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Heterosis in interspecific hybrids between *Solanum melongena* L. and species from the primary and secondary gene pools

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Abstract

Solanum melongena L. (Solanaceae) is an important species both nutritionally and economically. Having a better knowledge of the effects of heterosis could help to improve the characteristics of eggplant crops. The aim of the study was to identify interspecific hybrids with agromorphological characteristics superior to those of their parents, as well as the parental accessions that produced the best interspecific hybrid combinations. 15 agromorphological parameters were used to characterize eight accessions of *S. melongena*, eight accessions from the primary and secondary gene pools species and 36 interspecific hybrid progenies obtained between *S. melongena* and species from different gene pools. The results showed that heterosis effects were more important for vegetative growth characteristics than for production. The M4 × IS3 interspecific hybrid was the best in terms of heterosis effects for both vegetative growth and production characteristics. The parental accessions IS3 from the primary gene pool and DS1 from the secondary pool gave hybrids with the greatest heterosis effects. The phenotypic characteristics of the parental accessions and the heterosis effects of hybrids offer interesting prospects for eggplant breeding by introgression of genes from wild species in the cultivated species *S. melongena*.

Keywords : *eggplant, breeding, hybrid vigor, Côte d'Ivoire.*

Résumé

Hétérosis chez des hybrides interspécifiques entre *Solanum melongena* et des espèces des pools géniques primaire et secondaire

Solanum melongena L. (Solanaceae) est une espèce importante aussi bien sur le plan nutritionnel qu'économique. Comprendre les effets de l'hétérosis pourrait contribuer à améliorer les caractéristiques des cultures d'aubergine. L'objectif de l'étude a été d'identifier des hybrides interspécifiques présentant des caractéristiques agromorphologiques supérieures à celles de leurs parents, ainsi que les accessions parentales ayant permis d'obtenir les meilleures combinaisons hybrides interspécifiques. 15 paramètres agromorphologiques ont été utilisés pour caractériser huit accessions de *S. melongena*, huit accessions d'espèces des pools géniques primaire et secondaire ainsi que 36 descendances hybrides interspécifiques obtenues entre *S. melongena* et les espèces des différents pools géniques. Les résultats ont montré que les effets hétérosis sont plus importants pour les caractéristiques de croissance végétative que de production. L'hybride interspécifique M4 × IS3 est le meilleur pour ce qui concerne les effets hétérosis à la fois pour les caractéristiques de croissance végétative et de production. Les accessions parentales IS3 du pool génique primaire et DS1 du pool secondaire ont donné des hybrides ayant les effets hétérosis les plus importants. Les caractéristiques phénotypiques des accessions parentales et les effets hétérosis des hybrides offrent des perspectives intéressantes pour l'amélioration de l'aubergine par l'introgression de gènes des espèces sauvages chez l'espèce cultivée *S. melongena*.

Mots-clés : *aubergine, amélioration, vigueur hybride, Côte d'Ivoire.*

1. Introduction

Solanum melongena L. (Solanaceae) also known as eggplant or aubergine is an important species in tropical and subtropical regions of the world. In these regions, this plant is mainly grown for its fruits used in diet. With world production estimated at 59.31 tonnes in 2022 [1], this crop has a major economic interest. Despite its nutritional and economic importance, *S. melongena* has to cope with various biotic and abiotic stresses. Faced with these stresses, this species has only partial resistance, often at levels insufficient to ensure tolerance or effective resistance of the plant to these stresses [2, 3]. Eggplant has significant plant genetic resources, consisting of around 500 cultivated and wild *Solanum* species that make up the *Leptostemonum* subgenus [4, 5]. The different species belonging to eggplant genetic resources show a wide variability in resistance to various biotic and abiotic stresses [6, 7]. These species therefore represent sources of genes of agronomic importance that could be exploited to improve eggplant. Crosses between different species can be used to improve a number of eggplant traits by exploiting the heterosis effect. Heterosis refers to a phenomenon whereby the hybrid offspring obtained from genetically different individuals outperform the parents for given traits. These include vegetative vigor, yield components, adaptability and resistance to biotic and abiotic stress factors. Heterosis thus contributes to improving agricultural production [8, 9]. Heterosis is a highly variable phenomenon, and the degree to which the characteristics considered in hybrids increase varies according to the genetic distance between the parents and their mode of reproduction [10, 11]. To this end, it has been reported that when two homozygous and genetically different lines are crossed, the hybrids obtained are generally more vigorous than the two parents for given traits [12, 13]. *S. melongena* and its relatives belong to different gene pools [5;14] and are preferentially self-pollinating and therefore highly homozygous [15]. Thus, interspecific hybridization between *S. melongena* and related species maximizes the effects of heterosis [16, 17]. This could make it possible to obtain eggplant varieties with very good performance in terms of both production components and adaptation to environmental conditions. Obtaining such varieties requires a better understanding of the effects of heterosis. This should help to rationalize its use to improve the characteristics of eggplant crops. The aim of the present study was to identify interspecific hybrids with agromorphological characteristics superior to those of their parents, as well as the parental accessions that produced the best interspecific hybrid combinations.

2. Material and methods

2-1. Plant material

The plant material comprised 16 accessions of cultivated and wild species. All these accessions come from seven species, two of which are cultivated and five wilds: *S. melongena*, *S. insanum*, *S. anguivi*. *S. dasyphyllum*, *S. aethiopicum*, *S. linneanum* and *S. tomentosum* ***(Table 1)***. The 16 accessions are composed of eight accessions of *S. melongena* coded M1, M2, M3, M4, M5, M6, M7, M9 and eight accessions of species from the primary and secondary gene pools. The primary gene pool consists of two accessions of the species *S. insanum* (IS1, IS3). In the secondary pool, six accessions were used, including two of *S. anguivi* (AG1, AG2), one of *S. dasyphyllum* (DS1), one of *S. aethiopicum* (AT1), one of *S. linneanum* (LN1) and one of S. *tomentosum* (TM1) ***(Table 1)***. In addition, 36 first-generation (F1) interspecific hybrid progenies were used to measure agromorphometric traits. 15 of these hybrids were obtained with *S. insanum* accessions IS1 and IS3 from the primary gene pool. In the secondary gen pool, eight interspecific hybrids were obtained with accessions AG1 and AG2 of *S. anguivi*, five with the DS1 accession of *S. dasyphyllum*, three with the AT1 accession of the cultivated species *S. aethiopicum*, three with the TM1 accession of *S. tomentosum* and two with the LN1 accession of *S. linnaeanum* ***(Table 2)***.

Table 1 : *Cultivated and wild species accessions used to obtain interspecific hybrids*

Gene pool	Status	Species	Accessions	Origins	Codes
	Cultivated	*S. melongena*	BBS-118/B	Côte d'Ivoire	M1
			BBS-146	Côte d'Ivoire	M2
			BBS-175	Côte d'Ivoire	M3
			7145	Sri Lanka	M4
			8104	Sri Lanka	M5
			Ampara	Sri Lanka	M6
			Kermit	South East Asia	M7
			Jeffna Special	Sri Lanka	M9
primary	Wild	*S. insanum*	SLKINS-1	Sri Lanka	IS1
			MM 498	Japan	IS3
Secondary	Cultivated	*S. aethiopicum*	Aub21NB	Unknown (Source: Côte d'Ivoire)	AT1
	Wild	*S. anguivi*	BBS 119	Côte d'Ivoire	AG1
			BBS 125/B	Côte d'Ivoire	AG2
		S. dasyphyllum	MM 1153	Uganda	DS1
		S. linneanum	JPT0028	España	LN1
		S. tomentosum	MM 992	South Africa	TM1

Table 2 : *Parental accessions and their F1 interspecific hybrid progeny used to measure phenotypic characteristics in the field*

N°	Interspecific hybridizations	Crossed accessions	Codes of F1 hybrid progenies
1	*S. melongena* × *S. insanum*	M1 × IS1	BBS-118/B × SLKINS-1
2		M2 × IS1	BBS-146 × SLKINS-1
3		M3 × IS1	BBS-175 × SLKINS-1
4		M4 × IS1	7145 × SLKINS-1
5		M5 × IS1	8104 × SLKINS-1
6		M6 × IS1	Ampara × SLKINS-1
7		M7 × IS1	Kermit × SLKINS-1
8		M1 × IS3	BBS-118/B × MM 498
9		M4 × IS3	7145 × MM 498
10		M5 × IS3	8104 × MM 498
11		M6 × IS3	Ampara × MM 498
12		M7 × IS3	Kermit × MM 498
13		M9 × IS3	Jeffna Special × MM 498
14	*S. insanum* × *S. melongena*	IS3 × M3	MM 498 × BBS-175
15		IS3 × M6	MM 498 × Ampara
16	*S. melongena* × *S. anguivi*	M1 × AG1	BBS-118/B × BBS 119
17		M2 × AG1	BBS-146 × BBS 119
18		M3 × AG1	BBS-175× BBS 119
19		M4 × AG1	7145 × BBS 119
20		M5 × AG1	8104 × BBS 119
21		M6 × AG1	Ampara × BBS 119
22		M2 × AG2	BBS-146 × BBS 125/B
23		M5 × AG2	8104 × BBS 125/B
24	*S. melongena* × *S. dasyphyllum*	M2 × DS1	BBS-146 × MM 1153
25		M3 × DS1	BBS-175 × MM 1153
26		M5 × DS1	8104 × MM 1153
27		M6 × DS1	Ampara × MM 1153
28		M9 × DS1	Jeffna Special× MM 1153
29	*S. melongena* × *S. aethiopicum*	M4 × AT1	7145 × Aub21NB
30		M7 × AT1	Kermit × Aub21NB
31		M9 × AT1	Jeffna Special × Aub21NB
32	*S. linneanum* × *S. melongena*	LN1 × M1	JPT0028 ×BBS-118/B
33		LN1 × M6	JPT0028× Ampara
34	*S. tomentosum* × *S. melongena*	TM1 × M5	MM 992 × 8104
35		TM1 × M3	MM 992 × BBS-175
36	*S. melongena* × *S. tomentosum*	M2 × TM1	BBS-146 × MM 992

Note. M1, M2, M3, M4, M5, M6, M7, M9 = accessions of S. melongena; IS1 et IS3 = accessions of S. insanum; AG et AG2 = accessions of S. anguivi, DS1 = accession of S. dasyphyllum; AT1 = accession of S. aethiopicum; LN1 = accession of S. linneanum et TM1 = accession of S. tomentosum.

2-2. Methods

2-2-1. Measurement of agromorphological characteristics

Fifteen agromorphological parameters, taken from the descriptor for eggplant [18], including seven vegetative growth traits and eight production-related traits ***(Table 3)***, were used for the phenotypic characterization of parental accessions and their interspecific hybrid progenies. Vegetative growth traits were measured as soon as the first flower appeared. For production-related traits, floral parameters were assessed on four randomly selected inflorescences per plant. The number of stamens was counted on four flowers, chosen randomly. Fruit characteristics were also measured on four fruits per plant.

Table 3 : *Agromorphological traits used for the characterization of cultivated and wild relative's accessions of eggplant and their interspecific hybrid progenies*

Traits	Units	Abbreviations	Types of character
Plant Height	cm	PLHE	Vegetative growth traits
Plant Canopy diameter	cm	PLCD	
Branching index	—	BRIN	
Leaf blade length	cm	LBLE	
Leaf blade width	cm	LBWI	
Petiole length	cm	PELE	
Petiole diameter	mm	PEDI	
Number of flowers per inflorescence	—	NFLI	Yield-related traits
Number of stamens	—	NBST	
Fruit length	cm	FRLE	
Fruit width	cm	FRWI	
Fruit pedicel length	cm	FRPL	
Fruit pedicel diameter	mm	FRPD	
Number of fruits per infructescence	—	NFRI	
Fruit weight	g	FRWE	

2-2-2. Statistical analysis of collected data

2-2-2-1. Comparison of agromorphological characteristics of parental accessions and interspecific hybrid progeny

The discriminating power of all the agromorphological traits measured was assessed by multivariate analysis of variance (MANOVA) using the Wilks's Lambda test and the Snedecor *F* statistic at the 5 % risk of error. Variations in quantitative characteristics were assessed using basic statistics such as the mean and standard deviation. An analysis of variance (ANOVA) was used to compare the variances of each quantitative trait's values. The groups formed by *S. melongena* accessions, accessions of relatives' species and F1 hybrid progeny were considered. The mean phenotypic values of the groups considered were compared using the Student-Newman-Keuls (SNK) post ANOVA multiple comparison of mean test, with a 5 % risk of error. This made it possible to assess heterosis in hybrid progeny in relation to the phenotypic value of the best parental group.

2-2-2-2. Heterosis in interspecific hybrids compared with the mid-parent

For each quantitative trait, the value of heterosis was calculated in hybrid progeny obtained between *S. melongena* accessions and accessions of wild species from the primary and secondary gene pools. Heterosis (H) for a trait was calculated using the following ***Formula*** :

$$\mathrm{H}\ (\%) = \left(\frac{\mathrm{F1-MP}}{\mathrm{MP}}\right) \mathrm{x}\ 100 \qquad (1)$$

Where, F1 = mean phenotypic value of interspecific hybrids and MP = mean phenotypic value of both parents. All statistical analyses were performed using Statistica version 7.1, IBM, Statistical Package of Social Sciences (SPSS) Version 22.0 (IBM corp. Armonk, New York, USA).

3. Results

3-1. Comparison of agromorphological traits between parental accessions and their interspecific hybrid progeny

Multivariate analysis of variance (MANOVA) revealed significant differences between cultivated and wild parental accessions and their interspecific hybrid progeny. Agromorphological characteristics taken together were therefore able to discriminate between groups ($p < 0.001$) ***(Table 4)***. Significant differences were observed between the parental accessions of the cultivated eggplant, *S. melongena*, and those of the related wild species in terms of both vegetative growth and production characteristics ***(Table 5)***. In terms of parameters related to plant architecture, the Plant canopy diameter (PLCD) of *S. melongena* is greater than that of related wild species. There were no significant differences between the two groups of parental accessions for plant height (PLHE) and branching index (BRIN). Values for all other leaf characteristics were significantly higher in *S. melongena* accessions, with the exception of leaf blade width (LBWI), for which there was no difference between the two groups of parental accessions ***(Table 5)***. Overall, interspecific hybrids showed higher values of vegetative growth traits than both cultivated and wild parental accessions. However, the petiole length (PELE) of hybrids was less than that of the parental accessions of *S. melongena* and was not significantly different from that of the parental accessions of the wild species. On the other hand, the petiole diameter (PEDI) of *S. melongena* accessions was statistically similar to that of interspecific hybrids and these (PEDI) values were higher than those observed in wild parental accessions ***(Table 5)***. In terms of flowering characteristics, wild species accessions produced many more flowers per inflorescence (NFLI) than *S. melongena* accessions. However, the number of stamens (NBST) per flower was higher in *S. melongena* accessions ***(Table 6)***. With the exception of the number of fruits per infructescence (NFRI) for which the wild relatives had a higher mean, the two groups of parental accessions had statistically similar values, the values of all other fruit characteristics were significantly higher in *S. melongena* accessions ***(Table 6)***. For production-related traits, the values for hybrids were generally intermediate between those of *S. melongena* accessions and wild species. However, interspecific hybrids did not differ significantly from *S. melongena* accessions in terms of the number of flowers per inflorescence (NFLI) and fruit width (FRWI). The number of fruits per infructescence (NFRI) was identical between the hybrids and the wild parental accessions ***(Table 6)***.

Table 4 : *Evaluation of the discriminating power of the 15 agromorphologicals traits measured on F1 and their cultivated and wild relative's using MANOVA*

Factor	**Test**	**value**	***F***	**ddl of hypothesis**	**ddl of error**	***p***
Constant	Wilks' Lambda	0.005	2 349 045	15	180	< 0.001
Group	Wilks' Lambda	0.154	18 605	30	360	< 0.001

Note. F1: interspecific hybrids; MANOVA : multivariate analysis of variance; F: value of the statistic associated with the Fisher-Snedecor test; ddl : degree of freedom; p : probability value associated with the Fisher-Snedecor test.

Table 5 : *Descriptive statistics for vegetative growth traits of cultivated and wild relatives of eggplant and their interspecific hybrid progenies*

	S. melongena **(N = 41)**	**Related species (N = 36)**	**F1 (120 ≤ N ≤ 170)**		
Traits	Mean ± SD	Mean ± SD	Mean ± SD	*F*	*p*
PLHE	75.85 ± 15.85 ^{a}	76.83 ± 29.57 ^{a}	93.78 ± 28.15 ^{b}	11.31	< 0.001
PLCD	128.84 ± 17.31 ^{b}	100.07 ± 28.47 ^{a}	145.57 ± 31.63 ^{c}	37.36	< 0.001
BRIN	5.73 ± 0.98 ^{a}	6.16 ± 4.03 ^{a}	7.20 ± 2.45 ^{b}	18.74	< 0.001
LBLE	24.57 ± 4.06 ^{b}	20.74 ± 7.91 ^{a}	26.79 ± 6.26 ^{c}	22 707	< 0.001
LBWI	17.20 ± 2.88 ^{a}	15.98 ± 5.63 ^{a}	21.21 ± 5.40 ^{b}	28.54	< 0.001
PELE	10.15 ± 2.77 ^{b}	7.91 ± 3.55 ^{a}	9.20 ± 2.33 ^{a}	6.83	0.001
PEDI	5.63 ± 1.12 ^{b}	4.31 ± 1.25 ^{a}	5.49 ± 1.37 ^{b}	20.11	< 0.001

Note. F1: interspecific hybrids; SD : standard deviation; N: number of observations; F : value of the statistic associated with Fisher's test; p : probability value associated with Fisher's test. Means indexed by the same letter on the same line are statistically identical according to the Student-Newman-Keuls post-ANOVA test at the 5 % probability level; PLHE : Plant Height; PLCD: Plant Canopy diameter; BRIN : Branching index ; LBLE : Leaf blade length; LBWI : Leaf blade width; PELE : Petiole length; PEDI : Petiole diameter

Table 6 : *Descriptive statistics for yield-related traits of cultivated and wild relatives of eggplant and their interspecific hybrid progenies*

	S. melongena **(N = 41)**	**Related species (N = 36)**	**F1 (120 ≤ N ≤ 170)**		
Traits	Mean ± SD	Mean ± SD	Mean ± SD	*F*	*p*
NFLI	2.85 ± 0.65 ^{a}	5.39 ± 3.03 ^{b}	4.72 ± 2.35 ^{b}	14.25	< 0.001
NBST	5.88 ± 0.81 ^{c}	5.19 ± 0.40 ^{a}	5.39 ± 0.49 ^{b}	17.69	< 0.001
FRLE	11.89 ± 4.00 ^{c}	2.97 ± 1.57 ^{a}	5.27 ± 4.45 ^{b}	56.89	< 0.001
FRWI	6.12 ± 1.61 ^{b}	3.31 ± 2.06 ^{a}	3.86 ± 1.74 ^{a}	30.59	< 0.001
FRPL	5.73 ± 1.61 ^{c}	2.06 ± 0.85 ^{a}	3.16 ± 1.24 ^{b}	106.48	< 0.001
FRPD	10.23 ± 2.42 ^{c}	4.74 ± 1.71 ^{a}	6.01 ± 3.36 ^{b}	61.08	< 0.001
NFRI	1.15 ± 0.42 ^{a}	2.08 ± 1.18 ^{b}	1.24 ± 0.62 ^{a}	21.27	< 0.001
FRWE	163.35 ± 52.02 ^{c}	29.32 ± 21.27 ^{a}	52.65 ± 50.72 ^{b}	121.18	< 0.001

Note. F1: interspecific hybrids; SD : standard deviation; N: number of observations; F : value of the statistic associated with Fisher's test; p : probability value associated with Fisher's test. Means indexed by the same letter on the same line are statistically identical according to the Student-Newman-Keuls post-ANOVA test at the 5 % probability level; NFLI : Number of flowers per inflorescence; NBST : Number of stamens; FRLE : Fruit length; FRWI : Fruit width; FRPL : Fruit pedicel length; FRPD : Fruit pedicel diameter; NFRI : Number of fruits per infructescence; FRWE : Fruit weight.

3-2. Mid-Parent heterosis observed in interspecific hybrids (F1)

In terms of vegetative growth parameters, heterosis effects were generally observed both in hybrids between accessions of the cultivated species, *S. melongena*, and those of wild species from the primary ***(Table 7)*** and secondary ***(Table 8)*** gene pools. The highest rates of increase were observed in the M9 × AT1 interspecific hybrid with 60.45 % and 70.39 % for PLHE and PLCD respectively. The highest increase in BRIN was observed in M2 × AG1. The strongest increases in leaf characteristics were shown by the M5 × IS1 and M2 × DS1 hybrids for LBLE with 15.19 % and LBWI with 36.94 % respectively ***(Tables 7 and 8)***. Overall, the highest rates of increase in vegetative growth traits were observed in interspecific hybrids obtained between *S. melongena* and accessions from species in the secondary gene pool. In terms of production-related traits, heterosis effects were mainly observed for NFLI. For this parameter, the highest heterosis value was observed in the M4 × AT1 interspecific hybrid with 129.41 % increase. For other production-related characteristics, the highest heterosis effects were found mainly in interspecific hybrids obtained with accessions of the species in the primary gene pool. These were: NBST (5.45 %) in M7 × IS3; FRLE (59.34 %) and FRWI (16.05 %) in M6 × IS3; FRPL (9.74 %) in M4 × IS3; FRPD (9.27 %) and FRWE (37.32 %) in IS3 × M6 ***(Tables 7 and 8)***. Overall, heterosis effects were greater for vegetative growth traits than for production-related traits. In hybrids obtained with accessions of primary gene pool species, the M4 × IS3 progeny showed hybrid vigor for all vegetative growth parameters. Progenies M1 × IS3, M7 × IS3 and M9 × IS3 also showed hybrid vigor for all vegetative growth traits with the exception of PELE, BRIN and PEDI respectively ***(Table 7)***. Considering production-related parameters in addition to vegetative growth characteristics, the M4 × IS3 progeny showed hybrid vigor for all the agromorphological characteristics measured except for the number of flowers per inflorescence (NFLI) and the number of fruits per infructescence (NFRI) ***(Table 7)***. In hybrids obtained with accessions of species from the secondary gene pool, the progenies M2 × DS1, M3 × DS1, M5 × DS1 and M9 × DS1 showed hybrid vigor for all vegetative growth parameters except BRIN ***(Table 8)***. Hybrid progenies obtained with the DS1 accession of the *S. dasyphyllum* species from the secondary pool showed the most vigor for vegetative growth parameters ***(Table 8)***. For production-related parameters, heterosis effects were mainly observed for NFLI in hybrids obtained with accessions from the secondary gene pool ***(Table 8)***.

Table 7 : *Heterosis values (%) calculated considering F1 between accessions of the cultivated species S. melongena and those of wild species in the primary gene pool*

	Vegetative growth traits							Yield-related traits							
	PLHE	PLCD	BRIN	LBLE	LBWI	PELE	PEDI	NFLI	NBST	FRLE	FRWI	FRPL	FRPD	NFRI	FRWE
IS3 × M3	-20.25	-15.00	29.63	-21.97	-20.04	-30.86	-17.46	-16.67	3.03	-17.38	-0.64	-1.43	-14.65	-23.08	-21.49
IS3 × M6	18.70	16.50	-19.75	3.96	7.42	-9.32	13.96	-4.76	-5.56	6.99	14.79	-8.59	0.30	-9.09	37.32
M1 × IS1	7.69	20.24	7.58	-5.26	1.88	-29.42	-13.58	-32.54	-5.56	-24.17	-9.68	-13.41	-14.26	-23.08	-41.96
M1 × IS3	12.60	6.11	6.90	6.95	8.43	0.00	8.46	-3.45	-1.64	1.05	8.97	-10.83	-16.02	-9.09	14.47
M2 × IS1	4.40	30.26	33.33	0.50	21.79	-13.98	-10.89	-12.73	-5.88	-29.79	-21.40	-5.72	-11.95	-23.08	-43.24
M3 × IS1	-10.09	20.45	15.25	-6.09	-5.53	-33.17	-21.74	-9.68	-3.70	-34.57	-8.91	-17.00	-13.80	-33.33	-54.46
M4 × IS1	7.70	23.21	26.44	-6.25	0.70	-33.91	-11.76	-13.58	-0.58	-9.39	-10.36	-15.76	-27.85	-23.08	-35.54
M4 × IS3	42.05	30.65	32.08	13.44	18.74	23.96	20.77	-7.14	3.45	12.91	5.36	9.74	2.86	-9.09	7.12
M5 × IS1	21.93	38.62	-3.85	15.19	19.40	-12.10	-6.91	-9.09	-3.85	-36.49	-7.57	-24.55	-25.09	-41.18	-61.11
M5 × IS3	16.52	22.63	-13.33	1.30	2.22	-8.70	-5.76	5.88	-5.66	0.13	4.66	-12.41	-18.81	-33.33	-11.64
M6 × IS1	13.41	28.03	11.86	-3.98	-1.55	-32.05	-20.35	3.70	-1.69	-30.80	5.21	-20.43	9.27	-23.08	-31.89
M6 × IS3	8.76	0.53	-11.11	3.47	7.87	-1.17	5.98	0.00	0.00	59.34	16.05	-10.66	-3.95	-9.09	27.45
M7 × IS1	33.33	57.37	14.58	-1.37	-3.64	-31.11	-19.61	-27.08	-1.23	-11.70	-9.05	-20.02	-6.50	-23.08	-10.71
M7 × IS3	13.95	31.38	-11.86	11.23	10.57	9.74	17.92	-21.21	5.45	2.81	-1.49	4.60	0.00	-9.09	-3.42
M9 × IS3	23.94	23.47	16.36	9.32	14.18	5.45	0.00	-33.33	-7.14	14.64	14.40	-4.91	-4.46	-9.09	32.81

Note. In bold, value of the "mid-parent" heterosis observed in interspecific hybrids (F1); a negative value means that the average value of the hybrid for the trait in question is lower than the average value of the parents; PLHE: Plant Height; PLCD : Plant Canopy diameter; BRIN : Branching index; LBLE : Leaf blade length; LBWI : Leaf blade width; PELE : Petiole length; PEDI : Petiole diameter; NFLI: Number of flowers per inflorescence; NBST : Number of stamens; FRLE : Fruit length; FRWI : Fruit width; FRPL: Fruit pedicel length; FRPD : Fruit pedicel diameter; NFRI : Number of fruits per infructescence; FRWE : Fruit weight.

Table 8I : *Heterosis values (%) calculated considering F1 between accessions of the cultivated species S. melongena and those of wild species in the secondary gene pool*

	Vegetative growth traits							**Yield-related traits**							
	PLHE	PLCD	BRIN	LBLE	LBWI	PELE	PEDI	NFLI	NBST	FRLE	FRWI	FRPL	FRPD	NFRI	FRWE
M1 × AG1	26.75	23.02	6.28	-17.34	-16.73	-52.20	-27.18	55.91	-15.25	-75.47	-59.87	-65.45	-75.78	-27.14	-97.60
M2 × AG1	29.12	69.08	71.43	-2.06	7.43	-7.27	-16.28	0.81	-11.11	-80.26	-68.52	-61.07	-74.56	-33.33	-98.43
M2 × AG2	-7.01	19.64	-0.43	-6.34	7.25	-12.69	-10.94	68.63	-13.04	-74.33	-62.83	-60.72	-78.30	-44.67	-97.03
M2 × DS1	48.28	3.03	-44.26	12.99	36.94	10.57	13.22	48.39	0.00	—	—	—	—	—	—
M2 × TM1	45.51	59.13	14.29	-12.95	-7.17	-27.14	-35.28	4.35	-13.04	-86.94	-85.23	-75.40	-64.39	-6.67	-98.99
M3 × AG1	15.71	60.03	0.00	-1.15	-0.70	-15.45	-12.79	-3.85	-5.66	-76.55	-56.49	-53.21	-67.28	-34.78	-95.59
M3 × DS1	57.60	0.27	-23.32	7.38	20.97	23.89	11.22	34.12	8.97	—	—	—	—	—	—
M4 × AT1	21.55	29.24	-2.78	4.64	-6.13	-32.76	-14.85	129.41	3.57	-64.19	-43.48	-22.34	-55.34	-16.67	-83.82
M4 × AG1	-24.08	15.75	40.63	-29.48	-34.40	-48.10	-40.25	-7.10	-10.71	-43.75	-53.94	-46.73	-59.84	-52.38	-94.81
M5 × AG1	27.03	55.98	-1.41	-11.47	-22.66	-45.97	-32.65	-4.48	-1.96	-79.01	-58.77	-55.85	-52.43	-60.00	-95.59
M5 × AG2	13.15	47.01	11.76	-5.49	-13.38	-37.68	-23.68	35.42	0.00	-66.89	-59.43	-56.09	-67.35	5.26	-94.45
M5 × DS1	42.67	2.31	-36.70	10.89	27.73	22.02	11.23	80.79	2.22	—	—	—	—	—	—
M6 × AG1	9.61	21.04	-12.82	3.06	13.66	-11.73	-3.77	14.75	-13.79	-71.08	-56.25	-55.63	-66.09	10.95	-95.64
M6 × DS1	51.69	14.97	-51.44	2.83	13.49	-23.14	0.82	67.32	5.26	—	—	—	—	—	—
M7 × AT1	40.08	47.56	-7.05	12.65	14.67	-22.72	7.14	41.03	-3.30	-64.73	-65.73	-11.94	-65.04	4.17	-85.62
M9 × AT1	60.45	70.39	10.81	12.30	14.45	-23.88	-7.11	116.67	3.70	-6.41	8.94	-14.03	-65.92	0.00	-80.64
M9 × DS1	47.19	27.51	-40.06	5.79	15.06	13.70	8.63	55.28	-0.94	—	—	—	—	—	—
TM1 × M3	36.14	36.23	7.89	5.35	0.00	-7.33	-15.79	4.92	-3.85	-76.78	-54.26	-55.08	-62.22	3.70	-98.46
TM1 × M5	-1.58	-27.81	34.29	-39.63	-37.95	-37.12	-37.08	-41.80	0.00	-79.79	-59.92	-69.08	-50.14	-26.44	-98.51
LN1 × M1	39.30	58.40	-49.73	15.12	22.12	-4.70	-19.30	87.50	-13.79	-29.00	-6.16	-1.30	-3.63	-14.29	-60.71
LN1 × M6	-27.48	-37.86	24.65	-14.04	-20.59	-36.34	-15.18	-18.03	-6.43	-80.76	-55.23	-64.81	-44.72	-42.86	-84.04

Note. In bold, value of the "mid-parent" heterosis observed in interspecific hybrids (F1); a negative value means that the average value of the hybrid for the trait in question is lower than the average value of the parents; PLHE : Plant Height; PLCD : Plant Canopy diameter; BRIN : Branching index; LBLE : Leaf blade length; LBWI : Leaf blade width; PELE : Petiole length; PEDI : Petiole diameter; NFLI : Number of flowers per inflorescence; NBST : Number of stamens; FRLE : Fruit length; FRWI : Fruit width; FRPL : Fruit pedicel length; FRPD : Fruit pedicel diameter; NFRI : Number of fruits per infructescence; FRWE : Fruit weight.

4. Discussion

Agromorphological traits showed a large range of variability. In this study, *S. melongena* has vegetative growth and fruit parameters superior compared to species in the primary and secondary gene pools. The characterization of eggplant in Spain showed that wild species had larger plants than the cultivated species *S. melongena*. Moreover, fruit parameters are similar to those of our study [19]. This difference in vegetative growth of wild species could be explained by environmental differences between the characterization areas. Interspecific hybrids had higher vegetative growth traits than *S. melongena* accessions and wild species. In addition, production-related parameters in interspecific hybrids were intermediate between those of *S. melongena* accessions and wild species. These results suggest that genes with additive effects are important, in expression of eggplant's production traits that are polygenic [19, 20]. The higher rates of increase in vegetative growth traits observed in interspecific hybrids obtained between *S. melongena* and accessions from species in the secondary gene pool testify to the impact of parentage on heterosis effects. Indeed, the heterosis effect is stronger the further apart the parents are genetically distant, as is the case in interspecific hybridization [11, 12]. The strongest heterosis effects, in terms of production parameters, were found in interspecific hybrids obtained with accessions of the species from the primary gene pool. Heterosis studies in eggplant fruit characters [21, 22] indicate that crosses between *S. melongena* and accessions of species from the primary gene pool could be advantageous in improving fruit characteristics and yield for commercial eggplant genotypes. The importance of heterosis for vegetative growth traits suggests the existence of overdominance in allelic interactions of genes controlling these traits [17, 22]. Similar results were obtained by study on utilization of crop heterosis showed greater heterosis effects for vegetative growth traits in interspecific hybridization [11]. The greater vigor for vegetative growth traits makes it possible to envisage the use of these interspecific hybrids as rootstocks in eggplant breeding programs for adaptation to edaphic conditions.

The better performance observed in the M4 × IS3 hybrid obtained between the coded accessions M4 of *S. melongena* and IS3 of *S. insanum* makes the IS3 accession of the wild *S. insanum* species a promising candidate for use in eggplant improvement programs. Works in eggplant characterization for drought tolerance shown that the hybrid progeny obtained with the *S. insanum* species has drought tolerance abilities superior to those of their parents [23, 24]. For interspecific hybrids obtained with accessions of species from the secondary gene pool, hybrid progeny obtained with the DS1 accession of *S. dasyphyllum* showed greater vigor for vegetative growth parameters. These could help to improve eggplant resistance to abiotic stresses such as drought. Study on the mechanisms of response to drought using transcriptome profiles showed that the species *S. dasyphyllum* is a potential source of genes for obtaining drought-resistant eggplant varieties [25]. These heterosis effects could be explained by the genetic recombination of genes in certain hybrids. The mixing of two different genomes may be one of the reasons for the increased vigor of hybrids. This is because the dominant alleles from one parent complement their recessive counterparts from the second parent, ultimately resulting in a more vigorous phenotype [12, 26]. Autogamy is the preferred mode of reproduction for eggplant and its wild relatives, and homozygosity is high in *Leptostemonum* subgenus. Indeed, it has been documented that the increase resulting from heterozygosity when homozygous lines are crossed can enhance hybrids vigor, particularly when the parents are genetically distant, as this study's parent are [11, 17]. Interspecific hybridization maximizes genetic and phenotypic diversity and therefore heterotic response [16]. Moreover, after crossing *S. melongena* and *S. aethiopicum*, it was shown that interspecific hybrids have been more vigorous than the parents [27]. When characterizing interspecific hybrids between *S. melongena* and related species from the primary and secondary gene pools, authors also reported greater vegetative vigor in the interspecific hybrids [19]. However, depending on the parental accessions considered, there were significant differences between the progeny of eggplant and a given wild relative. The existence of different allelic variations in the genes governing agromorphological traits in several accessions of the same species may explain these results.

5. Conclusion

The characterization of accessions of the *S. melongena* species and of species from the primary and secondary gene pools using agromorphological descriptors enabled us to understand the variation in heterosis effects in hybrids obtained between *S. melongena* and species from the primary and secondary gene pools. It was found that, in eggplant, heterosis effects are more important for vegetative growth characteristics than for production. The M4 × IS3 interspecific hybrid was the best, as it showed the best heterosis effects for both vegetative growth and production characteristics. In terms of the parents used to obtain the interspecific hybrids, the best parental accessions are, in the primary gene pool, the MM 498 accession coded IS3 in this study and the MM 1153 accession coded DS1 in the secondary pool. These parental accessions in each gene pool produced the hybrids with the greatest heterosis effects. Information obtained in the study on the phenotypic characteristics of the parental accessions and the heterosis effects of hybrids between *S. melongena* and wild species opens up interesting prospects for the improvement of eggplant through the introgression of genes from the species into the cultivated species *S. melongena*.

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