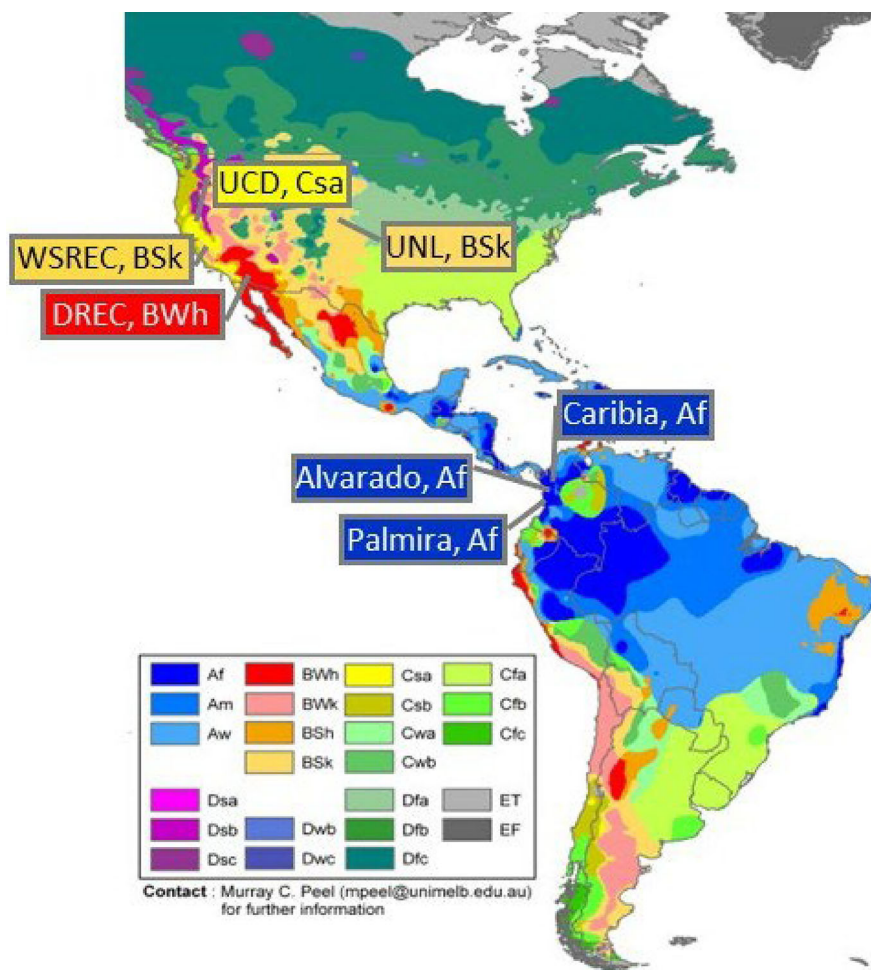
Accession ID	Crop ontology <sup>a</sup>										Source
	Taxa <sup>b</sup>	Panel of 22 GH <sup>c</sup>	PSC	SSC	SCP	SDBR	SSZ	Type	Country	State	
DOR390	v		I1b	Black	0	Dull	Medium	Bred line	Mexico		USDA
G40001	a		IIIb	White	0	Dull	Small	Landrace	Mexico	Veracruz	CIAT
G40019	a	✓	I1b	Black	0	Shiny	Small	Landrace	Mexico	Oaxaca	CIAT
G40022	a	✓	IIIb	White	0	Dull	Small	Landrace	USA	Arizona	CIAT
G40027	a		IIIb	White	0	Dull	Small	Landrace	Costa Rica		CIAT
G40036	a	✓	I1b	Black	0	Shiny	Small	Landrace	Mexico	Oaxaca	CIAT
G40056	a	✓	IIIb	Cream-beige	Black	Speckled	Small	Wild	Mexico	Sonora	CIAT
G40068	a	✓	IIIb	Yellow	0	Dull	Medium	Landrace	USA	Arizona	CIAT
G40084	a	✓	IIIb	Cream-beige	Black	Speckled	Small	Landrace	Mexico	Durango	CIAT
G40111	a	✓	IIIb	Black	0	Dull	Small	Landrace	Mexico	Campeche	CIAT
G40119	a	✓	IIIb	Black	0	Semi-shiny	Small	Landrace	Mexico	Oaxaca	CIAT
G40141	a		IIIb	White	0	Dull	Small	Landrace	Mexico	Sinaloa	CIAT
G40142	a	✓	IIIb	Cream-beige	0	Semi-shiny	Small	Landrace	Mexico	Sonora	CIAT
G40148	a	✓	IIIb	White	0	Dull	Small	Landrace	Mexico	Sonora	CIAT
G40161	a	✓	IIIb	Cream-beige	0	Semi-shiny	Small	Landrace	Mexico	Sonora	CIAT
G40168	a	✓	IIIb	Other	White	Speckled	Small	Wild	Mexico	Sinaloa	CIAT
G40173A	a	✓	IIIb	Yellow	0	Dull	Small	Landrace	Mexico	Sonora	CIAT
G40200	a	✓	IIIb	Black	White	Speckled	Small	Landrace	Costa Rica		CIAT
G40237A	a	✓	IIIb	Pink	0	Dull	Small	Landrace	Mexico	Saltillo	CIAT
G40264	m	✓	IIIb	Cream-beige	Black	Mottled	Small	Wild	Mexico		CIAT
G40274	a	✓	IIIb	Cream-beige	Black	Mottled	Small	Wild	Mexico	Baja California	CIAT
G40279	a	✓	IIIb	White	0	Dull	Small	Landrace	Mexico	Sonora	CIAT
G40284	a	✓	IIIb	White	0	Dull	Small	Landrace	USA	Arizona	CIAT
G40287	a	✓	IIIb	Cream-beige	Brown	Speckled	Small	Wild	Mexico	Sonora	CIAT
SEF10-1	v		I1a	Red	0			Bred line			CIAT
SEF60	v		I1a	Red	0			Bred line			CIAT
SEN52	v		I1b	Black	0	Dull	Small	Bred line			CIAT
TARS-Tep 22	a	✓	IIIb	White	0	Semi-shiny	Small	Bred line			Porch et al. (2013, 2022)
TARS-Tep 23	a	✓	IIIb	Black	0	Dull	Medium	Bred line			
TARS-Tep 32	a		IIIb	Yellow	0	Dull	Medium	Bred line			

Abbreviations: CIAT, International Center for Tropical Agriculture; GH, growth habit; PSC, primary seed color; SCP, seed color pattern; SDBR, seed brilliance; SSC, secondary seed color; SSZ, seed size; TARS, Tropical Agriculture Research Station; USDA, United States Department of Agriculture.

<sup>a</sup>Crop ontology: [https://croponontology.org/term/CO\\_335:0001018](https://croponontology.org/term/CO_335:0001018).

<sup>b</sup>Taxa: a: *P. acutifolius*; m: *P. montanus* (previously *P. parvifolius*, Debouck 2021); v: *Phaseolus vulgaris*.

<sup>c</sup>GH: Growth habit according to Singh (1982).



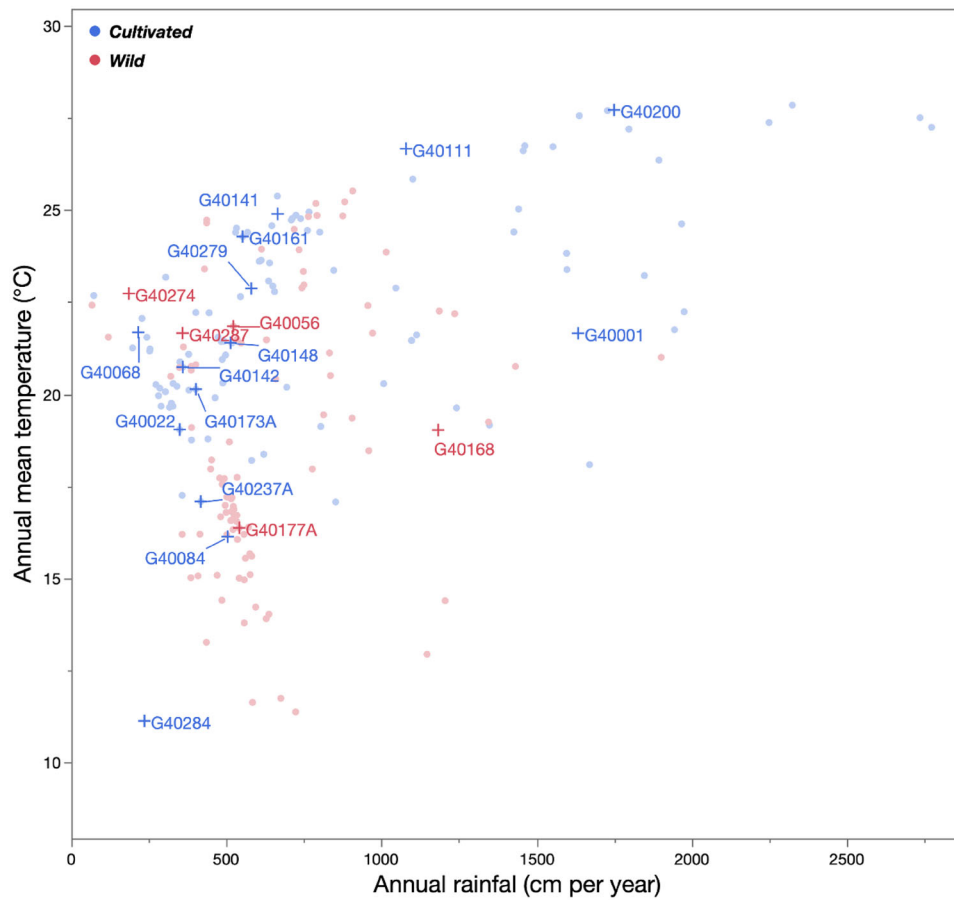
**FIGURE 1** Geographic and climate distribution of field site locations. Climate symbols are from Beck et al. (2018); Rubel and Kottek (2010): Af, tropical, humid; Bsk, arid, steppe, colder winter; Bwh, arid, desert, hot; Csa, temperate, dry and hot summer. DREC, Desert Research and Extension Center; UCD, University of California, Davis; UNL, University of Nebraska Lincoln; WSREC, West Side Research and Extension Center.

## 2 | MATERIALS AND METHODS

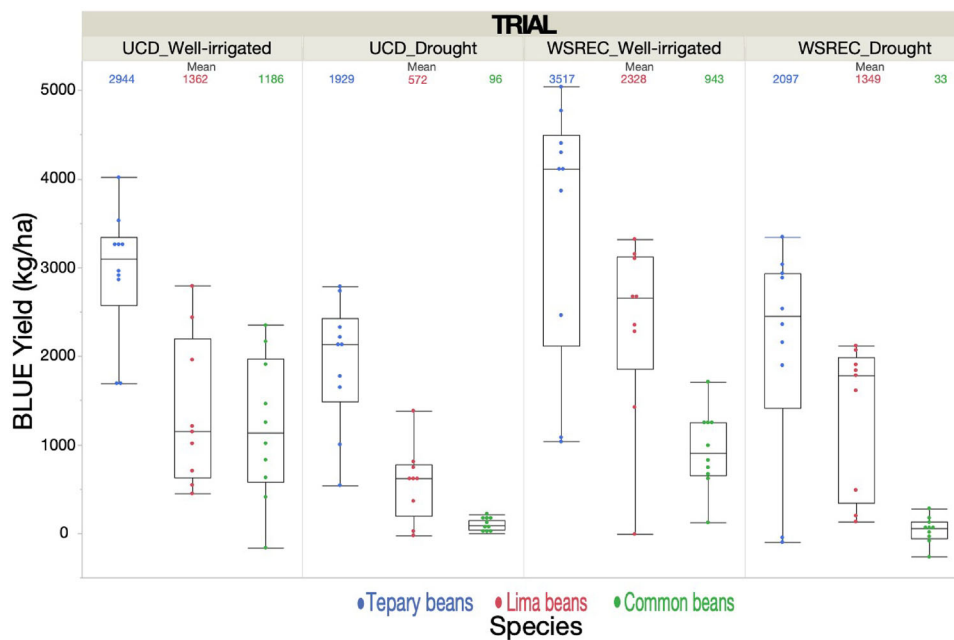
### 2.1 | Drought evaluation of three domesticated *Phaseolus* species (Experiment 1)

To compare the drought stress response among key domesticated *Phaseolus* species, 10 genotypes of each of the common bean and tepary bean and nine genotypes of the Lima bean (Table S1) were evaluated under well-irrigated and terminal drought conditions during the summer of 2016 in two locations in California (Table 1). These 29 genotypes are representative of the genetic diversity in these three species, as they include representatives of the two domestications in common and Lima beans (e.g., Garcia et al., 2021; Kwak & Gepts, 2009) and their breeding status (landraces vs. improved varieties). Field trials were conducted at the University of California, Agricultural and Natural Resources WSREC (Bsk climate, i.e., arid, cold steppe type climate, according to the Köppen–Geiger classification: Beck et al., 2018; Peel et al., 2007; Rubel & Kottek, 2010), and the University of

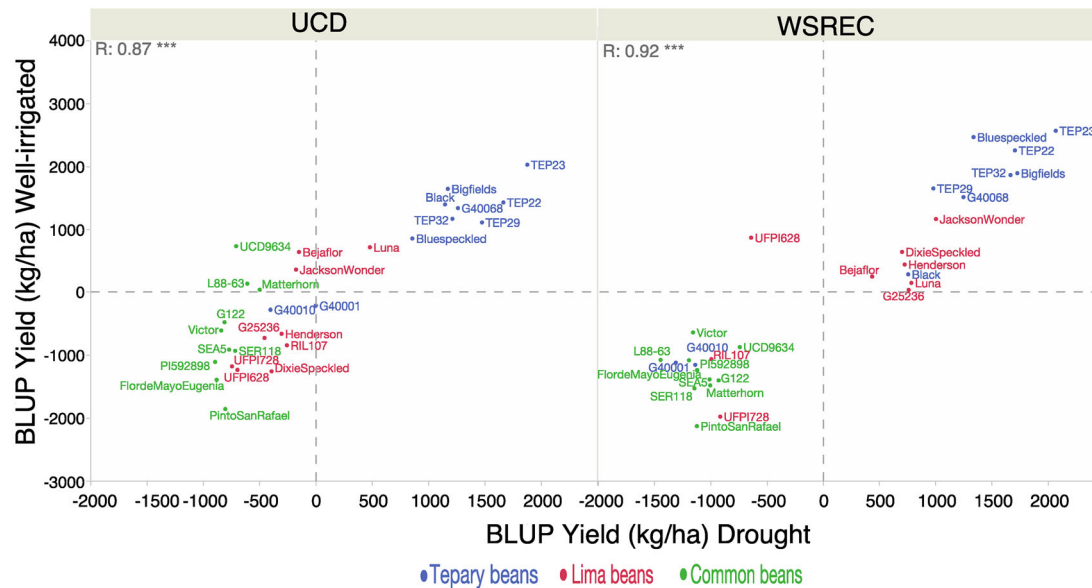
California, Davis, Plant Science Field Facility (UC Davis) (Csa climate: temperate with hot, dry summer), which differ in altitude, soil type, and average weather data such as precipitation, temperature, and relative humidity (Table 1). The plant material was obtained from the seed inventory of the Bean Breeding Program, Department of Plant Sciences, University of California, Davis. Drought/irrigated field trials in both locations were planted side by side in a row-column randomized design with three replications. Individual plots consisted of two 3 m-rows (50 seeds/row), spaced 0.76 m apart. The drought stress was terminal, with irrigation reduced by 50% at WSREC and 75% at UC Davis between flowering and harvesting compared with the well-irrigated trial. Trials were agronomically maintained using standard common bean commercial procedures (Long et al., 2010). To control for spatial variability in each trial, best linear unbiased estimators (BLUES) and best linear unbiased predictors (BLUPs) of yield (kg/ha) were fitted using the SPATs package (Rodríguez-Álvarez et al., 2018) in the Mr. Bean App (Aparicio et al., 2019) (Figures 3 and 4). Genetic correlations of the



**FIGURE 2** Environmental conditions (annual precipitation and annual temperature data from the Worldclim database (Hijmans et al., 2005) of the tepary bean accessions' locations of origin used in this multi-environment trials (MET) study. Unlabeled accessions were not included in the METs.



**FIGURE 3** Best linear unbiased estimators (BLUEs) of yield (kg/ha). Tepary beans (blue), Lima beans (red), and common beans (green). Data from drought and well-irrigated trials planted at the University of California, Davis (UCD) and West Side Research and Extension Center (WSREC).



**FIGURE 4** Best linear unbiased predictors (BLUPs) of yield (kg/ha). Tepary beans (blue), Lima beans (red), and common bean (green). Data from well-irrigated trial versus drought conditions. Data from trials planted at the University of California, Davis (UCD) and West Side Research and Extension Center (WSREC). R, Pearson's correlation coefficient \*\*\*  $p < 0.0001$ .

locations were obtained using the statistical program EchnaMMS (Gilmour, 2020). The analysis of variance (ANOVA) was conducted using the lme4 package (Bates et al., 2015) in R (R Core Team, 2023). The model, which was fitted with the lmer function (Bates et al., 2015), included species, genotype, locations, and irrigation/drought treatment as fixed effects. Analysis of variance (ANOVA) calculations utilized the Kenward and Roger (1997) method for determining the denominator degrees of freedom to enhance the accuracy of  $F$ -tests and  $t$ -tests for fixed effects. Mean comparisons were performed with the emmeans function using the Tukey test to compare the estimated marginal means (Bates et al., 2015).

## 2.2 | Evaluation of tepary beans to drought and heat stress throughout multi-environment trials (MET) study (Experiment 2)

### 2.2.1 | Drought stress trials

To determine the drought tolerance of tepary beans across different environments, we evaluated 22 tepary bean genotypes (Table 2) in three drought-stressed and well-irrigated trials in three locations in 2017 and 2018. These 22 lines were chosen to represent germplasm accessions or landraces (G entries) and improved cultivars (Tropical Agriculture Research Station [TARS]-Tep entries) (Table 2) and were selected from a wide range of annual mean temperature and annual rainfall (Figure 2). For the purpose of comparison, four *P. vulgaris* breeding lines were also added (DOR, SEN, and SEF lines)

(Table 2). Field trials were conducted in a humid tropical environment at the International Center for Tropical Agriculture (now called Alliance Bioversity and CIAT), Palmira, Colombia (DrPAL; Af climate); a semi-arid temperate environment at the University of California, Davis, CA (DrUCD); and a semi-arid temperate climate at the University of Nebraska, Panhandle Research and Extension Center, Scottsbluff, NE (DrUNL; Bsk climate) (Table 1). Trials were planted during the summer seasons in the two temperate locations and during the low precipitation season in the tropical location. Environmental conditions such as altitude, soil type, and weather data such as precipitation, temperature, and relative humidity differed across the three locations (Table 1). Drought stress in Palmira was intermittent and moderate, with water supply reduced by 28% compared to the well-irrigated trial. Drought stress in Davis was terminal and severe, with water supply to the crop reduced by ~75% compared to the well-irrigated trial. Drought stress in Scottsbluff was terminal and severe, with water supply reduced by 74% compared to the well-irrigated trial (Table 1). Drought and well-irrigated trials were planted side-by-side in a randomized complete block design with three replicates in Palmira, Colombia (PAL), five in Davis, CA (UC Davis), and two in Scottsbluff, NE. Individual plots in Davis consisted of two rows (50 seeds/row), 3 m long and 0.76 m apart; in Palmira, the trials were planted in four-row, 3-m-long plots, spaced 0.6 m apart; in Scottsbluff, trials were planted in two-row, 3.65 m-long plots, spaced 0.6 m apart. Trials were agronomically maintained using local, standard common bean commercial procedures.

## 2.2.2 | High heat trials

To evaluate the heat tolerance of tepary beans across different environments, we evaluated the same 22 drought-tolerance-tested tepary bean genotypes (Table 2) under heat stress in three distinct locations in 2017 and 2018 (Table 1). It has been reported that minimum temperatures (i.e., night temperatures) above 20°C and maximum temperatures (i.e., day temperatures) above 30°C negatively impact the yield production in the common bean (Porch, 2006; Porch & Jahn, 2001). Thus, locations above the 20/30°C night/day threshold were selected to conduct the heat stress trials. Field trials were planted in two hot and humid tropical locations in Alvarado (HtALV; Department of Tolima, Colombia; Af climate) and Caribia (HtCAR; Department of Magdalena, Colombia; Af climate), and one desert climate at the Desert Research and Extension Center, University of California, Holtville, CA (HtDREC; Bwh climate) (Table 1). Reduction of water supplied (by rainfall and irrigation, Table 1) provided an additional environment in Holtville that combined heat and drought stress. High heat trials were planted at low altitudes in tropical locations and during the summer season in the desert. Environmental conditions such as altitude, soil type, and weather data such as precipitation, temperature, and relative humidity differed across the three locations (Table 1). Field trials were planted in a randomized complete block experimental design, with three replicates in all three locations. Plots in Alvarado consisted of two rows (50 seeds/row), 3 m long, and 0.6 m apart; in Caribia, the plots consisted of 4 rows (50 seeds/row), 3 m long, and 0.6 m apart; in Holtville, California, plots included 2 rows (50 seeds/row), 3 m long, and 0.76 m apart. Trials were agronomically maintained using standard common bean commercial procedures.

## 2.3 | MET data analysis

The genotype  $\times$  environment ( $G \times E$ ) interaction was modeled using a linear mixed model known as factor analytic structure of order 2 (FA2) in ASREML-R 4 (Butler et al., 2017). The variance matrix for the residuals was assumed to be block diagonal so that  $R = \bigoplus_{j=1}^t R_j$  where  $R_j = \text{var}(e_j) = \sigma_j^2$  is the variance for the residuals for the  $j$ th trial, and  $t$  is the number of trials. The FA MET was modeled as:

$$y_{ijkl} = \mu + \text{trial}_i + \text{gen}(\text{trial})_{ij} + e_{ijkl}$$

where  $y_{ijkl}$  is the observation of the  $j$ th genotype in the  $i$ th environment (trial),  $\mu$  is the intercept,  $\text{trial}_i$  is the effect for the  $i$ th environment, and  $e_{ijkl}$  is the plot error effect corresponding to  $y_{ijkl}$ . For the FA2 MET, the genotype and  $G \times E$  factors were combined into a single compound model factor of genotype nested within the environment:  $\text{gen}(\text{trial})_{ij}$ .

This formulation then allowed us to specify the pattern of genotypic variances within environments and also the correlation structure for the effects of a common genotype across environments (Isik et al., 2017).

$$\text{gen}(\text{trial})_{ij} = u_{gij} = \lambda_{1i} f_{1j} + \lambda_{2i} f_{2j} + \delta_{ij}$$

where  $\lambda_{1i}$  is the loading for the environment  $i$  on the first factor;  $f_{1j}$  is the genetic effect (score) of genotype  $j$  on the first factor;  $\lambda_{2i}$  is the loading for the environment  $i$  on factor 2;  $f_{2j}$  is the score of genotype  $j$  on factor 2, and  $\delta_{ij}$  is the deviation of the observed genetic effect of genotype  $j$  in environment  $i$  from its predicted value based on the multiplicative factor model fit (Isik et al., 2017). A dendrogram showing the relationships among the testing environments in Experiment 2 (Figure 5a), genetic correlation plots (Figure 5b,c,d), and biplots (Figure 6a,b) were generated with ASREML-R (Butler et al., 2017) using the FA2 statistical analysis.

## 3 | RESULTS

### 3.1 | Drought evaluations of *Phaseolus* species (Experiment 1)

To evaluate the inter- and intraspecific variation for terminal drought response in *Phaseolus* species, we planted several genotypes of common bean ( $n = 10$ ), Lima bean ( $n = 9$ ), and tepary bean ( $n = 10$ ) in two locations in California (WSREC and UC Davis) during the summer of 2016 (Experiment 1; Table 1). The drought stress imposed in these two trials reduced average, experiment-wide grain yield by a statistically significant  $\sim 50\%$ , indicative of a desired intermediate stress (Experiment 1: Tables 1 and 2; Table S2). When comparing species, grain yield was reduced by terminal drought stress in comparison to the well-irrigated treatment by 34%, 58%, and 92% in tepary bean, Lima bean, and common bean, respectively, at UCD, while the reduction at WSREC was 40%, 42%, and 96%, respectively (Figure 3). When examining the three-way combinations (Species  $\times$  Irrigation Treatment  $\times$  Location) (Table S2), the combinations with the highest grain yield included *P. acutifolius* under well-irrigated conditions and then drought stress, at WSREC and then at UC Davis.

An ANOVA of grain yield showed that the main factors (irrigation treatment, species, genotype across species, and location) showed statistically significant differences at the  $p = 0.001$  level (Table 3). Among the two-way interactions tested, only the irrigation treatment  $\times$  genotype ( $p = 0.05$ ) and genotype  $\times$  location ( $p = 0.001$ ) showed statistically significant differences. Consistent with this observation, genetic correlations of yield (kg/ha) among drought and well-irrigated trials were above 70%, indicating that the phenotypic response

**TABLE 3** Analysis of variance of grain yield variation across two irrigation treatments, two locations, and 29 *Phaseolus* species genotypes (*Phaseolus vulgaris*, *P. lunatus*, and *P. acutifolius*) (Experiment 1).

	Sum square	Mean square	No. of DF	DenDF	F value	Pr(> F)	Statistical significance
Irrigation treatment	83,507,985	83,507,985	1	84.7	360.2	3.00E-32	***
Species	4,953,467	2,476,734	2	83.8	10.7	7.37E-05	***
Genotype	23,360,887	898,496	26	84.5	3.9	1.25E-06	***
Location	9,607,654	9,607,654	1	114.6	41.4	2.93E-09	***
Treatment × species	413,959	206,980	2	83.8	0.9	4.13E-01	Ns
Treatment × genotype	10,228,797	393,415	26	84.2	1.7	3.70E-02	*
Treatment × location	194,195	194,195	1	115.1	0.8	3.62E-01	Ns
Species × location	801,068	400,534	2	113.4	1.7	1.82E-01	Ns
Genotype × location	27,050,653	1,040,410	26	114.3	4.5	1.08E-08	***
Genotype × block	6,913,145	238,384	29	84.8	1.0	4.44E-01	Ns
Treatment × species × location	628,858	314,429	2	113.4	1.4	2.62E-01	Ns
Treatment × genotype × location	11,664,716	448,643	26	114.7	1.9	9.43E-03	**

\* $p < 0.01$ . \*\*\* $p < 0.001$ . ns, not significant.

of the three *Phaseolus* species was similar in both locations (Figure S1). Among three-way interactions, the Irrigation Treatment × Genotype × Location interaction was statistically significant ( $p = 0.01$ ) but not the Treatment × Species × Location (Table 3). The overall yield was higher in both water treatments (drought and well-irrigated) at WSREC than at UC Davis (Figure S1), which is explained by the high yield of tepary beans at WSREC (Figure 3). On the other hand, the common bean entries did not tolerate drought stress when they were planted in dry climates since their yield at UCD was only 96 kg/ha and 33 kg/ha at WSREC (Figure 3). The intraspecific variation analysis showed that eight of 10 tepary genotypes ranked in the top 30% with positive best linear unbiased predictor (BLUP) values in both locations (WSREC and UCD) and under both water treatments (Figure 3). The improved tepary genotypes (TARS-Tep 22 and TARS-Tep 23; Porch et al., 2013; Porch et al., 2022) had the best genotypic values in both locations and both water treatments (Figure 4). Conversely, the performance of most common bean genotypes was inferior, with negative BLUP values in both locations and both water treatments. Only UCD9364, L88-63, and ‘Matterhorn’ had positive BLUPs in the well-irrigated treatment (Figure 4).

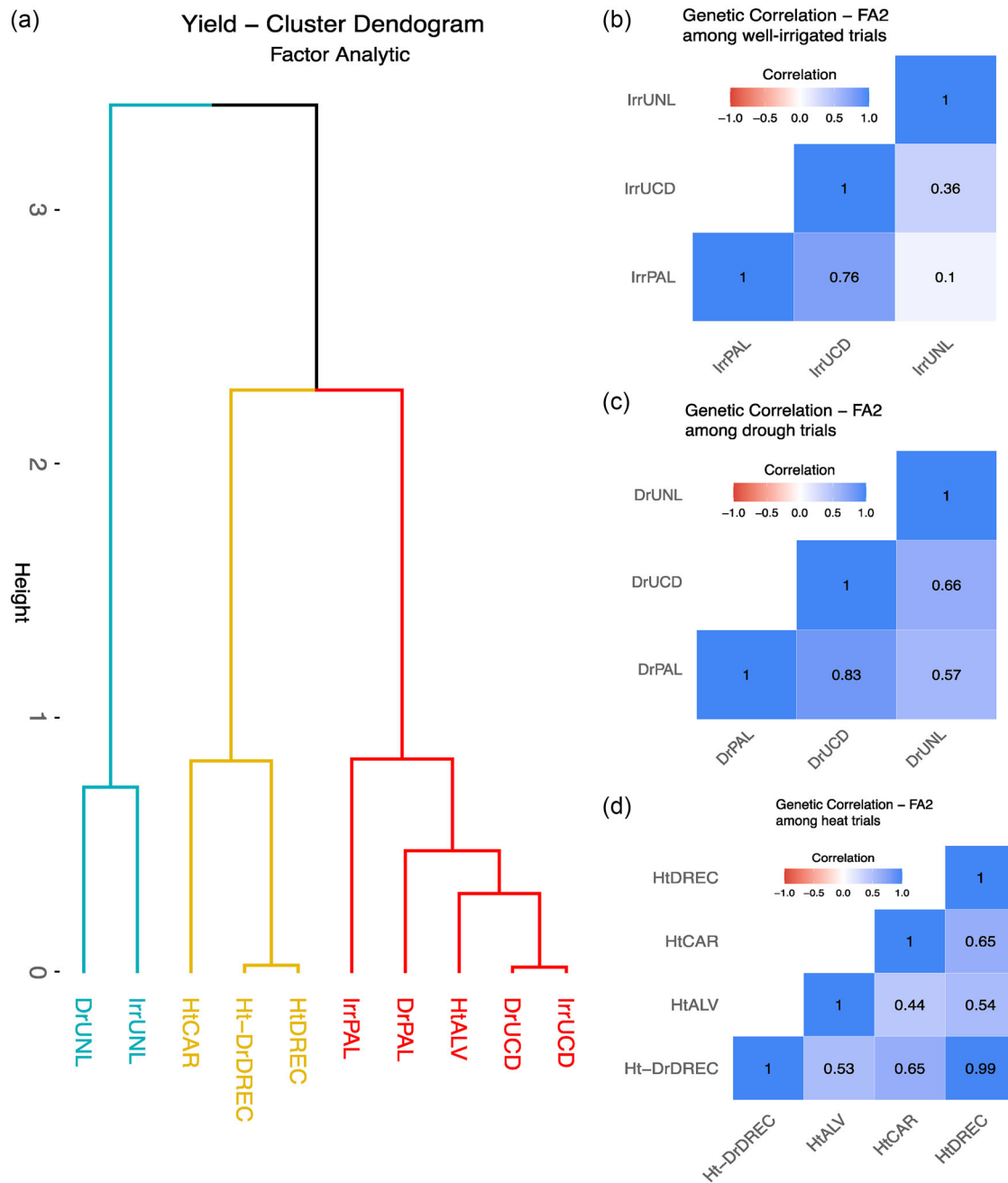
### 3.2 | MET study of tepary beans (Experiment 2)

To evaluate tepary beans’ drought and heat tolerance across different environments, we conducted a MET study. To capture G × E interactions, the whole yield (kg/ha) data set was modeled using an extended factor analytic of second-

order (XFA2), which is a prudent approach that captures the complexity of multiple covariances among a large set of environments (Smith et al., 2001). The effects of drought stress, as well as the effects of heat stress under irrigation on tepary bean yield, were assessed in several locations in Colombia and the United States (Table 1: Experiment 2). The yield (kg/ha) results showed that trials conducted in Scottsbluff, NE, regardless of their water regime, were different from all the other trials (Figure 5a). Trials conducted under heat stress in Caribia, Colombia, and Holtville, CA, were grouped, as well as trials conducted in Davis (UCD), Alvarado, and Palmira (PAL; Figure 5a). These close cluster associations were grouped according to the location, indicating that the environment influences the yield response of tepary beans more than the stress condition.

Since a cluster association does not necessarily represent a genetic correlation, we determined genetic correlations between stress conditions. We found that heat stress trials and drought stress trials were positively correlated (Figure 5c,d). The only trials that were not correlated were well-irrigated trials conducted in Scottsbluff, NE, and Palmira, Colombia (genetic correlation value = 0.1; Figure 5b).

Among trials at different locations, the highest correlations were found between well-irrigated trials (genetic correlation value = 0.76; Figure 5b) and drought trials (genetic correlation value = 0.83; Figure 5c) in Palmira, Colombia, and Davis, CA, respectively. Genetic correlations among heat stress trials were similar, with Holtville, CA, and Caribia, Colombia, the two locations with the highest genetic correlation (genetic correlation value = 0.65; Figure 5d). The highest genetic correlation was observed, not surprisingly, for the heat stress versus heat and drought stress at the same



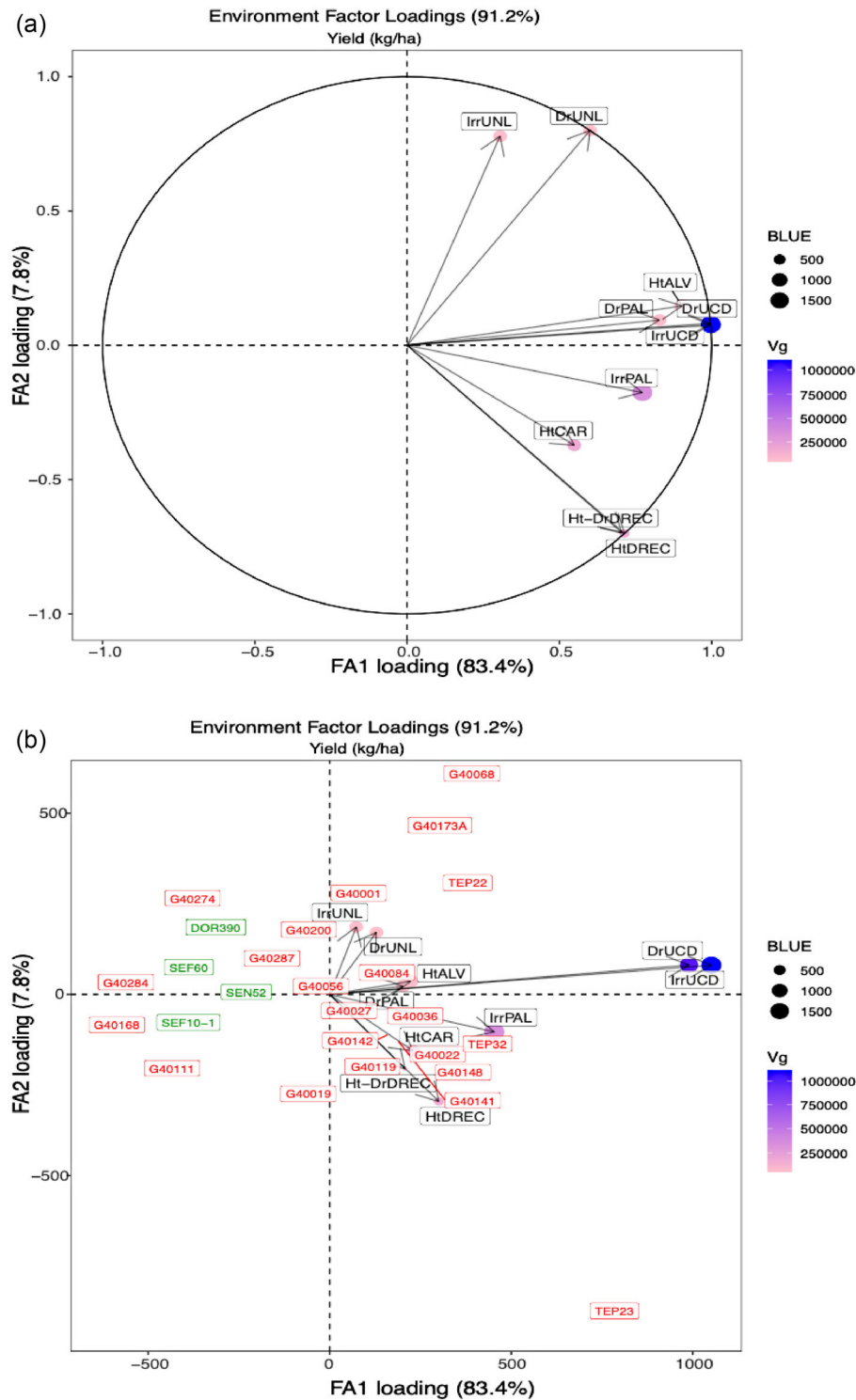
**FIGURE 5** Cluster association, genetic correlation, and heritability of yield (kg/ha). Data evaluated on the tepary bean response to drought heat and well-irrigated conditions across multiple trials (ALV, Alvarado, Colombia; CAR, Caribia, Colombia; Dr, drought trials; DREC, Desert Research and Extension Center = Holtville, CA; Ht, heat trials; Ht-Dr, drought + heat trials; Irr, well-irrigated trials; PAL, CIAT, Palmira, Colombia; UCD, University of California, Davis, CA; UNL, University of Nebraska Lincoln Scottsbluff, NE) (a) Clustering of trials according to yield. (b) Genetic correlation among well-irrigated trials. (c) Genetic correlation among drought-stress trials (d) Genetic correlation among heat-stress trials.

location at the DREC in Holtville, CA (genetic correlation = 0.99; Figure 5d).

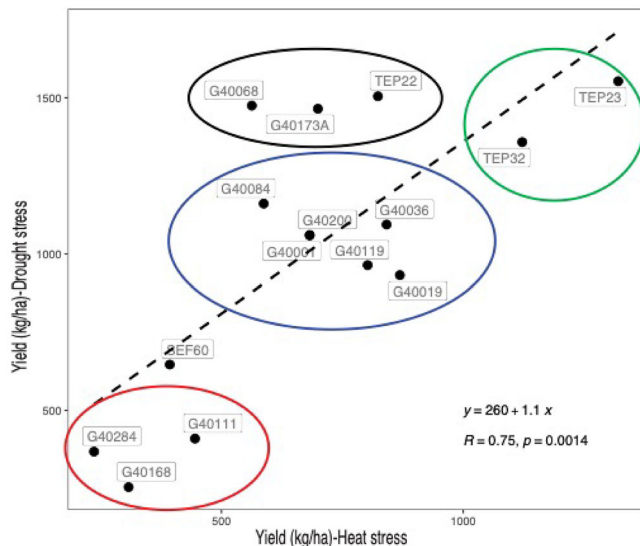
When the genetic variances for each environment were separated, a factor loading showed that the genetic response of tepary bean is driven more by the location than the stress condition, that is, heat or drought (Figure 6a). Also, environments with high genetic variances, such as Davis (UCD) and Palmira

(PAL), explained most of the variance (~84%) present in the MET experiment (Figure 6a). Additionally, we observed environments with low genetic variances, such as Scottsbluff, NE (UNL), and Holtville, CA (DREC) (Figures 6a,b and 7).

Also, three tepary beans (TARS-Tep 22, G40068, and G40173A) performed better under drought stress than under heat stress conditions across environments (Figures 6b



**FIGURE 6** Biplots from the factor analytic model were used to determine the genotype  $\times$  environment effects. The yields (kg/ha) of tepary bean (red boxes) and common bean (green boxes) were used to create the biplots. Data from heat, drought, and well-irrigated conditions across multiple environment trials (ALV, Alvarado, Colombia; CAR, Caribia, Colombia; Dr, drought trials; DREC, Desert Research and Extension Center = Holtville, CA; FA 1 and FA2, factor analytic order 1 and order 2, respectively; Ht, heat trials; Ht-Dr, drought + heat trials; Irr, well-irrigated trials; PAL, CIAT, Palmira, Colombia; UNL, University of Nebraska Lincoln Scottsbluff, NE). Genetic variances (vg) of each trial are represented by the color of the dots. The best linear unbiased estimators (BLUEs) of each trial are represented by the size of the dots. (a) Factor loadings determined based on trial effect. (b) Factor loadings determined based on trial effect and genotype effect (red labels).



**FIGURE 7** Linear regression of yield (kg/ha) evaluated under heat and drought stresses in tepary genotypes. Heat and drought data set were combined from multiple environment trials. Circles indicate the grouping of the tepary genotypes (explained in the main text) according to their yield under both stresses.

and 7). A previous study reported that shoot traits such as canopy biomass, harvest index, and photosynthetic mobilization evaluated as pod harvest index (PHI) explained most of the adaptation to drought stress in G40068 (Rao et al., 2013).

In contrast, tepary beans, such as TARS-Tep 23, G40019, G40119, G40141, and G40148, performed better under heat stress trials than drought trials, indicating a  $G \times E$  interaction associated with the evaluation under multiple environments and stress conditions (Figure 6b). We also found numerous tepary beans, such as G40284, G40168, G40287, and G40111, with low performance under both drought and heat stresses across locations (Figure 6b), indicating that there is variation in the tepary bean, and not all tepary bean genotypes tolerate heat and drought. The common bean lines planted in this experiment had the lowest yield across environments and stress conditions, confirming the vulnerability of common beans to drought and heat stresses (Figure 6b).

To determine the yield response of tepary genotypes only among drought and heat trials, we estimated a linear regression in a data set that combined data for 15 genotypes that had been tested under both drought and heat stress. We found a significant ( $p$ -value = 0.0014) positive correlation ( $R = 0.75$ ) between drought and heat stress trials, indicating that some tepary beans tolerate both stress conditions (Figure 7). It also showed that a possible indirect selection between heat and stress conditions could be conducted. We also identified four groups of tepary genotypes: a drought and heat susceptible group (G40111, G40168, and G40284; Figure 7: red group); an intermediate drought and heat tolerant group

(G40001, G40019, G40036, G40084, G40119, and G40200; Figure 7: blue group); a group that had higher drought tolerance than heat tolerance (G40068, G40173A, and TARS-Tep 22; Figure 7: black group); and two exceptional tepary genotypes that were highly tolerant to both drought and heat stresses (TARS-Tep 23 and TARS-Tep 32; Figure 7: green group). The tolerance to drought was higher than the tolerance to heat stress in all tested tepary genotypes but the susceptible group (Figure 7).

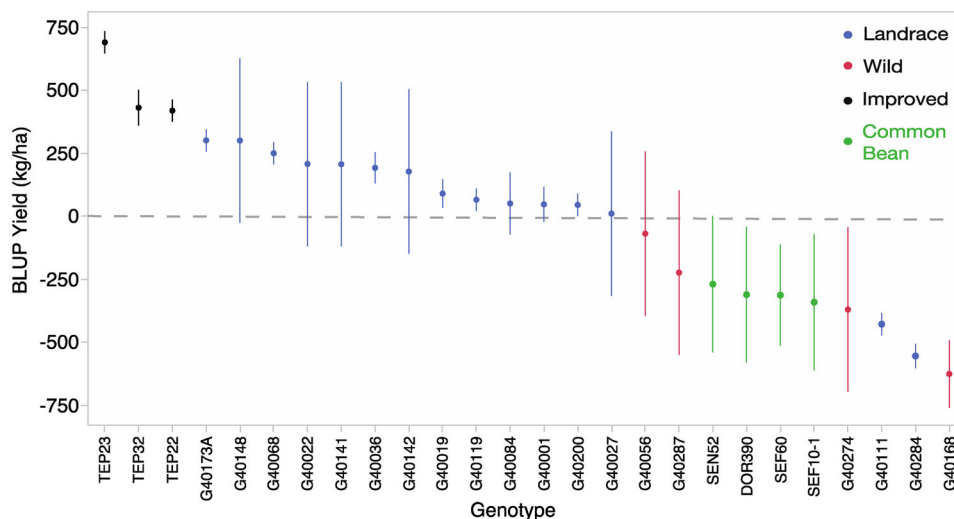
To identify the genotypes with better overall performance, we estimated the BLUPs of yield (kg/ha) by combining the whole data set. We found that 16 out of 22 tepary bean genotypes had positive (values > 0) BLUP values, indicating the high level of tolerance to drought and heat stress across multiple environments in tepary beans (Figure 8). We also found that the improved tepary beans (TARS-Tep 22, TARS-Tep 23, and TARS-Tep 32) had the highest overall performance, followed by landraces and wild tepary genotypes (Figure 8). This result highlights the importance of breeding tepary beans and the rapid progress that can be made. Also, as expected, the overall performance of common beans was negative (BLUP values < 0) (Figure 8), confirming that common bean has a lower genetic response compared with tepary bean when it comes to drought and heat constraints.

## 4 | DISCUSSION

### 4.1 | Drought evaluations of *Phaseolus* species show that tepary beans performed better under drought stress than Lima and common beans (Experiment 1)

The terminal drought stresses imposed on the three *Phaseolus* species (Tables 1 and 2) reduced grain yield by some 50%. In our experience, this intermediate yield reduction is strong enough to identify genetic variation in drought stress tolerance between and within species. Both lighter and stronger stresses than the ones observed here generally prevent this identification because they limit phenotypic variation.

In these trials, we found that, compared with common bean and Lima bean, tepary bean has the highest tolerance to terminal drought stress, confirming the ability of the tepary bean to use water efficiently and thrive under severe drought conditions (Markhart, 1985). A previous study also reported tepary beans with higher tolerance levels to drought stress than common bean (Rao et al., 2013). However, this is the first study that compares the drought tolerance of common beans, tepary beans, and Lima beans in multiple environments. We also found that the tepary beans tested in this study had the highest yield of all three species evaluated, consistent with the high inherent productivity of the species, especially under heat and drought stresses (Figures 3 and 4; Nabhan & Felger, 1978;



**FIGURE 8** The performance of tepary beans (improved in black, Landraces in blue, Wild in red) and common bean controls (green) was evaluated across multiple environment trials. Performance was estimated as best linear unbiased predictors (BLUPs) of yield (kg/ha).

Pratt & Nabhan, 1988). Tepary and Lima beans also showed more intraspecific phenotypic diversity associated with terminal drought tolerance in tepary bean and Lima bean than in common bean (Figures 3 and 4), which suggests that there is more potential to maximize genetic diversity and select tepary and Lima genotypes under drought conditions. Reports indicate that genetic diversity among domesticated and wild tepary beans is limited (Blair et al., 2012; Gujaria-Verma et al., 2016; Schinkel & Gepts, 1988, 1989). However, these studies have based their reports only on molecular diversity studies.

Although the performance of common bean on the whole as a species was inferior to that of tepary and Lima beans, this assessment was not uniform across the common bean genotypes tested. A positive response of UCD9364 was expected since this line was bred at the University of California, Davis. Thus, this line is already adapted to the California climate and irrigated agronomic conditions. In contrast, L88-63 was the result of a genetic experiment to study the inheritance of terminal drought stress tolerance in the lowland tropics (Frahm et al., 2004). The cultivar ‘Matterhorn’ was bred at Michigan State University and has broad adaptation in the U.S. (Kelly et al., 1999). Lima beans had an intermediate performance under both water treatments and both locations (Figure 4). Lima bean was also the *Phaseolus* species that had more variation between both sites (Figure 4), indicating a strong  $G \times E$  interaction in this species.

A combination of both molecular and phenotypic studies across multiple environments is needed to better determine the genetic basis of productivity and drought tolerance of tepary beans. Quantitative Trait Loci and Genome-Wide Association analyses will help in understanding the inheritance of stress tolerance in tepary bean in comparison to Lima bean and common bean (Asfaw et al., 2017; Berny Mier y Teran, Konzen,

Medina, et al., 2019; Berny Mier y Teran, Konzen, Palkovic, et al., 2019; Blair et al., 2012; Garcia et al., 2021; Nabateregga et al., 2019; Polania et al., 2016). What is evident in this study is that improved tepary beans have a better performance to drought stress than landraces, emphasizing the usefulness and need to continue breeding tepary beans (Mwale et al., 2020, 2022; Porch et al., 2022).

## 4.2 | Evaluation of tepary beans to drought and heat stress through MET reveals that the environment influences the tepary beans response more than the stress condition itself (Experiment 2)

In this study, we conducted field experiments to test a diverse sample of tepary bean, which included wild populations, landraces, and improved lines, under a wide range of temperate and tropical environments with different climate and stress conditions. We found that some tepary beans have a broad adaptation to temperate and tropical climate zones. For example, we confirmed that TARS-Tep 23 (Porch et al., 2022) shows strong heat and drought tolerances extending across a broad range of climates (Figure 7: green ellipse). The tepary bean’s ability to adapt to different climate zones could be an important characteristic to introduce into common bean due to the narrow climate adaptation of the latter (Beebe, 2012). Similarly, some tepary beans were widely adapted to distinct heat (Figure 7: blue ellipse, below the regression line) and drought stress (Figure 7: black ellipse) conditions.

However, we also observed that the testing location or environment was more important in affecting the response of tepary beans than the stress conditions themselves. These results, along with the high correlation among conditions

(heat, drought, and well-irrigated trials), indicate that including additional environments in a selection program is more important than including multiple stress conditions in the same environment. The existence of a strong  $G \times E$  interaction effect is consistent with the presence among tepary bean accessions of a narrow adaptation, that is, that limited adaptation across environments and stress conditions (Figures 6b and 7). Although previous studies had already reported on the tolerance of tepary beans to drought (Mohamed et al., 2005; Rao et al., 2013) and heat stressors (Suárez et al., 2020), these studies were mainly focused on the physiological response of tepary genotypes, and the environment effect was not considered.

Taken together, the results indicate that tepary bean selection for yield under heat and drought constraints could be conducted either in tropical (Colombia) or temperate (California) climates, expecting an interchangeable positive response. However, low correlations between trials conducted in Scottsbluff, NE, and those conducted in other locations and low genetic variances of Scottsbluff trials (Figure 6a) suggest that Scottsbluff, NE, was not optimal for selecting tepary beans. This surprising observation could be attributed to one or more causes, including the lack of adaptation of the assayed tepary lines to the Nebraska Panhandle climatic and soil conditions and the specific cultivation practices used in this experiment, which may have been unsuitable for tepary beans.

This study also showed that improved tepary genotypes, such as TARS-Tep 22, TARS-Tep 23, and TARS-Tep 32, performed better for yield than landrace and wild tepary genotypes (Figures 7 and 8), which is consistent with the evaluation of the three *Phaseolus* species, previously described (Figure 4). These results once again strengthen the importance of breeding tepary beans to either improve common beans through interspecific introgressions or use them as an alternative crop to overcome the impact of climate change, including extended drought seasons, warmer weather, and water scarcity. Although interspecific gene transfer from tepary to common bean has been hampered by strong reproductive isolation (Mejía-Jiménez et al., 1994; Muñoz et al., 2004; Souter et al., 2017; Waines et al., 1988), recent progress in crossability studies of this interspecific cross has led to the identification of three interspecific VAP lines that facilitate the crossability between common and tepary beans by avoiding the embryo rescue process in the initial cross (Barrera et al., 2022; Cruz et al., 2023). In turn, this increased crossability may hopefully increase the size and widen the chromosome locations of introgressed fragments from either species in reciprocal crosses, compared to the current situation in which introgressed fragments are very small and limited to distal chromosome locations (Lobaton et al., 2018).

## 5 | CONCLUSION

We confirmed that tepary beans on average have a greater adaptation to terminal drought than Lima and common beans and a broad adaptation to different heat stress conditions. Nevertheless, we also report within-species variation for tolerance to drought and heat with the tepary bean species across multiple temperate and tropical arid environments. We found an important  $G \times E$  interaction, which should be considered in a tepary bean selection program. The tepary genotypes that perform better across locations and trials can be included in an interspecific crossing program between tepary and common beans, a breeding effort to introduce tolerance to drought and heat stresses and other traits of agronomic importance, such as disease and pest resistances, into the common bean. Alternatively, tepary beans can be developed as a more drought- and heat-resilient grain legume crop in the face of global climate heating.

## AUTHOR CONTRIBUTIONS

**Santos Barrera:** Conceptualization; formal analysis; investigation; writing—original draft; writing—review and editing. **Jorge C. Berny Mier y Teran:** Conceptualization; formal analysis; investigation; writing—review and editing. **Johan Aparicio:** Formal analysis; investigation. **Jairo Diaz:** Formal analysis; investigation. **Rommel Leon:** Formal analysis; investigation. **Steve Beebe:** Conceptualization; funding acquisition; writing—review and editing. **Carlos A. Urrea:** Conceptualization; formal analysis; funding acquisition; investigation; writing—original draft; writing—review and editing. **Paul Gepts:** Conceptualization; funding acquisition; writing—original draft; writing—review and editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Raw data for Experiments 1 and 2 are available from DRYAD (<https://doi.org/10.5061/dryad.zpc866tgq>).

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## REFERENCES

- Aparicio, J., Ariza-Suarez, D., & Raatz, B. (2019, 15–19 July). *Web application for spatial modelling of field trials*. XXIX Simposio Internacional de Estadística, Barranquilla, Colombia. <https://cgspace.cgiar.org/handle/10568/103767>
- Araújo, S. S., Beebe, S., Crespi, M., Delbreil, B., González, E. M., Gruber, V., Lejeune-Henaut, I., Link, W., Monteros, M. J., Prats, E., Rao, I., Vadez, V., & Patto, M. C. V. (2015). Abiotic stress responses in legumes: Strategies used to cope with environmental challenges. *Critical Reviews in Plant Sciences*, *34*, 237–280. <https://doi.org/10.1080/07352689.2014.898450>
- Asfaw, A., Ambachew, D., Shah, T., & Blair, M. W. (2017). Trait associations in diversity panels of the two common bean (*Phaseolus vulgaris* L.) gene pools grown under well-watered and water-stress conditions. *Frontiers in Plant Science*, *8*, Article 733. <https://doi.org/10.3389/fpls.2017.00733>
- Barrera, S., Berny Mier Y Teran, J. C., Lobaton, J. D., Escobar, R., Gepts, P., Beebe, S., & Urrea, C. A. (2022). Large genomic introgression blocks of *Phaseolus parvifolius* Freytag bean into the common bean enhance the crossability between tepary and common beans. *Plant Direct*, *6*, e470. <https://doi.org/10.1002/pld3.470>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Baudoin, J. P., & Mergeai, G. (2001). Haricot de lima, *Phaseolus lunatus* L. In R. H. Raemaekers (Ed.), *Agriculture en Afrique Tropicale* (pp 356–361). Direction Générale de la Coopération Internationale.
- Beck, H. E., Zimmermann, N. E., McVicar, T. R., Vergopolan, N., Berg, A., & Wood, E. F. (2018). Present and future Köppen–Geiger climate classification maps at 1-km resolution. *Scientific Data*, *5*, 180214. <https://doi.org/10.1038/sdata.2018.214>
- Beebe, S. (2012). Common bean breeding in the tropics. In J. Janick (Ed.), *Plant Breeding Reviews* (pp. 357–426). Wiley. <https://doi.org/10.1002/9781118358566.ch5>
- Beebe, S., Ramirez, J., Jarvis, A., Rao, I. M., Mosquera, G., Bueno, J. M., & Blair, M. W. (2011). Genetic improvement of common beans and the challenges of climate change. In S. S. Yadav, R. J. Redden, J. L. Hatfield, H. Lotze-Campen, & A. E. Hall (Eds.), *Crop adaptation to climate change* (pp. 356–369). Wiley-Blackwell. <https://doi.org/10.1002/9780470960929.ch25>
- Beebe, S. E., Rao, I. M., Blair, M. W., & Acosta-Gallegos, J. A. (2013). Phenotyping common beans for adaptation to drought. *Frontiers in Physiology*, *4*, Article 35. <https://doi.org/10.3389/fphys.2013.00035>
- Berny Mier Y Teran, J. C., Konzen, E. R., Medina, V., Palkovic, A., Ariani, A., Tsai, S. M., Gilbert, M. E., & Gepts, P. (2019). Root and shoot variation in relation to potential intermittent drought adaptation of Mesoamerican wild common bean (*Phaseolus vulgaris* L.). *Annals of Botany*, *124*, 917–932. <https://doi.org/10.1093/aob/mcy221>
- Berny Mier Y Teran, J. C., Konzen, E. R., Palkovic, A., Tsai, S. M., Rao, I. M., Beebe, S., & Gepts, P. (2019). Effect of drought stress on the genetic architecture of photosynthate allocation and remobilization in pods of common bean (*Phaseolus vulgaris* L.), a key species for food security. *BMC Plant Biology*, *19*, 171. <https://doi.org/10.1186/s12870-019-1774-2>
- Bettinger, R., Richerson, P., & Boyd, R. (2009). Constraints on the development of agriculture. *Current Anthropology*, *50*, 627–631. <https://doi.org/10.1086/605359>
- Blair, M. W., Pantoja, W., & Carmenza Muñoz, L. (2012). First use of microsatellite markers in a large collection of cultivated and wild accessions of tepary bean (*Phaseolus acutifolius* A. Gray). *Theoretical and Applied Genetics*, *125*, 1137–1147. <https://doi.org/10.1007/s00122-012-1900-0>
- Bornowski, N., Hart, J. P., Palacios, A. V., Ogg, B., Brick, M. A., Hamilton, J. P., Beaver, J. S., Buell, C. R., & Porch, T. (2023). Genetic variation in a tepary bean (*Phaseolus acutifolius* A. Gray) diversity panel reveals loci associated with biotic stress resistance. *The Plant Genome*, *16*, e20363. <https://doi.org/10.1002/tpg2.20363>
- Burbano-Erazo, E., León-Pacheco, R., Cordero-Cordero, C., López-Hernández, F., Cortés, A., & Tofiño-Rivera, A. (2021). Multi-environment yield components in advanced common bean (*Phaseolus vulgaris* L.) × tepary bean (*P. acutifolius* A. Gray) interspecific lines for heat and drought tolerance. *Agronomy*, *11*, 1978. <https://doi.org/10.3390/agronomy11101978>
- Butler, D. G., Cullis, B. R., Gilmour, A. R., Gogel, B. J., & Thompson, R. (2017). *ASReml-R Reference Manual Version 4*. VSN International Ltd. <https://www.mmade.org/wp-content/uploads/2019/01/asremLRMfinal.pdf>
- Cruz, S., Lobatón, J., Urban, M. O., Ariza-Suarez, D., Raatz, B., Aparicio, J., Mosquera, G., & Beebe, S. (2023). Interspecific common bean population derived from *Phaseolus acutifolius* using a bridging genotype demonstrate useful adaptation to heat tolerance. *Frontiers in Plant Science*, *14*, 1145858. <https://doi.org/10.3389/fpls.2023.1145858>
- Debouck, D. G., Dohle, S., Marquez, D., Pratt, R., Santaella, M., Santos, L. G., & Urban, M. (2023). Report on *Phaseolus* exploration in New Mexico, USA. USDA-ARS—New Mexico State University—Alliance Bioversity & CIAT. <https://hdl.handle.net/10568/134726>
- Delgado, A., & Gama López, S. (2015). Diversidad y distribución de los frijoles silvestres en México. *Universidad Nacional Autónoma de México Revista Digital Universitaria*, *16*. <https://www.revista.unam.mx/vol.16/num2/art10/>
- Dwivedi, S. L., Chapman, M. A., Abberton, M. T., Akpojotor, U. L., & Ortiz, R. (2023). Exploiting genetic and genomic resources to enhance productivity and abiotic stress adaptation of underutilized pulses. *Frontiers in Genetics*, *14*, 1193780. <https://doi.org/10.3389/fgene.2023.1193780>
- Federici, C. T., Ehdaie, B., & Waines, J. G. (1990). Domesticated and wild tepary bean: Field performance with and without drought-stress. *Agronomy Journal*, *82*, 896–900. <https://doi.org/10.2134/agronj1990.00021962008200050010x>
- Fernández, F., Gepts, P., & López, M. (1983). *Etapas de desarrollo de la planta de frijol común: guía de estudio [Stages of development of the common bean plant: Study guide]* (Serie 04EB-09.03). CIAT.
- Frahm, M. A., Rosas, J. C., Mayek-Perez, N., Lopez-Salinas, E., Acosta-Gallegos, J. A., & Kelly, J. D. (2004). Breeding beans for resistance to terminal drought in the lowland tropics. *Euphytica*, *136*, 223–232. <https://doi.org/10.1023/B:euph.0000030671.03694.bb>

- García, T., Duitama, J., Zullo, S. S., Gil, J., Ariani, A., Dohle, S., Palkovic, A., Skeen, P., Bermudez-Santana, C. I., Debouck, D. G., Martínez-Castillo, J., Gepts, P., & Chacón-Sánchez, M. I. (2021). Comprehensive genomic resources related to domestication and crop improvement traits in lima bean. *Nature Communications*, *12*, 702. <https://doi.org/10.1038/s41467-021-20921-1>
- Gilmour, A. R. (2020). *Echidna mixed model software*. <http://www.EchidnaMMS.org>
- Gujaria-Verma, N., Ramsay, L., Sharpe, A. G., Sanderson, L.-A., Debouck, D. G., Tar'an, B., & Bett, K. E. (2016). Gene-based SNP discovery in tepary bean (*Phaseolus acutifolius*) and common bean (*Phaseolus vulgaris*) for diversity analysis and comparative mapping. *BMC Genomics*, *17*, 1–16. <https://doi.org/10.1186/s12864-016-2499-3>
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978. <https://doi.org/10.1002/joc.1276>
- Isik, F., Holland, J., & Maltecca, C. (2017). *Genetic data analysis for plant and animal breeding*. Springer.
- Kelly, J. D., Hosfield, G. L., Varner, G. V., Uebersax, M. A., & Taylor, J. (1999). Registration of 'Matterhorn' great northern bean. *Crop Science*, *39*, 589–590. <https://doi.org/10.2135/cropsci1999.0011183X003900020058x>
- Kenward, M. G., & Roger, J. H. (1997). Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics*, *53*, 983–997. <https://doi.org/10.2307/2533558>
- Kwak, M., & Gepts, P. (2009). Structure of genetic diversity in the two major gene pools of common bean (*Phaseolus vulgaris* L., Fabaceae). *Theoretical and Applied Genetics*, *118*, 979–992. <https://doi.org/10.1007/s00122-008-0955-4>
- IPCC. (2023). Climate change 2023: AR6 synthesis report. In H. Lee & J. Romero (Eds.), *Contribution of working groups I, II, and III to the sixth assessment report of the intergovernmental panel on climate change core writing team* (pp. 35–115). IPCC <https://doi.org/10.59327/IPCC/AR6-9789291691647>
- Lobaton, J. D., Miller, T., Gil, J., Ariza, D., De La Hoz, J. F., Soler, A., Beebe, S., Duitama, J., Gepts, P., & Raatz, B. (2018). Re-sequencing of common bean identifies regions of inter-gene pool introgression and provides comprehensive resources for molecular breeding. *The Plant Genome*, *11*, 170068. <https://doi.org/10.3835/plantgenome2017.08.0068>
- Long, R., Temple, S., Schmierer, J., Canevari, M., & Meyer, R. D. (2010). *Common dry bean production in California, second edition* (UC ANR Publication 8402). University of California Agriculture and Natural Resources. <http://ucanr.org/pubs.cfm>
- Nabateregga, M., Mukankusi, M., Raatz, B., Edema, R., Nkalubo, S., & Alladassi, B. M. E. (2019). Quantitative trait loci (QTL) mapping for intermittent drought tolerance in BRB 191 × SEQ 1027 Andean Intragene cross recombinant inbred line population of common bean (*Phaseolus vulgaris* L.). *African Journal of Biotechnology*, *18*, 452–461. <https://doi.org/10.5897/AJB2019.16768>
- Markhart, A. H. (1985). Comparative water relations of *Phaseolus vulgaris* L. and *Phaseolus acutifolius* Gray. *Plant Physiology*, *77*, 113–117. <https://doi.org/10.1104/pp.77.1.113>
- Martínez-Castillo, J., Araujo, A. S. F., Chacón-Sánchez, M. I., Santos, L. G., Lopes, A. C. A., Gibson, K., Gomes, R. L. F., Andueza-Noh, R. H., Bitochi, E., Ballina-Gómez, H. S., Peralta, E., Ormeño-Orrillo, E., Espinoza, L., Nieto, C., Murillo, A., Jadán-Veriñas, E., García, T., Duitama, J., Aguirre-Liguori, J. A., ... Debouck, D. G. (2023). International lima bean network: From the origin of the species to modern plant breeding. *Genetic Resources and Crop Evolution*, *70*, 1575–1583. <https://doi.org/10.1007/s10722-023-01603-x>
- Mejía-Jiménez, A., Muñoz, C., Jacobsen, H. J., Roca, W. M., & Singh, S. P. (1994). Interspecific hybridization between common and tepary beans: Increased hybrid embryo growth, fertility, and efficiency of hybridization through recurrent and congruity backcrossing. *Theoretical and Applied Genetics*, *88*, 324–331. <https://doi.org/10.1007/bf00223640>
- Moghaddam, S. M., Oladzad, A., Koh, C., Ramsay, L., Hart, J. P., Mamidi, S., Hoopes, G., Sreedasyam, A., Wiersma, A., Zhao, D., Grimwood, J., Hamilton, J. P., Jenkins, J., Vaillancourt, B., Wood, J. C., Schmutz, J., Kagale, S., Porch, T., Bett, K. E., ... McClean, P. E. (2021). The tepary bean genome provides insight into evolution and domestication under heat stress. *Nature Communications*, *12*, 2638. <https://doi.org/10.1038/s41467-021-22858-x>
- Mohamed, F., Mohamed, M., Schmitz-Eiberger, N., Keutgen, & Noga, M. (2005). Comparative drought postponing and tolerance potentials of two tepary bean lines in relation to seed yield. *African Crop Science Journal*, *13*, 49–60.
- Muñoz, L. C., Blair, M. W., Duque, M. C., Tohme, J., & Roca, W. (2004). Introgression in common bean × tepary bean interspecific congruity-backcross lines as measured by AFLP Markers. *Crop Science*, *44*, 637–645. <https://doi.org/10.2135/cropsci2004.6370>
- Mwale, S. E., Shimelis, H., Mafongoya, P., & Mashilo, J. (2020). Breeding tepary bean (*Phaseolus acutifolius*) for drought adaptation: A review. *Plant Breeding*, *139*, 821–833. <https://doi.org/10.1111/pbr.12806>
- Mwale, S. E., Shimelis, H., Nkhata, W., Sefasi, A., Fandika, I., & Mashilo, J. (2022). Genotype-by-environment interaction in tepary bean (*Phaseolus acutifolius* A. Gray) for seed yield. *Agronomy*, *13*, 12. <https://doi.org/10.3390/agronomy13010012>
- Nabhan, G. P., & Felger, R. S. (1978). Teparies in southwestern North America. *Economic Botany*, *32*, 3–19. <https://doi.org/10.1007/BF02906725>
- Parker, T. A., Acosta Gallegos, J., Beaver, J., Brick, M., Brown, J. K., Cichy, K., Debouck, D. G., Delgado-Salinas, A., Dohle, S., Ernest, E., Estevez de Jensen, C., Gomez, F., Hellier, B., Karasev, A. K., Kelly, J. D., McClean, P., Miklas, P., Myers, J. R., Osorno, J. M., ... Gepts, P. (2023). Genetic resources and breeding priorities in *Phaseolus* beans: Vulnerability, resilience, and future challenges. In I. Goldman (Ed.), *Plant breeding reviews* (pp. 289–420). <https://doi.org/10.1002/9781119874157.ch6>
- Parker, T. A., & Gepts, P. (2021). Population genomics of *Phaseolus* spp.: A domestication hotspot. In O. P. Rajora (Ed.), *Population genomics: Crop plants* (pp. 1–83). Springer Nature. [https://doi.org/10.1007/13836\\_2021\\_89](https://doi.org/10.1007/13836_2021_89)
- Pathak, T., Maskey, M., Dahlberg, J., Kearns, F., Bali, K., & Zaccaria, D. (2018). Climate change trends and impacts on California agriculture: A detailed review. *Agronomy*, *8*, 25. <https://doi.org/10.3390/agronomy8030025>
- Peel, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Köppen–Geiger climate classification. *Hydrology and Earth System Science*, *11*, 1633–1644. <https://doi.org/10.5194/hess-11-1633-2007>
- Polania, J. A., Poschenrieder, C., Beebe, S., & Rao, I. M. (2016). Effective use of water and increased dry matter partitioned to grain contribute to yield of common bean improved for drought resistance.

- Frontiers in Plant Science*, 7, 660. <https://doi.org/10.3389/fpls.2016.00660>
- Porch, T., Barrera, S., Berny Mier Y Teran, J. C., Díaz-Ramírez, J., Pastor-Corrales, M., Gepts, P., Urrea, C. A., & Rosas, J. C. (2022). Release of tepary bean TARS-Tep 23 germplasm with broad abiotic stress tolerance and rust and common bacterial blight resistance. *Journal of Plant Registrations*, 16, 109–119. <https://doi.org/10.1002/plr2.20180>
- Porch, T. G. (2006). Application of stress indices for heat tolerance screening of common bean. *Journal of Agronomy and Crop Science*, 192, 390–394. <https://doi.org/10.1111/j.1439-037X.2006.00229.x>
- Porch, T. G., Beaver, J. S., & Brick, M. A. (2013). Registration of tepary germplasm with multiple-stress tolerance, TARS-Tep 22 and TARS-Tep 32. *Journal of Plant Registrations*, 7, 358–364. <https://doi.org/10.3198/jpr2012.10.0047crg>
- Porch, T. G., & Jahn, M. (2001). Effects of high-temperature stress on microsporogenesis in heat-sensitive and heat-tolerant genotypes of *Phaseolus vulgaris*. *Plant, Cell & Environment*, 24, 723–731. <https://doi.org/10.1046/j.1365-3040.2001.00716.x>
- Porch, T. G., Rosas, J. C., Cichy, K., Lutz, G. G., Rodriguez, I., Colbert, R. W., Demosthene, G., Hernández, J. C., Winham, D. M., & Beaver, J. S. (2023). Release of tepary bean cultivar ‘USDA Fortuna’ with improved disease and insect resistance, seed size, and culinary quality. *Journal of Plant Registrations*, 18, 42–52. <https://doi.org/10.1002/plr2.20322>
- Pratt, R. C., & Nabhan, G. P. (1988). Evolution and diversity of *Phaseolus acutifolius* genetic resources. In P. Gepts (Ed.), *Genetic resources of Phaseolus beans* (pp. 409–440). Springer, Dordrecht. [https://doi.org/10.1007/978-94-009-2786-5\\_17](https://doi.org/10.1007/978-94-009-2786-5_17)
- R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org>
- Rainey, K. M., & Griffiths, P. D. (2005). Inheritance of heat tolerance during reproductive development in snap bean (*Phaseolus vulgaris* L.). *Journal of the American Society for Horticultural Science*, 130, 700–706. <https://doi.org/10.1007/s10722-004-1811-2>
- Rao, I., Beebe, S., Polania, J., Ricaurte Oyola, J., Cajiao, C., Garcia, R., & Rivera, M. (2013). Can tepary bean be a model for improvement of drought resistance in common bean? *African Crop Science Journal*, 21, 265–281. <https://doi.org/10.4314/ACSJ.V21I4>
- Richerson, P. J., Boyd, R., & Bettinger, R. L. (2001). Was agriculture impossible during the Pleistocene but mandatory during the Holocene? *American Antiquity*, 66, 387–411. <https://doi.org/10.2307/2694241>
- Rodríguez-Álvarez, M. X., Boer, M. P., Van Eeuwijk, F. A., & Eilers, P. H. C. (2018). Correcting for spatial heterogeneity in plant breeding experiments with P-splines. *Spatial Statistics*, 23, 52–71. <https://doi.org/10.1016/j.spasta.2017.10.003>
- Rosas, J. C., Castro, A., & Flores, E. (2000). Mejoramiento genético del frijol rojo y negro mesoamericano para Centroamérica y El Caribe. *Agronomía Mesoamericana*, 11, 37–43.
- Rubel, F., & Kotteck, M. (2010). Observed and projected climate shifts 1901–2100 depicted by world maps of the Köppen–Geiger climate classification. *Meteorologische Zeitschrift*, 19, 135–141. <https://doi.org/10.1127/0941-2948/2010/0430>
- Schinkel, C., & Gepts, P. (1988). Phaseolin diversity in the tepary bean, *Phaseolus acutifolius* A. Gray. *Plant Breeding*, 101, 292–301. <https://doi.org/10.1111/j.1439-0523.1988.tb00301.x>
- Schinkel, C., & Gepts, P. (1989). Allozyme variability in the tepary bean, *Phaseolus acutifolius* A. Gray. *Plant Breeding*, 102, 182–195. <https://doi.org/10.1111/j.1439-0523.1989.tb00336.x>
- Shonnard, G. C., & Gepts, P. (1994). Genetics of heat tolerance during reproductive development in common bean. *Crop Science*, 34, 1168–1175. <https://doi.org/10.2135/cropsci1994.0011183x003400050005x>
- Singh, S. P. (1982). A key for identification of different growth habits of *Phaseolus vulgaris* L. *Annual Report of the Bean Improvement Cooperative*, 25, 92–95.
- Smith, A., Cullis, B., & Thompson, R. (2001). Analyzing variety by environment data using multiplicative mixed models and adjustments for spatial field trend. *Biometrics*, 57, 1138–1147. <https://doi.org/10.1111/j.0006-341x.2001.01138.x>
- Souter, J. R., Gurusamy, V., Porch, T. G., & Bett, K. E. (2017). Successful introgression of abiotic stress tolerance from wild tepary bean to common bean. *Crop Science*, 57, 1160–1171. <https://doi.org/10.2135/cropsci2016.10.0851>
- Suárez, J. C., Polanía, J. A., Contreras, A. T., Rodríguez, L., Machado, L., Ordoñez, C., Beebe, S., & Rao, I. M. (2020). Adaptation of common bean lines to high temperature conditions: Genotypic differences in phenological and agronomic performance. *Euphytica*, 216, 28. <https://doi.org/10.1007/s10681-020-2565-4>
- Waines, J. G., Manshardt, R. M., & Wells, W. C. (1988). Interspecific hybridization between *Phaseolus vulgaris* and *P. acutifolius*. In P. Gepts (Ed.), *Genetic resources of Phaseolus beans* (pp. 485–502). Springer.
- Yuan, Y., Ton, B. L., Thomas, W. J. W., Batley, J., & Edwards, D. (2023). Supporting crop plant resilience during climate change. *Crop Science*, 63, 1816–1828. <https://doi.org/10.1002/csc2.21019>
- Zabel, F., Müller, C., Elliott, J., Minoli, S., Jägermeyr, J., Schneider, J. M., Franke, J. A., Moyer, E., Dury, M., Francois, L., Folberth, C., Liu, W., Pugh, T. A. M., Olin, S., Rabin, S. S., Mauser, W., Hank, T., Ruane, A. C., & Asseng, S. (2021). Large potential for crop production adaptation depends on available future varieties. *Global Change Biology*, 27, 3870–3882. <https://doi.org/10.1111/gcb.15649>

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