

SPECIAL ISSUE ARTICLE

Adapting Agriculture to Climate Change: A Walk on the Wild Side

Genetic parameters of drought tolerance for agromorphological traits in eggplant, wild relatives, and interspecific hybrids

Abou Bakari Kouassi¹  | Koffi Brice Aymar Kouassi¹ | Zakaria Sylla¹ | Mariola Plazas² | Ramya Malkanthi Fonseka³ | Auguste Kouassi¹ | Hemal Fonseka⁴ | Assanvo Simon-Pierre N'guetta¹ | Jaime Prohens²

¹ Laboratoire de Génétique, UFR-Biosciences, Univ. Félix Houphouët-Boigny (UFHB), 22 BP 582, Abidjan 22, Côte d'Ivoire

² Instituto de Conservación y Mejora de la Agrodiversidad Valenciana, Univ. Politècnica de València, Camino de Vera 14, Valencia 46022, Spain

³ Dep. of Crop Science, Faculty of Agriculture, Univ. of Peradeniya, Peradeniya 20400, Sri Lanka

⁴ Onesh Agriculture Pvt. Ltd., 100. Kent Road, Colombo 9, Sri Lanka

Correspondence

Jaime Prohens, Instituto de Conservación y Mejora de la Agrodiversidad Valenciana, Univ. Politècnica de València, Camino de Vera 14, 46022 Valencia, Spain.
Email: jprohens@btc.upv.es

Assigned to Associate Editor Benjamin Kilian.

Funding information

Universitat Politècnica de València, Grant/Award Number: PAID-06-18; Ministerio de Ciencia e Innovación, Grant/Award Number: RTI-2018-094592-B-I00; Generalitat Valenciana, Grant/Award Number: APOSTD/2018/014; Global Crop Diversity Trust, Grant/Award Number: GS20001

Abstract

Crop wild relatives (CWRs) have barely been used in eggplant (*Solanum melongena*) breeding. However, introgression breeding may help in coping with the challenges posed by climate change. During the rainy and dry seasons, we evaluated nine accessions of eggplant, nine accessions of seven related species (of which six are CWRs and one is a cultivated relative), and 12 interspecific hybrids. Drought tolerance scores, calculated as ratios of growing rates and ratios of mean values during the rainy and dry seasons, were obtained for vegetative growth and yield-related traits. Considering the vegetative growth and yield-related traits evaluated, the F₁ hybrid progenies of eggplant with *S. insanum* MEL1 × INS2 and MEL4 × INS3, *S. anguivi* MEL6 × ANG1, and *S. dasyphyllum* MEL6 × DAS1, plus the *S. sysimbriifolium* accession SIS1, displayed drought tolerance. Small to large gaps were observed between phenotypic and genotypic CVs of drought tolerance scores, reflecting variable influence of environmental factors on drought tolerance of the traits evaluated. In addition, the narrow-sense heritability was generally moderate, indicating that genes with dominance and/or epistasis effects may be involved in the expression of drought tolerance. High genotypic correlations for drought tolerance scores between pairs of traits such as branching index and leaf length, leaf petiole diameter and plant height, number of stamens per flower, and fruit pedicel length suggest that drought tolerance of these traits is controlled by genes that are in linkage disequilibrium and/or have pleiotropic effects. The results are relevant for the development of drought-tolerant cultivars of eggplant.

Abbreviations: CWR, crop wild relative.

1 | INTRODUCTION

Availability of water is an essential factor for the growth, development, and productivity of crop plants (Condon,

Richards, Rebetzke, & Farquhar, 2004). In a context where water resources are already scarce and likely to become scarcer, it is now imperative to improve the tolerance of plants to drought in order to guarantee food security. Drought can be defined as a climatic phenomenon that is characterized by a deviation from the average or normal values of rainfall (Grieu, Maury, Debaeke, & Sarrafi, 2008). Quantitative elements related to drought, such as duration (intermittent or prolonged drought), period of occurrence, geographic extension, the dynamics of establishment (sudden or progressive), and the time of its onset in the crop cycle, have consequences for agriculture (Gaufichon, Piroul, & Bachelier, 2010). In fact, in drought conditions, crop plants in general have lower yields and are subject to higher production costs and deterioration in farming practices. Irrigation, as a means of mitigating drought, has its own environmental and economic costs, making this option unsuitable for all scenarios. It is hence necessary to find effective ways to increase or at least stabilize crop production under drought conditions, which are expected to become more common due to climate change. In this way, genetic improvement is crucial to develop improved varieties of crop plants that are well adapted to restricting environmental conditions (Nakashima & Suenaga, 2017).

Eggplant (*Solanum melongena* L.) is included in the Annex 1 of the International Treaty on Plant Genetic Resources for Food and Agriculture, which is a recognition of its importance for food security, especially in tropical and subtropical regions (Fowler, Moore, & Hawtin, 2003). Given that many areas of cultivation of eggplant may become prone to drought in the near future, there is a need for drought-tolerant improved varieties of eggplant. In particular for eggplant, diverse degrees of drought tolerance have been observed in some available accessions and varieties, and they are potentially usable to face this problem. For instance, Delfin, Manaday, Canama, Ocampo, and Maghirang (2013) observed significant differences between a hundred varieties of eggplant and its crop wild relatives (CWRs), for morphological and physiological characteristics, subjected to drought conditions in a greenhouse, indicating that there are possibilities of selection of drought-resistant eggplant varieties. Similarly, Tani et al. (2018) obtained different reactions of two eggplant genotypes subjected to separate and simultaneous effects of drought and infection by the pathogenic fungus *Verticillium dahliae*, whereas Plazas et al. (2019) found differences in the physiological and biochemical response to drought stress of four eggplant cultivars. In addition, Plazas, Rahma, Rodríguez-Burruezo, Prohens, and Fita (2016) identified accessions of the wild species *S. anguivi* Lam. and *S. insanum* L., as well as interspecific hybrids, with enhanced drought tolerance. These data and those of other authors (Daunay, 2008; Daunay & Hazra, 2012; Kashyap et al., 2003) sug-

gest that the use of eggplant CWRs as sources of genes of agronomic interest for adaptation to drought in breeding programs may be an appropriate strategy. Indeed, these species can be found in a wide range of environmental conditions (Vorontsova & Knapp, 2016) and may therefore present a great allelic diversity for important agronomic characteristics, as well as for adaptation to various environmental conditions. They are able to grow on soils infested with pathogens (Daunay, 2008; Gisbert, Prohens, & Nuez, 2011; Rotino, Sala, & Toppino, 2014) and in extreme climatic conditions such as desertic areas, environments with large thermal amplitudes, in particular night temperatures below 0 °C, marshy areas, etc. (Daunay & Hazra, 2012; Ranil et al., 2017; Vorontsova & Knapp, 2016). Thus, the use of interspecific hybridization has allowed the introgression of genes from wild species into the genetic background of eggplant (Kouassi et al., 2016; Kouassi, Kouassi, Alla-N'nan, Kouassi, & N'guetta, 2019; Plazas, Vilanova, et al., 2016) and may lead to the widening of its genetic variability. However, the evaluation of drought tolerance of the new genotypes and their use in breeding programs require the definition of reliable phenotypic criteria, transmissible from parental accessions to progenies (Gaufichon et al., 2010).

In the present study, we analyzed the drought tolerance of accessions of eggplant, some relatives, and their interspecific F₁ hybrid progenies using drought tolerance scores for the agromorphological characteristics. The objective was to identify, on the one hand, accessions of eggplant, CWRs, and interspecific hybrid progenies presenting drought tolerance or resistance abilities and, on the other hand, to quantify genetic parameters (genotypic and phenotypic CVs, heritability, and genotypic and phenotypic correlation coefficients) for drought tolerance scores of agromorphological characteristics assessed in open field conditions.

2 | MATERIALS AND METHODS

2.1 | Site of the study

This study was performed in Côte d'Ivoire, in an experimental farm of the National Center for Agronomic Research (CNRA) located in Adiopodoumé/Yopougon, 17 km from Abidjan. The geographic coordinates of the plot are 5°19'51.6" N, 4°08'20.6" W, and an altitude of 37 m asl. Two experiments were carried out in 2018, one during the main dry season and the other in the rainy season, which extend respectively from December to April and from May to July. The plants were transplanted in January and May 2018 for the assessments in dry and rainy seasons, respectively. In the dry season, the average

monthly precipitation was 63.85 mm of rain and the average temperature was 28.55 °C. In the rainy season, the average monthly precipitation was 204.59 mm of rain and the average temperature was 26.51 °C.

2.2 | Plant material and growing conditions

The plant material consisted of nine eggplant (*S. melongena*) accessions, nine accessions of six CWRs and one cultivated relative of eggplant from the primary, secondary, and tertiary gene pools (Table 1), and 12 F₁ interspecific hybrids between eggplant and wild and cultivated relatives (Table 2).

Seeds of parental accessions and of F₁ hybrid progenies were germinated according to the recommendations of Ranil et al. (2015). Briefly, it consisted of soaking the seeds in water for 24 h, then in a 500 mg kg⁻¹ solution of gibberellic acid for 24 h. The seeds were then sown in Petri dishes filled with cotton and paper soaked in a 1,000 mg kg⁻¹ KNO₃ solution. In case the seeds were sown in peat or potting soil, watering was carried out with the 1,000 mg kg⁻¹ KNO₃ solution.

The seedlings were left in the nursery for 45 d and then transplanted to the field in a completely randomized Fisher block. Each parental accession and each F₁ offspring were represented by a row of three to five plants with a spacing of 1.5 and 1 m, respectively, between and within rows. The 12–22–22 N–P–K fertilizer was applied at a rate of 25 g per plant per month. The fungicide Ivory 80 WP (composition: mancozeb 80 g kg⁻¹) and the insecticide Cypercal 50 EC (composition: cypermethrin 50 g L⁻¹) were applied at the rates of 2 kg ha⁻¹ and 1 L ha⁻¹, respectively, when fungal and pest attacks were observed. The experimental plot was also regularly weeded.

2.3 | Measurement of agromorphological traits

The plants were characterized, in open field conditions, during the dry and rainy seasons using 18 agromorphological traits selected from the descriptors list of eggplant (IBPGR, 1990) (Table 3). In each season, the vegetative growth traits were measured 3 and 10 wk after transplanting the seedlings. The floral traits were evaluated on three to four inflorescences chosen randomly on each plant. When the inflorescence consisted of more than three flowers, the stamens were counted on three flowers also chosen randomly. The characteristics of the fruits were measured on three to four fruits per plant. Data have been stored

in the Germinate 3 database (<https://ics.hutton.ac.uk/cwr/eggplant/#home>; Shaw et al., 2020).

2.4 | Drought tolerance assessment

A new method, based on agromorphological traits, has been defined for the assessment of drought tolerance abilities of parental accessions and F₁ hybrid progenies. During the dry and rainy seasons, vegetative growth traits were scored 3 and 10 wk after transplanting (3 WAT and 10 WAT, respectively). The growing rate of each vegetative growth trait was then calculated according to the formula below:

$$\frac{(\text{Mean value of the vegetative growth trait 10 WAT}) - (\text{Mean value of the vegetative growth trait 3 WAT})}{\text{Mean value of the vegetative growth trait 3 WAT}}$$

Subsequently, for each vegetative growth trait, the drought tolerance score (DTS1) of each accession was evaluated based on the following formula:

$$\text{DTS1} = \frac{\text{Growing rate of the vegetative growth trait in the rainy season}}{\text{Growing rate of the vegetative growth trait in the dry season}}$$

For yield-related traits, drought tolerance scores (DTS2) of each accession were evaluated based on the following ratio:

$$\text{DTS2} = \frac{\text{Mean value of the yield – related parameter in the rainy season}}{\text{Mean value of the yield – related parameter in the dry season}}$$

For each agromorphological character, when the DTS ratio is equal to 1 ± 0.1 , this indicates that the growing rates are similar in the dry and rainy seasons. When the ratio is greater than 1 ± 0.1 , this indicates that the plants grow better in the rainy season than in the dry season. Reciprocally, when the ratio is less than 1 ± 0.1 , this indicates better growth in the dry season compared with the rainy season.

2.5 | Data analysis

Drought tolerance scores were calculated using Microsoft Excel 2013. For each agromorphological trait, a mixed linear model, based on the restricted maximum likelihood (REML) method, was used to estimate variance components (additive genetic variance, phenotypic variance, and

TABLE 1 Accessions of eggplant (*Solanum melongena*) and wild and cultivated relatives used in the study

Gene pool	Statute	Species	Code	Accession	Origin
Primary	Cultivated	<i>S. melongena</i>	MEL1	BBS-118/B	Côte d'Ivoire
			MEL2	BBS-146	Côte d'Ivoire
			MEL3	BBS-175	Côte d'Ivoire
			MEL4	7145	Sri Lanka
			MEL5	8104	Sri Lanka
			MEL6	Ampara	Sri Lanka
			MEL7	Kermit	South Est Asia
			MEL8	Listada de Gandia	Spain
			MEL9	Jeffna Special	Sri Lanka
Secondary	Wild	<i>S. insanum</i>	INS1	SLKINS-1	Sri Lanka
			INS3	MM498	Japan
			AET1	Aub2INB	Unknown (source: Côte d'Ivoire)
	Cultivated	<i>S. aethiopicum</i>	ANG1	BBS-119	Côte d'Ivoire
			ANG2	BBS-125/B	Côte d'Ivoire
			DAS1	MM1153	Uganda
	Wild	<i>S. anguivi</i>	LIN3	MM195	Tunisia
			PYR1	SOLN-66	Unknown (source: Germany)
			SIS1	SOLN-78	Unknown (source: USA)
Tertiary	Wild	<i>S. sisymbriifolium</i>			

TABLE 2 Interspecific F_1 hybrid progenies obtained from hybridization of accessions of eggplant (*Solanum melongena*) with those of wild and cultivated relatives

Interspecific hybridizations	Crossed accessions	Codes of F_1 hybrid progenies
<i>S. melongena</i> × <i>S. insanum</i>	BBS-118/B × SLKINS-1	MEL1 × INS1
	BBS-118/B × SLKINS-2	MEL1 × INS2
	BBS-118/B × MM498	MEL1 × INS3
	7145 × MM498	MEL4 × INS3
	8104 × MM498	MEL5 × INS3
<i>S. melongena</i> × <i>S. anguivi</i>	Ampara × MM498	MEL6 × INS3
	BBS-146 × BBS-119	MEL2 × ANG1
	BBS-175 × BBS-119	MEL3 × ANG1
<i>S. melongena</i> × <i>S. dasyphyllum</i>	Ampara × BBS-119	MEL6 × ANG1
	BBS-175 × MM1153	MEL3 × DAS1
	Ampara × MM1153	MEL6 × DAS1
<i>S. melongena</i> × <i>S. aethiopicum</i>	7145 × Aub21NB	MEL4 × AET1

residual variance) and genetic parameters (coefficients of genotypic and phenotypic correlations) of drought tolerance scores (Patterson & Thompson, 1971) with the Variance Components Estimation (VCE) package, version 6.0.2 (Groeneveld, Kovač, & Mielenz, 2010). The matrix notation of the model is $\mathbf{Y} = \mu + \mathbf{Z}\boldsymbol{\alpha} + \mathbf{e}$, where $\mathbf{Y}$ is the vector of drought tolerance scores, μ is the overall mean drought tolerance score, $\mathbf{Z}$ is the incidence matrix of random additive genetic effects, $\boldsymbol{\alpha}$ is the vector of random additive genetic effects, and $\mathbf{e}$ is the vector of random residual effects (i.e., other genetic effects such as dominance, epistasis, and nongenetic effects; Kruuk, 2004; Mrode & Thompson, 2014).

Narrow-sense heritability (h^2), as well as phenotypic (PCV) and genotypic (GCV) CVs, were calculated based on the different variance–covariance matrices provided by the VCE 6.0.2 package. The heritability was considered low, medium, and high when its value was <.20, between .20 and .50, and >.50, respectively (Johnson, Robinson, & Comstock, 1955; Stanfield, 1975). The GVC and PVC were considered low, moderate, and high when their values were <11%, between 11 and 20%, and >20%, respectively (Sumathi, Sumanth, & Veerabhadhiran, 2010). Genetic parameters were calculated according the following formulas:

$$h^2 = \frac{\sigma_a^2}{\sigma_p^2}$$

$$\text{PCV} = \left(\frac{\sqrt{\sigma_p^2}}{\mu} \right) \times 100$$

$$\text{GCV} = \left(\frac{\sqrt{\sigma_a^2}}{\mu} \right) \times 100$$

$$r = \frac{\text{cov}(x, y)}{\sqrt{\sigma_x^2 \sigma_y^2}}$$

where σ_a^2 , σ_p^2 , and μ are the additive genetic variance, the phenotypic variance, and the mean value of the drought tolerance score of a given agromorphological character, respectively; $\text{cov}(x, y)$ is the covariance of drought tolerance scores of two traits (x and y); and σ_x^2 and σ_y^2 are the variances of drought tolerance scores of the traits x and y , respectively.

3 | RESULTS

3.1 | Drought tolerance scores of parental accessions and F_1 hybrid progenies

Drought tolerance scores of the accessions SIS1 of *S. sisymbriifolium* Lam., MEL3 of *S. melongena* (Table 4), as well as the interspecific F_1 progenies MEL4 × INS3, MEL6 × ANG1, and MEL6 × DAS1 (Table 5) were less than or equal to 1 ± 0.1 regarding plant height (PLHE), canopy width (PLWI) and plant branching index (BRIN). The vegetative growth of these genotypes was relatively higher in the dry season than in the rainy season. Regarding these three traits, for the accessions INS3 of *S. insanum* and MEL4 of *S. melongena* (Table 4), as well as the hybrids MEL1 × INS2,

TABLE 3 Agromorphological traits used for the characterization of accessions of eggplant (*Solanum melongena*) wild and cultivated relatives and their interspecific hybrid progenies

No.	Traits	Units	Abbreviations	Organs	Types of character
1	Plant Height	cm	PLHE	Stems	Vegetative growth traits
2	Plant canopy width	cm	PLWI		
3	Branching index	–	BRIN		
4	Leaf blade length	cm	LBL	Leaves	
5	Leaf blade width	cm	LBWI		
6	Petiole length	cm	PELE		
7	Petiole diameter	mm	PEDI		Yield-related traits
8	Flowering time	d	FLTM	Flowers	
9	No. of flowers per inflorescence	–	NFLIN		
10	Style length	mm	STLE		
11	No. of stamens	–	NBST		
12	Fruit length	cm	FRLE	Fruits	
13	Fruit width	cm	FRWI		
14	Fruit pedicel length	mm	FRPL		
15	Fruit pedicel diameter	mm	FRPD		
16	Fruit weight	g	FRWE		
17	No. of seeds per fruit	–	NSEF		
18	Weight of 100 seeds	g	100S		

TABLE 4 Drought tolerance scores of some accessions of eggplant (*Solanum melongena*) and wild and cultivated relatives, regarding agromorphological traits

Accessions	Vegetative growth traits ^a						Floral traits ^a						Fruit traits ^a					
	PLHE	PLWI	BRIN	LBLE	LBWI	PELE	PEDI	FLTM	NFLIN	STLE	NBST	FRLE	FRWI	FRPL	FRPD	FRWE	NSEF	100S
AET1	0.66	1.52	2.20	3.84	7.12	2.46	0.06	1.14	1.32	4.33	1.02	0.96	0.93	0.99	0.98	0.80	1.46	1.08
ANG1	0.64	1.77	5.65	0.02	0.26	0.27	0.00	0.97	0.38	2.17	1.04	1.09	1.11	0.60	1.05	1.17	1.02	1.00
ANG2	1.08	2.44	2.31	1.72	0.55	0.67	0.31	1.07	3.22	2.50	1.00	0.98	0.95	1.11	1.09	1.17	1.04	1.00
DAS1	1.56	0.92	1.82	0.66	0.71	9.58	0.33	1.12	1.25	0.67	1.00	1.11	1.15	1.19	0.11	1.00	1.04	1.00
INS1	0.90	2.80	5.20	2.85	2.77	15.00	0.96	1.34	1.90	0.93	0.98	1.12	1.08	1.14	1.29	0.54	0.89	0.93
INS3	0.58	0.77	2.84	0.66	0.47	2.63	3.17	1.27	0.86	0.93	0.96	1.26	1.35	0.58	1.54	0.51	1.13	1.00
LIN3	1.17	0.85	13.50	1.97	1.57	4.76	3.00	1.05	0.83	1.20	1.00	1.67	1.83	1.50	1.60	4.52	4.32	1.06
MEL1	2.35	2.24	10.20	1.83	0.98	13.46	0.40	1.27	1.11	0.35	1.08	1.53	1.27	1.82	0.15	1.25	1.35	2.27
MEL2	1.86	1.78	1.11	0.92	0.70	0.81	3.89	1.09	1.33	0.33	1.10	0.88	1.04	1.17	0.93	1.21	0.86	1.11
MEL3	1.08	0.89	0.57	1.90	1.58	3.67	1.41	0.71	1.67	0.60	0.98	1.50	1.17	1.33	0.17	1.06	1.25	1.11
MEL4	0.99	0.66	1.33	0.94	0.63	6.74	0.50	1.11	1.20	1.07	1.16	1.20	1.28	0.87	0.16	1.36	1.24	1.06
MEL5	1.09	1.27	6.00	5.21	2.21	29.23	0.23	1.28	0.93	0.00	1.09	1.55	1.23	1.40	1.60	1.50	1.33	1.34
MEL6	1.41	1.04	4.67	0.46	0.43	0.67	2.21	1.14	1.10	0.27	1.06	1.87	0.78	1.37	0.19	1.22	0.84	0.25
MEL7	1.32	1.71	2.16	0.66	0.12	9.26	0.00	1.11	0.75	0.97	1.09	1.16	1.18	1.22	1.50	1.00	1.34	0.82
MEL8	1.61	2.09	2.33	2.93	1.51	2.65	1.46	1.22	1.00	0.47	1.08	1.14	0.97	1.18	1.15	1.06	1.02	1.03
MEL9	1.72	1.12	3.90	2.07	0.22	1.19	0.03	1.19	1.67	0.50	0.93	1.32	1.03	1.39	1.23	0.77	1.01	0.90
PYR1	1.56	0.98	5.65	0.71	1.69	0.83	0.33	1.22	0.85	4.75	1.00	9.83	1.25	1.18	1.00	8.57	0.99	1.00
SIS1	0.68	0.73	0.75	0.05	0.31	0.23	0.94	1.00	0.84	0.64	0.87	1.22	1.39	1.14	1.26	5.87	0.80	1.14

Note. Drought tolerance scores that are less than or equal to 1 ± 0.1 are shown in bold.

^aPLHE, plant height; PLWI, plant canopy width; BRIN, branching index; LBLE, leaf blade length; LBWI, leaf blade width; PELE, petiole length; PEDI, petiole diameter; FLTM, flowering time; NFLIN, number of flowers per inflorescence; STLE, style length; NBST, number of stamens; FRLE, fruit length; FRWI, fruit width; FRPL, fruit pedicel length; FRPD, fruit pedicel diameter; FRWE, fruit weight; NSEF, number of seeds per fruit; 100S, weight of 100 seeds.

TABLE 5 Drought tolerance scores of F₁ hybrid progenies of some accessions of eggplant (*Solanum melongena*) and wild and cultivated relatives regarding agromorphological traits

Hybrid progenies	Vegetative growth traits ^a							Floral traits ^a				Fruit traits ^a						
	PLHE	PLWI	BRIN	LBLE	LBWI	PELE	PEDI	FLTM	NFLIN	STLE	NBST	FRLE	FRWI	FRPL	FRPD	FRWE	NSEF	100S
MEL1 × INS1	1.24	1.46	15.42	1.56	2.64	2.83	0.19	1.29	0.61	5.50	1.02	1.29	1.20	1.02	1.75	1.67	1.23	1.82
MEL1 × INS3	1.21	1.65	6.20	0.96	1.01	6.13	0.20	1.21	0.75	0.57	0.98	1.36	1.26	1.64	1.86	0.92	2.68	1.26
MEL1 × INS2	1.06	0.96	4.96	0.27	0.42	0.32	0.18	1.18	1.00	0.33	0.98	1.07	1.17	0.98	1.64	0.97	1.76	1.73
MEL2 × ANG1	1.18	0.83	5.01	2.38	0.00	0.23	0.37	1.15	1.17	3.68	0.83	–	–	–	–	–	–	–
MEL3 × ANG1	0.69	1.56	8.00	0.08	0.16	1.01	0.52	1.29	1.17	0.75	0.96	–	–	–	–	–	–	–
MEL3 × DAS1	0.67	0.41	1.50	0.24	0.18	0.90	1.56	1.09	1.94	0.57	1.02	–	–	–	–	–	–	–
MEL4 × AET1	1.03	0.93	3.35	1.53	18.82	1.25	0.28	1.19	1.82	0.91	1.04	–	–	–	–	–	–	–
MEL4 × INS3	0.71	0.39	1.00	0.06	0.02	0.11	0.67	1.08	0.84	0.11	1.11	1.06	1.08	1.23	1.10	0.63	0.00	0.00
MEL5 × INS3	0.93	0.68	5.33	0.33	0.35	1.20	0.24	1.22	1.38	0.22	1.08	1.03	0.04	0.98	1.83	0.87	1.48	1.16
MEL6 × ANG1	0.53	0.71	0.44	0.08	0.73	0.25	0.36	1.05	0.93	1.25	0.92	0.87	0.91	0.84	0.75	0.10	1.63	0.40
MEL6 × DAS1	0.89	0.64	1.00	0.37	0.30	0.96	0.89	1.14	1.60	0.00	0.91	–	–	–	–	–	–	–
MEL6 × INS3	1.98	0.98	4.47	0.40	0.22	0.53	0.11	1.18	0.70	0.11	0.98	1.27	0.92	1.28	1.19	0.72	1.18	1.05

Note. Drought tolerance scores that are less than or equal to 1 ± 0.1 are shown in bold.

^aPLHE, plant height; PLWI, plant canopy width; BRIN, branching index; LBLE, leaf blade length; LBWI, leaf blade width; PELE, petiole length; PEDI, petiole diameter; FLTM, flowering time; NFLIN, number of flowers per inflorescence; STLE, style length; NBST, number of stamens; FRLE, fruit length; FRWI, fruit width; FRPL, fruit pedicel length; FRPD, fruit pedicel diameter; FRWE, fruit weight; NSEF, number of seeds per fruit; 100S, weight of 100 seeds.

MEL3 × DAS1, MEL4 × AET1, and MEL5 × INS3 (Table 5), only plant height and plant canopy width grew faster in the dry season.

Leaves of the accession SIS1 and the hybrids MEL1 × INS2, MEL3 × ANG1, MEL4 × INS3, MEL6 × ANG1, MEL6 × DAS1, and MEL6 × INS3 grew faster in the dry season than in the rainy season (Tables 4 and 5). Their drought tolerance scores were indeed less than or equal to 1 ± 0.1 for leaf blade length and leaf blade width, as well as petiole length and petiole diameter. The same was true for leaf blade length and leaf blade width of the accessions ANG1, DAS1, INS3, MEL2, MEL4, MEL6, and MEL7 and of the hybrids MEL1 × INS3, MEL3 × DAS1, and MEL5 × INS3 (Tables 4 and 5).

Apart from the accession MEL3, which flowered earlier during the rainy season, drought tolerance scores of all the other parental accessions and of the F_1 hybrid progenies were greater than or equal to 1 ± 0.1 for flowering time. Indeed, flowering time of the accessions ANG1, ANG2, LIN3, and MEL2, as well as the hybrid progenies MEL3 × DAS1, MEL4 × INS3, and MEL6 × ANG1, were generally similar during the rainy and dry seasons. However, most of parental accessions and hybrid progenies flowered earlier in the dry season (Tables 4 and 5). Among the genotypes whose flowering times remained stable or which were earlier in the dry season, the parental accessions INS3, MEL5, MEL6, MEL7, MEL8, and SIS1, as well as the hybrid progenies MEL1 × INS3, MEL1 × INS2, and MEL6 × INS3, produced more flowers per inflorescence, longer styles on average, and more stamens per flower during the dry season. Drought tolerance scores of all the others parental accessions and F_1 hybrid progenies were not significantly different from 1 ± 0.1 for the number of stamens per flower, which was thus stable in the two seasons. This was also the case for style length, except of the accessions AET1, ANG1, ANG2, LIN3, and PYR1, as well as the hybrids MEL1 × INS1, MEL2 × ANG1, and MEL6 × ANG1 (Tables 4 and 5).

Drought tolerance scores of parental accessions and F_1 hybrid progenies were mainly greater than or equal to 1 ± 0.1 for fruit characteristics, indicating that the fruits were, on average, smaller in the dry season. However, drought tolerance scores of the accession AET1, as well as the hybrids MEL4 × INS3, MEL5 × INS3, and MEL6 × ANG1, were less than or equal to 1 ± 0.1 for fruit weight, length, and width. These genotypes produced thus larger and heavier fruits in the dry season (Tables 4 and 5). Drought tolerance scores of the accessions ANG1, ANG2, DAS1, INS1, MEL2, MEL6, MEL8, MEL9, PYR1, and SIS1 were less than or equal to 1 ± 0.1 for the number of seeds per fruit and the weight of 100 seeds. Fruits of these accessions therefore produced, in the dry season, much more seeds, which were also heavier.

Considering all the vegetative growth and yield-related traits, the hybrid progenies MEL1 × INS2, MEL4 × INS3, MEL6 × ANG1, and MEL6 × DAS1 were considered as drought tolerant (Table 5). Indeed, drought tolerance scores of these progenies were greater than 1 ± 0.1 for the flowering time, indicating earlier flowering in the dry season. Their drought tolerance scores were furthermore less than 1 ± 0.1 for almost all the growth vegetative traits and yield-related traits. The accession SIS1 also exhibited drought tolerance abilities for vegetative growth traits and floral traits, but no positive effect was observed on fruit characteristics, except of the number of seeds per fruit (Table 4).

3.2 | Genotypic and phenotypic coefficients of variation of drought tolerance scores

For all the studied agromorphological traits, PCVs of drought tolerance scores were higher than GCVs. For plant height and flowering time, GCVs of drought tolerance scores were low, <11%. Medium GCV values, varying from 11 to 20%, were observed for the drought tolerance score of the number of stamens per flower. High GCVs, >20%, were observed for drought tolerance scores of all the other agromorphological traits. Except of the flowering time, whose drought tolerance score presented a PCV of 17.89%, for all the other agromorphological traits, PCVs of the drought tolerance scores were >20% (Table 6).

Very variable gaps were observed between PCV and GCV of the drought tolerance scores. Small gaps, <11%, were observed for the plant width, the flowering time, and the number of stamens per flower. Moderate gaps, from 11 to 20%, were observed for the branching index, the number of flowers per inflorescence, and the fruit width. Large differences, >20%, were observed between the PCVs and the GCVs of drought tolerance scores of the other agromorphological parameters (Table 6).

3.3 | Narrow-sense heritability of drought tolerance scores

Moderate narrow-sense heritability values, from 20 to 50%, were observed for drought tolerance scores of plant height, flowering time, number of seeds per fruit, and weight of 100 seeds. Drought tolerance scores of all the other agromorphological traits presented high heritability values, >50% (Table 6).

T A B L E 6 Genetic parameters of drought tolerance scores for agromorphological traits of some accessions of eggplant (*Solanum melongena*) and wild and cultivated relatives

Types of traits ^b	Genetic parameters ^a				% _____		
	σ_a^2	σ_p^2	μ	GCV	PCV	Gap (PCV – GCV)	$h^2 \pm SD$
Vegetative growth trait							
PLHE	0.22	0.46	1.14	3.92	59.27	55.35	.48 ± 0.02
PLWI	0.26	0.41	1.23	41.45	52.13	10.68	.63 ± 0.17
BRIN	15.68	22.89	4.30	92.19	111.39	19.20	.69 ± 0.13
LBLE	2.57	3.80	1.26	127.70	155.41	27.70	.68 ± 0.12
LBWI	24.48	40.70	1.62	304.90	393.19	88.30	.60 ± 0.08
PELE	303.07	530.53	3.99	435.90	576.72	140.83	.57 ± 0.05
PEDI	3.63	6.11	0.89	215.04	279.25	64.21	.59 ± 0.08
Yield-related traits							
FLTM	0.01	0.04	1.15	9.95	17.89	7.94	.31 ± .11
NFLIN	0.50	0.77	1.20	58.62	72.75	14.13	.65 ± .11
STLE	29.16	38.52	1.31	412.20	473.76	61.56	.76 ± .04
NBST	0.03	0.05	1.01	16.58	22.37	5.80	.55 ± .06
FRLE	9.86	17.39	1.57	199.57	265.05	65.48	.57 ± .08
FRWI	0.50	0.71	1.10	64.43	76.52	12.10	.71 ± .06
FRPL	0.89	1.46	1.17	25.59	103.83	78.30	.60 ± .05
FRPD	2.19	3.84	1.09	136.50	180.68	44.18	.57 ± .05
FRWE	18.10	31.80	1.62	263.01	348.60	85.59	.57 ± .07
NSEF	5.35	12.54	1.37	168.98	258.66	89.67	.43 ± .05
100S	1.39	3.02	1.11	106.60	157.34	50.74	.46 ± .05

^a σ_a^2 , additive genetic variance; σ_p^2 , phenotypic variance; μ , mean value; GCV, genotypic coefficient of variation; PCV, phenotypic coefficient of variation; h^2 , narrow-sense heritability; SD, standard deviation.
^bPLHE, plant height; PLWI, plant canopy width; BRIN, branching index; LBLE, leaf blade length; LBWI, leaf blade width; PELE, petiole length; PEDI, petiole diameter; NFLIN, number of flowers per inflorescence; STLE, style length; NBST, number of stamens; FRLE, fruit length; FRWI, fruit width; FRPL, fruit pedicel length; FRPD, fruit pedicel length; FRWE, fruit weight; NSEF, number of seeds per fruit; 100S, weight of 100 seeds.

3.4 | Genotypic and phenotypic correlations of drought tolerance scores

Drought tolerance scores of the studied agromorphological traits had mostly very weak genotypic and phenotypic correlations. However, drought tolerance score of branching index was positively correlated with drought tolerance scores of leaf blade length (genotypic correlation [r_g] = .83, phenotypic correlation [r_p] = .66) and plant width (r_g = .51, r_p = .06). Drought tolerance scores of plant height and petiole diameter were positively correlated (r_g = .71, r_p = .14). Drought tolerance score of flowering time was positively correlated with those of leaf blade length (r_g = .50, r_p = .31) and width (r_g = .22, r_p = .60). Drought tolerance score of the number of flowers per inflorescence was also positively correlated with those of leaf blade width (r_g = .59, r_p = .52) and petiole length (r_g = .55, r_p = .36). Drought tolerance score of fruit pedicel diameter was positively correlated with that of leaf blade width (r_g = .56, r_p = .35). Positive genotypic and phenotypic correlations were also observed for drought tolerance scores of the number of stamens per flower and fruit pedicel length (r_g = .81, r_p = .76), on the one hand, and drought tolerance scores of leaf blade width and fruit weight (r_g = .54, r_p = .33), on the other hand.

Drought tolerance score of leaf blade width was negatively correlated with those of fruit pedicel diameter (r_g = -.57, r_p = -.43) and fruit width (r_g = -.51, r_p = -.47). Drought tolerance scores of petiole length and style length (r_g = -.65, r_p = -.61), on the one hand, and drought tolerance scores of the weight of 100 seeds and fruit weight (r_g = -.52, r_p = -.49), on the other hand, were also negatively correlated.

4 | DISCUSSION

Drought tolerance scores of each parental accession and each F_1 hybrid progeny varied significantly from a given agromorphological character to another. In addition, for each agromorphological character, drought tolerance scores of parental accessions and F_1 hybrid progenies were significantly different. Thus it appears, as reported by other authors, that effects of water deficit on plants are organ dependent (Tambe, Kusalkar, Shinde, & Shinde, 2019) and genotype dependent (Delfin et al., 2013; Plazas, Vilanova, et al., 2016; Plazas et al., 2019; Tani et al., 2018). Interspecific hybrids MEL1 $\times$ INS2, MEL4 $\times$ INS3, MEL6 $\times$ ANG1, and MEL6 $\times$ DAS1, as well as the accession SIS1, exhibited drought tolerance with respect to vegetative growth traits and floral characteristics. Agromorphological parameters of these genotypes were indeed stable or grew better during the dry season compared with the rainy sea-

son. *Solanum sisymbriifolium* is a wild species native of tropical America. This species is perennial and can also be annual. It is more hardy and more tolerant and resistant to drought and pathogens than the other cultivated species of the genus *Solanum*, such as potato (*S. tuberosum* L.), tomato (*S. lycopersicum* L.), eggplant (*S. melongena*), or peppers (*Capsicum* spp.) (Jagatheeswari, 2014). Plants of *S. sisymbriifolium* can also reach fairly large sizes when the growing conditions are favorable (Daunay, 2008). The performance of the accession SIS1 could therefore be explained by the drought tolerance abilities acquired by the species *S. sisymbriifolium* during its evolution as a result of its adaptation to the environmental conditions of its area of origin. This adaptation may result from better absorption of water from the soil. Indeed, according to Gueye and Renard (1982), the root system is the first factor that determines physiological and growing efficiency of the plant in case of water deficit. Thus, unlike cultivated species, wild species, which only benefit from rainfalls for their growth, have developed root systems more suitable for water extraction from the soil in cases of water deficit.

Kaushik, Prohens, Vilanova, Gramazio, and Plazas (2016), Kouassi et al. (2019), and Prohens et al. (2012) reported heterosis effects for traits related to vegetative growth traits in F_1 progenies of some accessions of eggplant and CWRs. As previously reported by Plazas, Vilanova, et al. (2016), vigorous vegetative growth of interspecific hybrids could explain the fact that, unlike their parents, the progenies MEL1 $\times$ INS2, MEL4 $\times$ INS3, MEL6 $\times$ ANG1, and MEL6 $\times$ DAS1 expressed drought tolerance abilities with regard to vegetative growth characteristics. Indeed, Engelbrecht, Kursar, and Tyree (2005) showed that interspecific inheritance of phenotypic traits favors drought resistance abilities of hybrid progenies. These drought tolerance abilities could result from the maintenance of important physiological functions such as growth in case of water stress (Clavel, Drame, Diop, & Zuiluy-Fodil, 2005; Oladosu et al., 2019).

Many parental accessions and interspecific hybrids flowered earlier during the dry season. Flowering is a complex phenomenon that depends on exogenous and endogenous factors. In fact, in some plants, variations of seasonal temperature and humidity can trigger flowering (Hamès et al., 2008; Khan, Ai, & Zhang, 2014). In eggplant, flowering and fruiting also depend on environmental conditions. This earlier flowering of parental accessions during the dry season could therefore result from lower precipitation and higher temperatures. In addition to early flowering, some genotypes had larger numbers of flowers per inflorescence and longer styles during the dry season. The increase in these parameters can lead to an increase in fruiting of these genotypes. Indeed, the perception of stresses such as heat and water deficit could trigger a survival mechanism that

would promote reproduction at the expense of vegetative growth (McDowell et al., 2008). Overall, the number of stamens per flower was stable over the two seasons. Therefore, this character seems to be unaffected by water stress.

Fruits of most of the parental accessions and F_1 progenies were smaller during the dry season. This reduction in fruit sizes could be explained by the fact that after the fertilization of flowers, plants need more water for the proper development of the young fruits (Spollen, Sharp, Saab, & Wu, 1993). However, some genotypes such as the accession AET1 of *S. aethiopicum* L., as well as the hybrid progenies MEL4 $\times$ INS3, MEL5 $\times$ INS3, and MEL6 $\times$ ANG1, produced larger and heavier fruits with heavier seeds during the dry season. These genotypes could therefore be considered drought tolerant with regard to fruit characteristics.

Drought tolerance scores of all the studied agromorphological traits had higher PCVs compared with GCVs. The gaps between PCVs and GCVs ranged from low to high and reflect variable influences of environmental factors on the expression of drought tolerance abilities with regard to vegetative growth traits and yield-related traits (Lakshmana, Biradar, & Ravikumar, 2009). Combination of information relating to PCVs and GCVs with heritability values makes it possible to identify the best parents to be crossed in order to obtain the desired characteristics in the descendants (Burton & Devane, 1953). Values of narrow-sense heritability of drought tolerance scores were moderate to high and ranged from .31 to .76, indicating variable contributions of genes with additive effects in the expression of drought tolerance abilities. The small differences between GCVs and PCVs associated with moderate heritability values indicate the involvement of genes with nonadditive genetic effects such as dominance and/or epistasis in the expression of drought tolerance.

In general, very weak to moderate positive or negative phenotypic and genotypic correlations were observed between drought tolerance scores of all the agromorphological characteristics. However, as we reported for phenotypic values of some agromorphological traits (Kouassi et al., 2019), strong positive genotypic correlations were observed between drought tolerance scores of branching index and leaf blade length, the number of stamens per flower and fruit pedicel length, and petiole diameter and plant height, respectively. These strong positive genotypic correlations suggest that drought tolerance abilities, regarding these characteristics, are controlled by genes in linkage disequilibrium and/or with pleiotropic effects (Falconer & Mackay, 1996; Wricke & Weber, 1986). Indeed, strong genotypic correlations were observed between drought tolerance scores of vegetative growth traits, on the one hand, and those of yield-related traits, on the other hand.

5 | CONCLUSIONS

This study used an original approach to estimate drought tolerance scores of some accessions of eggplant and wild and cultivated relatives for vegetative growth characteristics and yield-related traits. The data showed that the accession SIS1 of *S. sysimbriifolium* and the F_1 hybrid progenies MEL1 $\times$ INS2, MEL4 $\times$ INS3, MEL6 $\times$ ANG1, and MEL6 $\times$ DAS1, resulting from interspecific crosses of some accessions of eggplant (*S. melongena*) and the CWRs *Solanum insanum*, *S. anguivi*, and *S. dasyphyllum* Schumacher & Thonn. have drought tolerance abilities. However, the variability of their responses to water stress suggests that they have different drought tolerance mechanisms, which could be combined in future eggplant breeding programs. Estimates of genotypic and phenotypic coefficients of variation and narrow-sense heritability of drought tolerance scores revealed that environmental factors have variable effects on expression of drought tolerance abilities that also involve genes with dominant, additive, epistatic, and/or pleiotropic effects. Thus, our results give an insight on the more reliable agromorphological traits to be considered for an efficient selection of drought tolerant eggplant varieties.

ACKNOWLEDGMENTS

This work was undertaken as part of the initiative “Adapting Agriculture to Climate Change: Collecting, Protecting and Preparing Crop Wild Relatives,” which is supported by the Government of Norway. The project is managed by the Global Crop Diversity Trust with the Millennium Seed Bank of the Royal Botanic Gardens, Kew, and implemented in partnership with national and international gene banks and plant breeding institutes around the world. For further information, see the project website: <http://www.cwrdiversity.org/>. Funding was also received from Ministerio de Ciencia, Innovación y Universidades, Agencia Estatal de Investigación and Fondo Europeo de Desarrollo Regional (Grant RTI-2018-094592-B-I00 from MCIU/AEI/FEDER, UE) and from Vicerrectorado de Investigación, Innovación y Transferencia de la Universitat Politècnica de Valencia (Ayuda a Primeros Proyectos de Investigación; PAID-06-18), Mariola Plazas is grateful to Generalitat Valenciana and Fondo Social Europeo for a postdoctoral contract (APOSTD/2018/014).

CONFLICT OF INTEREST

Authors declare that they have no conflict of interest.

ORCID

Abou Bakari Kouassi  <https://orcid.org/0000-0003-3529-2667>

REFERENCES

- Burton, G. W., & Devane, E. M. (1953). Estimating heritability in tall fescue (*Festuca arundinacea*) from replicated clonal material. *Agronomy Journal*, 45, 478–481. <https://doi.org/10.2134/agronj1953.00021962004500100005x>
- Clavel, D., Drame, N. K., Diop, N. D., & Zuily-Fodil, Y. (2005). Adaptation to drought and varietal creation: The case of groundnuts in the Sahelian zone. First part: Bibliographic review. (In French, with English abstract.) *Revue Bibliographique OCL*, 12, 248–260. <https://doi.org/10.1051/ocl.2005.0248>
- Condon, A. G., Richards, R. A., Rebetzke, G. J., & Farquhar, G. D. (2004). Breeding for high water-use efficiency. *Journal of Experimental Botany*, 55, 2447–2460. <https://doi.org/10.1093/jxb/erh277>
- Daunay, M. C. (2008). Eggplant. In J. Prohens-Tomás & F. Nuez (Eds.), *Handbook of plant breeding, vegetables II: Fabaceae, Liliaceae, Solanaceae, and Umbelliferae* (pp. 163–220). New York: Springer.
- Daunay, M. C., & Hazra, P. (2012). Eggplant. In K. V. Peter & P. Hazra (Eds.), *Handbook of vegetables* (Vol. I, pp. 257–322). Houston, TX: Studium Press.
- Delfin, E. F., Manaday, S. J. B., Canama, A. O., Ocampo, E. T., & Maghirang, R. (2013). Screening eggplant germplasm for drought tolerance under greenhouse condition. *NAST Transactions*, 35, 17.
- Engelbrecht, B. M. J., Kursar, T. A., & Tyree, M. T. (2005). Drought effects on seedling survival in a tropical moist forest. *Trees Structure and Function*, 19, 312–321. <https://doi.org/10.1007/s00468-004-0393-0>
- Falconer, D. S., & Mackay, T. F. C. (1996). *Introduction to quantitative genetics* (4th ed.). Harlow, UK: Longmans Green.
- Fowler, C., Moore, G., & Hawtin, G. (2003). *The international treaty on plant genetic resources for food and agriculture: A primer for the future harvest center of the CGIAR*. Rome: International Plant Genetic Resources Institute.
- Gaufichon, L., Piroul, J. L., & Bachelier, B. (2010). *What are the prospects for genetic improvement in drought-tolerant crop plants?* Paris: Foundation FARM.
- Gisbert, C., Prohens, J., & Nuez, F. (2011). Treatments for improving seed germination in eggplant and related species. *Acta Horticulturae*, 898, 45–51. <https://doi.org/10.17660/actahortic.2011.898.4>
- Grieu, P., Maury, P., Debaeke, P., & Sarrafi, A. (2008). Improving tolerance to drought in sunflowers: Contributions from ecophysiology and genetics. (In French, with English abstract) *Innovations Agronomiques*, 2, 37–51.
- Groeneveld, E., Kovač, M., & Mielenz, N. (2010). *VCE 6 user's guide and reference manual, version 6*. Neustadt, Germany: Institute of Farm Animal Genetics.
- Gueye, M., & Renard, C. (1982). Comparison of 2 rice cultivars (SE302-G and IR-442) subjected to drought at their early flowering stage. *Agronomie Tropicale*, 37, 81–88.
- Hamès, C., Ptchelkine, D., Grimm, C., Thevenon, E., Moyroud, E., Gérard, F., ... Müller, C. W. (2008). Structural basis for LEAFY floral switch function and similarity with helix-turn-helix proteins. *EMBO Journal*, 27, 2628–2637. <https://doi.org/10.1038/emboj.2008.184>
- IBPGR. (1990). *Descriptors for eggplant*. Rome: International Board of Plants Genetic Resources.
- Jagatheeswari, D. (2014). Morphological studies on flowering plants (Solanaceae). *International Letters of Natural Sciences*, 15, 36–43. <https://doi.org/10.18052/www.scipress.com/ilns.15.36>
- Johnson, H. W., Robinson, H. F., & Comstock, R. E. (1955). Estimates of genetic and environmental variability in soybeans. *Agronomy Journal*, 7, 314–318. <http://doi.org/10.2134/agronj1955.00021962004700070009x>
- Kashyap, V., Kumar, S. V., Collonnier, C., Fusarin, F., Haicour, R., Rotino, G. L., ... Rajam, M. V. (2003). Biotechnology of eggplant. *Scientia Horticulturae*, 97, 1–25. [https://doi.org/10.1016/s0304-4238\(02\)00140-1](https://doi.org/10.1016/s0304-4238(02)00140-1)
- Kaushik, P., Prohens, J., Vilanova, S., Gramazio, P., & Plazas, M. (2016). Phenotyping of eggplant wild relatives and interspecific hybrids with conventional and phenomics descriptors provides insight for their potential utilization in breeding. *Frontiers in Plant Science*, 7. <https://doi.org/10.3389/fpls.2016.00677>
- Khan, M. R., Ai, X. Y., & Zhang, J. Z. (2014). Genetic regulation of flowering time in annual and perennial plants. *Wiley Interdisciplinary Reviews: RNA*, 5, 347–359. <https://doi.org/10.1002/wrna.1215>
- Kouassi, A. B., Kouassi, K. B. A., Alla-N'nan, O., Kouassi, A., & N'guetta, A. S. P. (2019). Phenotypic and genotypic variability, heritability and correlation estimates for agro-morphological characteristics of eggplant (*Solanum melongena*) in Côte d'Ivoire. *International Journal of Current Research in Biosciences and Plant Biology*, 6, 15–23. <https://doi.org/10.20546/ijcrbp.2019.609.003>
- Kouassi, B., Prohens, J., Gramazio, P., Kouassi, A. B., Vilanova, S., Galán-Ávila, A., ... Plazas, M. (2016). Development of backcross generations and new interspecific hybrid combinations for introgression breeding in eggplant (*Solanum melongena*). *Scientia Horticulturae*, 213, 199–207. <https://doi.org/10.1016/j.scienta.2016.10.039>
- Kruuk, L. (2004). Estimating genetic parameters in natural populations using the 'animal model'. *Philosophical Transactions of the Royal Society B, Biological Sciences*, 359, 873–890. <https://doi.org/10.1098/rstb.2003.1437>
- Lakshmana, D., Biradar, B. D., & Ravikumar, R. L. (2009). Genetic variability studies for quantitative traits in a pool of restorers and maintainers lines of pearl millet (*Pennisetum glaucum* L.). *Karnataka Journal of Agricultural Science*, 22, 881–882.
- McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., ... Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, 178, 719–739. <https://doi.org/10.1111/j.1469-8137.2008.02436.x>
- Mrode, R. A., & Thompson, R. (2014). *Linear models for the prediction of animal breeding values* (3rd ed.). Wallingford, UK: CABI Publishing.
- Nakashima, K., & Suenaga, K. (2017). Toward the genetic improvement of drought tolerance in crops. *Japanese Agricultural Research Quarterly*, 51, 1–10. <https://doi.org/10.6090/jarq.51.1>
- Oladosu, Y., Raffi, M. Y., Samuel, C., Fatai, A., Magaji, U., Kareem, I., ... Kolapo, K. (2019). Drought resistance in rice from conventional to molecular breeding: A review. *International Journal of Molecular Sciences*, 20. <https://doi.org/10.3390/ijms20143519>
- Patterson, H. D., & Thompson, R. (1971). Recovery of inter-block information when block sizes are unequal. *Biometrika*, 58, 545–554. <https://doi.org/10.1093/biomet/58.3.545>
- Plazas, M., Nguyen, H. T., González-Orenga, S., Fita, A., Vicente, O., Prohens, J., & Boscaiu, M. (2019). Comparative analysis of the responses to water stress in eggplant (*Solanum melongena*)

- cultivars. *Plant Physiology and Biochemistry*, 143, 72–82. <https://doi.org/10.1016/j.plaphy.2019.08.031>
- Plazas, M., Rahma, A. F., Rodríguez-Burruezo, A., Prohens, J., & Fita, A. (2016). Screening for drought tolerance in eggplant relatives and interspecific hybrids. In K. Ertsey-Peregi, S. Füstös, G. Palotás, & G. Csilléry (Eds.), *Proceedings of the XVIth EUCARPIA Capsicum and Eggplant Working Group* (pp. 306–310). Budapest: Diamond Congress.
- Plazas, M., Vilanova, S., Gramazio, P., Rodríguez-Burruezo, A., Fita, A., Herraiz, F. J., ... Prohens, J. (2016). Interspecific hybridization between eggplant and wild relatives from different genepools. *Journal of the American Society for Horticultural Science*, 141, 34–44. <https://doi.org/10.21273/JASHS.141.1.34>
- Prohens, J., Plazas, M., Raigón, M. D., Seguí-Simarro, J. M., Stommel, J. R., & Vilanova, S. (2012). Characterization of interspecific hybrids and first backcross generations from crosses between two cultivated eggplants (*Solanum melongena* and *Solanum aethiopicum* Kumba group) and implications for eggplant breeding. *Euphytica*, 186, 517–538. <https://doi.org/10.1007/s10681-012-0652-x>
- Ranil, R. H. G., Niran, H. M. L., Plazas, M., Fonseka, R. M., Fonseka, H. H., Vilanova, S., ... Prohens, J. (2015). Improving seed germination of the eggplant rootstock *Solanum torvum* by testing multiple factors using an orthogonal array design. *Scientia Horticulturae*, 193, 174–181. <https://doi.org/10.1016/j.scienta.2015.07.030>
- Ranil, R. H. G., Prohens, J., Aubriot, X., Niran, H. M., Plazas, M., Fonseka, R. M., ... Knapp, S. (2017). *Solanum insanum* L. (subgenus *Leptostemonum* Bitter, Solanaceae), the neglected wild progenitor of eggplant (*S. melongena* L.): A review of taxonomy, characteristics and uses aimed at its enhancement for improved eggplant breeding. *Genetic Resources and Crop Evolution*, 64, 1707–1722. <https://doi.org/10.1007/s10722-016-0467-z>
- Rotino, G. L., Sala, T., & Toppino, L. (2014). Eggplant. In A. Pratap & J. Kumar (Eds.), *Alien gene transfer in crop plants. Volume 2: Achievements and impacts* (pp. 381–409). New York: Springer.
- Shaw, P. D., Raubach, S., Kilian, B., Dreher, K., Amri, A., Bassi, F. M., ... Werner, P. (2020). From bits to bites: Advancement of the Germinate platform to support genetic resources collections and pre-breeding informatics for crop wild relatives. *Crop Science*. <https://doi.org/10.1002/csc220250.20248> (in press).
- Spollen, W. G., Sharp, R. E., Saab, I. N., & Wu, Y. (1993). Regulation of cell expansion in roots and shoots at low water potentials. In J. A. C. Smith & H. Griffiths (Eds.), *Water deficits: Plant responses from cell to community* (pp. 37–52). Oxford, UK: Bio Scientific Publishers.
- Stanfield, W. D. (1975). *Genetics*. New York: Mc Graw-Hill.
- Sumathi, P., Sumanth, M., & Veerabadhiran, P. (2010). Genetic variability for different biometrical traits in pearl millet genotypes (*Pennisetum glaucum* LR BR.). *Electronic Journal of Plant Breeding*, 1, 437–440. <https://doi.org/10.5958/0975-928x.2017.00079.5>
- Tambe, S. A., Kusalkar, D. V., Shinde, G. S., & Shinde, M. S. (2019). Inheritance of morphological traits for drought tolerance in rabi sorghum [*Sorghum bicolor* (L.) Moench]. *International Journal of Current Research in Biosciences and Plant Biology*, 6, 24–32. <https://doi.org/10.20546/ijcrbp.2019.609.004>
- Tani, E., Kizis, D., Markellou, E., Papadakis, I., Tsamadia, D., Levantis, G., ... Karapanos, I. (2018). Cultivar-dependent responses of eggplant (*Solanum melongena* L.) to simultaneous *Verticillium dahliae* infection and drought. *Frontiers in Plant Science*, 9, <https://doi.org/10.3389/fpls.2018.01181>
- Vorontsova, M. S., & Knapp, S. (2016). A revision of the spiny solanums, *Solanum* subgenus *Leptostemonum* (Solanaceae) in Africa and Madagascar. *Systematic Botany Monographs*, 99, 1–436. <https://doi.org/10.5519/0055154>
- Wricke, G., & Weber, W. E. (1986). *Quantitative genetics and selection in plant breeding*. Berlin: Walter de Gruyter.

How to cite this article: Kouassi AB, Kouassi KBA, Sylla Z, et al. Genetic parameters of drought tolerance for agromorphological traits in eggplant, wild relatives, and interspecific hybrids. *Crop Science*. 2020;1–14. <https://doi.org/10.1002/csc2.20250>