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Genetic Analysis Indicate Superiority of Perfomance of Cape Gooseberry (*Physalis peruviana* L.) Hybrids

Genetic Analysis Indicate Superiority of Perfomance of Cape Gooseberry (*Physalis peruviana* L.) Hybrids

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ABSTRACT. The use of hybrids as a new type of cape gooseberry (*Physalis peruviana* L.) cultivars could improve yield in this crop, but little or no information is available on hybrid perfomance. We studied several vegetative characters, yield, fruit weight and fruit shape, soluble solids content (SSC), titratable acidity (TA) and ascorbic acid content (AAC) in three hybrids of cape gooseberry and their parents grown outdoors and in a glasshouse. The highest yields were obtained with hybrids, specially in a glasshouse. Interaction dominance x environment for yield was very important; a higher dominance effect was detected in the glasshouse, than that observed outdoors. Quality characters were highly affected by the environment and showed variable results for the different families. For fruit composition traits, the additive and additive x environment interactions were most important. Broad-sense heritability for all characters was high to medium (0.48-0.91), indicating that a high response to selection would be expected. Hybrids can improve cape gooseberry yield without impairing fruit quality.

KEYWORDS. Additivity, dominance, yield increase, fruit quality, heritability.

INTRODUCTION

Cape gooseberry (*Physalis peruviana* L.) is an Andean herbaceous crop grown for its edible fruits. It is usually cultivated as an annual crop, but in the absence of frosts it can be a perennial. Pollination is predominantly autogamous, although some degree of outcrossing can occur in the presence of wind or pollinating insects, like bees (McCain, 1993). Fruits are yellow-orange berries, 1 to 3.5 cm in diameter, very juicy, aromatic and with a peculiar bitter-sweet flavour. They are enclosed by the acrescent epicalyx, which gives them the shape of a bladder. The fruit can be eaten raw, as a dessert, as an appetizer or used for dish decoration. It can also be prepared in elaborated dishes, in cakes or used for making jam (National Research Council, 1989). It is high in vitamins A, B_1, B_2, B_{12}, C and PP (Branzati and Manaresi, 1980; Sarangi *et al*., 1989).

Cape gooseberry is mainly grown in the region of its origin (especially in Colombia) and in India, South Africa, New Zealand, Australia, and Hawaii (National Research Council, 1989; Fischer *et al*., 1990; Chattopadhyay, 1996). The increasing demand of this fruit in the exotic fruit markets from North America, Europe and Japan gives good prospects for the expansion of cape gooseberry as a new cash crop. The import of cape gooseberry by the European Union is estimated to be 150-500 t (Proctor, 1990; Zambrano, 1997).

Cape gooseberry can be grown and set fruit without problems if minimum temperatures are above 5 ºC (Péron *et al*., 1989; Prohens and Nuez, 1994). Glasshouse production, however, can result in continuous production in many regions where frosts are common during the cold season. Nonetheless, environmental differences between outdoors and glasshouse cultivation are important (Abak *et al*., 1994) and if genotype x environment interaction exists, it can be used for the selection of genotypes adapted to each of the environments, as is usual with many vegetable crops.

Most of research on this crop deals with the development and improvement of growing techniques (Klinac, 1986; Wolff, 1991; Chattopadhyay, 1996). There is a lack of breeding efforts; only some research relative to selection among different accessions (National Research Council, 1989), or to the development of *in vitro* culture protocols to obtain somaclonal variants, or as a first step for genetic transformation (Torres *et al*., 1991) has been conducted.

Genetic differences in yield and fruit quality characters found among accessions from different origins (Prohens and Nuez, 1994) can be exploited for cape gooseberry breeding. A simple breeding strategy is the development of hybrids to exploit heterosis for yield characters (Basra, 1999). It is well known that it is possible to develop such type of hybrids in other *Solanaceae* crops like tomato, pepper and eggplant (Bassett, 1986).

Genetic analysis of agronomically important traits in this species can provide relevant information for cape gooseberry breeding. Here, we use the components of means analysis in families formed by lines and their respective hybrids grown outdoors and in a glasshouse.

MATERIALS AND METHODS

Plant material

Three hybrids of cape gooseberry (ECU-197 x ECU-256, ECU-197 x AMS and ECU-256 x AMS) and parental lines (ECU-197, ECU-256 and AMS) were used. ECU-197 and ECU-256 originated in Ecuador (from accessions collected in Cashanpugro and Quito, respectively), wheras AMS came from fruits purchased in a market in Amsterdam. The origin of AMS is unknown, although it probably came from Colombia, as cape gooseberry is the 8th ranking export from Colombia to The Netherlands.

Growing conditions

Plants were grown in Valencia (Spain) under two different environments: outdoors and in a glasshouse. Plantlets from the nursery were transplanted to both environments in March. They were spaced 1 m between rows and 0.4 m within row. A drip irrigation system was used to water the plants. The greenhouse crop was trimmed to curtail its luxuriant vegetative growth; however, no trimming was necessary for the outdoors crop. No phytosanitary treatments were needed.

Characters studied

Vegetative characters

- Leaf length and width, petiole and internode length were recorded from adult leaves and stem characters were measured from the main stem (all in cm).

Yield

- Two traits were measured: yield per plant (g) and fruit weight (g).

Fruit quality

- Fruit shape was measured as the ratio of fruit length to fruit width.
- Soluble solids content (SSC) were measured with a manual refractometer, and expressed in º Brix.
- Titratable acidity (TA) was determined by titration with NaOH 0.025 N to the phenolphthalein end-point, and expressed as g of acid / 100 g of juice.
- Ascorbic acid content (AAC) was determined immediately after juice extraction by methaphosphoric acid extraction and titration with sodium 2,6-dichloroindophenolate hydrate. It was expressed in mg of ascorbic acid / 100 g of juice.

SSC, TA and AAC were measured in a juice sample obtained with a domestic juice extractor.

Experimental design

A 6 x 6 Latin square design was used in each of the environments. In this design randomization is restricted by grouping treatments in rows and columns, which allows removal of effects associated with row and column, although there are fewer degrees of freedom for the error term (Little and Hills, 1978). Rows corresponded to the drip irrigation lines and columns to the position of the genotype within the row. In this way, each row and column had six plots. Each plot included five plants. Thus 30 plants per genotype in each environment were available for study.

After the effects of rows and columns were removed, mean and standard error for each character of the lines and hybrids in each family in each environment were used to estimate the mean parent [m], environment [e], additive [d], dominance [h] and the additive x environment [d x e] and dominance x environment [h x e] interactions effects (Mather and Jinks, 1977). Coefficients used in each generation for the parameters estimated are shown in Table 1. The significance of this 6-parameter model cannot be tested with a χ^2 test. Thus, alternative models were tested in which some of the parameters were eliminated. For each family, 11 incomplete models representing different environmental, genetic and interaction effects were tested (Table 2). Among these models, the best fitting model (i.e, the one which had a higher probability in the χ^2 test) is used for further discussion.

Broad-sense heritabilities were estimated for yield and fruit traits from the estimates of genotypic and environmental variances obtained from an analysis of variance (Mather and Jinks, 1977). The estimates of the mean squares for error (MSEe) and for genotype (MSEg) were computed. MSEe and MSEg were used to obtain estimates of the environmental variance (σ_e^2) and genetic variance (σ_g^2). In this way, ECMe=σ_e^2 and ECMg=σ_e^2+r·σ_g^2, where r is the number of replicates. The estimates of the standard errors for the heritability were obtained as indicated by Nyquist (1991).

RESULTS

Vegetative characters

There were no differences among genotypes for these characters (Table 3). However, an important environmental effect was observed. All characters had higher values from plants grown in the glasshouse (Table 3). In all cases, the most relevant effects were [m] and [e], whereas the other parameters did not differ from zero.

Yield characters

Yield differences among different genotypes were high in the glasshouse. ECU-256 had a very low yield, but hybrids ECU-197 x ECU-256 and ECU-197 x AMS performed very well (Table 4). Differences outdoors were less important; the highest yielding genotype was a hybrid (ECU-197 x ECU-256).

The [d] values indicate that ECU-197 carries genes with additive effects that contributed to increased yield (Table 5). The family of hybrid ECU-197 x ECU-256 had a negative value for the [d x e] interaction, indicating that the additive effect of genes from ECU-197 in this cross was higher in the glasshouse than outdoors. The other crosses showed a negative value for the [h x e] interaction, indicating that an important heterotic effect was detected in the glasshouse, whereas it was lower outdoors.

The highest values for fruit weight were found in the hybrid ECU-256 x ECU-197, whereas the lowest values were found in ECU-197. Fruit weight was somewhat higher in the glasshouse than outdoors (Table 4). The additive value of ECU-197 was negative when compared to that of the other parents; also, the value of ECU-256 was negative when compared to AMS, indicating that AMS carries the alelles with a higher additive value for this character (Table 5). The heritabilities of yield and fruit weight were high (around 0.9) within the glasshouse, whereas they were somewhat smaller outdoors (Table 6).

Fruit quality characters

There were differences among genotypes for fruit shape (Table 4), the most elongated fruits being those of AMS. There was also an environmental effect on fruit shape. The fruit shape in the glasshouse was nearly rounded, with the length / width ratio being around 1, whereas outdoor fruits were more elongated (length / width ratio was around 1.1). Therefore, the estimate of [e] was positive in all cases. AMS carries the genes with a higher additive value for this character. The positive value of the [d x e] interaction in ECU-197 x ECU-256 indicates that the additive effect of the genes in this cross was larger outdoors. The opposite was the case with the cross ECU-256 x AMS. In the cross ECU-197 x ECU-256, there was, however, a positive value for [h], whereas in ECU-256 x AMS [h] it was negative. Heritability of the fruit shape was high, with values higher than 0.75 in both environments (Table 6).

Differences between environments were high for fruit composition traits (Table 4). Values for SSC were more than 2 º Brix higher outdoors than in the glasshouse. Parent ECU-197 had the highest number of additive genes with a negative effect on the character. There was a positive dominance effect in the cross ECU-197 x ECU-256, however (Table 5). The cross ECU-256 x AMS showed a negative value for the [h x e] interaction; for this reason, the dominance effect was positive in the glasshouse and negative outdoors.

The values of TA outdoors were twice those obtained in the glasshouse environment (Table 4). In the cross ECU-197 x AMS, we found an additive effect, such that genes of AMS contribute positively to the character (Table 5). A negative value for the [d x e] interaction was found in ECU-197 x ECU-256, indicating that the additive genes of ECU-197 had a positive effect on the character in the glasshouse and a negative effect outdoors. The effect of dominance was less important for this character, although a negative value in ECU-197 x AMS was observed.

For AAC, differences between environments were three-fold higher. In the glasshouse, the values for this character were around 90 mg/100 g. However, the values outdoors were much lower, around 25 mg/100 g (Table 4). In all crosses we found additive effects, AMS contributed a higher number of additive genes to the character.

Heritabilities for fruit composition characters were high (around 0.9) outdoors, and medium (around 0.5) in the glasshouse (Table 6). This shows that there are possibilities to improve these characters.

DISCUSSION

In general, a good agreement was obtained between the estimated values in the 6-parameter complete model and the values obtained with the best fitting incomplete models. However, in the latter case, the estimation of the errors improved (Mather and Jinks, 1977).

No dominance effects were found for the vegetative characters, showing that the hybrids were not heterotic for these characters. This indicates that there are no important differences among parents for the genes that control this character, or in the case that they exist, genes with additive effect are dispersed among parents and there is no dominance (Mather and Jinks, 1977).

The opposite was the case for yield, where heterosis was found. The higher than 1 ratio for [h]/[d] for yield and weight of the fruit in families ECU-197 x ECU-256 and ECU-256 x AMS indicates that the development of hybrids can be a suitable strategy for cape gooseberry breeding. In fact, hybrid ECU-197 x ECU-256 gave the highest yields in both environments. Furthermore, there were no important differences in quality characters between hybrids and parent lines.

Cape gooseberry is usually grown outdoors, so there has been no selection under these conditions. Therefore, this crop probably presents little adaptation to these conditions. It has been suggested that heterozygotes have an adaptative advantage when they are moved to new conditions or are placed under stress, because their intralocus variation can result in a higher developmental homestasis than that of homozygotes (Lerner, 1954; Blum, 1988; Nuez *et al*., 1997; Kang, 1998), which could explain the better behaviour of hybrids grown in the glasshouse.

There has been a very important environmental effect for the yield characters studied. SSC and TA were lower in the glasshouse. Probably a higher vegetative development of the plants in the glasshouse resulted in a lower light incidence per leaf area, which could lead to a lower accumulation of solids in fruits (Pearcy, 1990). The lower values of SSC and TA make the fruit less tasty, which could decrease the acceptance of these fruits. However, fruits can be harvested about a month earlier, and their high AAC, which can have an important influence in the consumer, may justify the use of glasshouses to grow cape gooseberry.

The interactions between additive and dominant effects with the environment for some characters indicates that there are differences in the genetic systems that control these characters in different environments. Kang (1998) has reviewed the scientific literature related to interactions between additive and dominant effects, and reports many cases where interactions of this type have been found. Physiological effects that act in one environment can be different to those that act in another one, and penetration, expressivity and the mode of gene action of genes that control a character in a given environment can be different to those acting in a different environment (Herrera-Estrella and Simpson, 1990). In fact, Falconer and Mackay (1996) indicate that a character measured in two different environments should not be considered as a single character, but as two different characters. In this way, if the expression of a genotype for one character depends on environmental conditions, heritability measurements can vary from one environment to another (Mazer and Schick, 1991; Kang, 1998).

We found that heritability for yield characters was higher in the glasshouse, probably due to the largest differences among genotypes and to the lower environmental variation in this environment. However, for fruit quality characters, there is a lower heritability was lower in the glasshouse, probably due to a higher variation among plants that in the end leads to a higher interplant variation and therefore, to a higher error term. Thus in the glasshouse environment, due to the luxuriant vegetative development, solar radiation was more unequally distributed among leaves than outdoors. This can influence sugar accumulation in fruits, so that those in the most shaded part of the plant accumulate less photosynthates, because leaves that supply photosynthates to them receive less solar radiation (Pearcy, 1990). Anyway, in all the cases and in all the environments tested, heritabilities were medium to high, indicating that there are good prospects for cape gooseberry breeding and for the development of new cultivars.

The development of hybrids can be a good strategy of breeding for this crop, especially when looking for good adaptation to glasshouse cultivation. Moreover, cape gooseberry hybrid seed is easy to produce, because the flower has a low sensitivity to manipulation and a considerable number of seed (more that 300) per fruit are usually obtained from each crossing. The use of hybrids can improve the yield performance of cape gooseberry without affecting fruit quality.

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TABLE 1. Coefficients used for the estimation of genetic parameters and their interaction with the environment.

Environment		Parameters[x]					
		[m]	[e]	[d]	[h]	[d x e]	[h x e]
Outdoors	Parent 1[y]	1	1	1	0	1	0
Glasshouse	Parent 1 [y]	1	-1	1	0	-1	0
Outdoors	Parent 2 [y]	1	1	-1	0	-1	0
Glasshouse	Parent 2 [y]	1	-1	-1	0	1	0
Outdoors	Hybrid	1	1	0	1	0	1
Glasshouse	Hybrid	1	-1	0	1	0	-1

[x] Mean parent [m], environment [e], additive [d], dominance [d] and the additive x environment [d x e] and dominance x environment [h x e] interactions effects.

[y] For the cross ECU-197 x ECU-256, parent 1 was ECU-197 and parent 2 was ECU-256.

For the cross ECU-197 x AMS, parent 1 was ECU-197 and parent 2 was AMS.

For the cross ECU-256 x AMS, parent 1 was ECU-256 and parent 2 was AMS.

TABLE 2. Incomplete models tested. Values of 1 indicate the parameters that have been taken in account in each model, whereas values of 0 indicate those that were discarded.

	Parameter[x]					
Effect type in the model	[m]	[e]	[d]	[h]	[d x e]	[h x e]
No effect	1	0	0	0	0	0
Environmental [e]	1	1	0	0	0	0
Additive [d]	1	0	1	0	0	0
Dominance [h]	1	0	0	1	0	0
Environmental + additive	1	1	1	0	0	0
Environmental + dominance	1	1	0	1	0	0
Environmental + additive + dominance	1	1	1	1	0	0
Environmental + additive + interaction [d x e]	1	1	1	0	1	0
Environmental + dominance + interaction [h x e]	1	1	0	1	0	1
Environmental + additive + dominance + interaction [d x e]	1	1	1	1	1	0
Environmental + additive + dominance + interaction [h x e]	1	1	1	1	0	1

[x] Mean parent [m], environment [e], additive [d], dominance [d] and the additive x environment [d x e] and dominance x environment [h x e] interactions effects.

TABLE 3. Means ∀ SE for the vegetative characters studied in the glasshouse and outdoors.

Genotype	Leaf length (cm)	Leaf width (cm)	Petiole length (cm)	Stem diameter (cm)	Internode length (cm)
			Outdoors		
ECU-197	51.7 ± 4.6	39.4 ± 4.5	51.2 ± 2.8	2.12 ± 0.11	30.8 ± 4.0
ECU-256	56.0 ± 5.5	45.7 ± 5.8	52.7 ± 1.7	2.05 ± 0.28	32.5 ± 8.2
AMS	59.5 ± 4.7	44.4 ± 5.7	57.1 ± 4.0	2.24 ± 0.16	37.6 ± 7.0
ECU-197 x ECU-256	56.3 ± 6.1	44.7 ± 6.9	53.3 ± 2.0	2.37 ± 0.20	31.5 ± 5.2
ECU-197 x AMS	59.8 ± 5.3	45.9 ± 4.8	54.7 ± 1.3	2.09 ± 0.17	40.6 ± 2.9
ECU-256 x AMS	55.7 ± 5.0	45.0 ± 5.9	52.8 ± 2.7	2.00 ± 0.23	32.0 ± 7.2
Parental mean	55.7	43.2	53.7	2.14	33.6
Hybrid mean	57.3	45.2	53.6	2.15	34.7
			Glasshouse		
ECU-197	88.6 ± 3.2	66.9 ± 3.7	116.6 ± 3.1	3.41 ± 0.12	69.9 ± 15.1
ECU-256	93.2 ± 8.0	74.2 ± 8.6	123.1 ± 5.0	3.60 ± 0.47	73.8 ± 23.4
AMS	87.6 ± 7.7	68.9 ± 6.2	119.4 ± 4.9	3.17 ± 0.43	88.2 ± 34.7
ECU-197 x ECU-256	87.4 ± 8.8	68.2 ± 7.1	118.5 ± 4.5	3.35 ± 0.32	75.0 ± 14.2
ECU-197 x AMS	86.8 ± 5.8	68.5 ± 6.5	119.0 ± 4.3	3.34 ± 0.49	64.8 ± 14.9
ECU-256 x AMS	88.5 ± 4.9	70.9 ± 6.4	120.2 ± 2.8	3.46 ± 0.26	86.2 ± 13.5
Parental mean	89.8	70.0	119.7	3.39	77.3
Hybrid mean	87.6	69.2	119.2	3.38	75.3

TABLE 4. Means ∀ SE for the yield and fruit quality characters studied in the glasshouse and outdoors..

	Yield (g)	Fruit weight (g)	Fruit shape (length/width)	CSS (º Brix)	TA (g /100g)	AAC (mg / 100g)
Genotype	Outdoors					
ECU-197	210.2 ± 45.6	1.55 ± 0.18	1.12 ± 0.02	12.7 ± 0.4	1.00 ± 0.06	20.6 ± 0.8
ECU-256	166.3 ± 33.8	1.95 ± 0.19	1.03 ± 0.03	15.0 ± 0.7	1.29 ± 0.09	28.7 ± 2.3
AMS	182.2 ± 50.4	1.95 ± 0.15	1.15 ± 0.06	13.5 ± 0.8	1.20 ± 0.10	27.7 ± 1.0
ECU-197 x ECU-256	231.0 ± 39.2	2.02 ± 0.25	1.10 ± 0.01	14.3 ± 0.6	1.05 ± 0.05	24.1 ± 1.9
ECU-197 x AMS	160.8 ± 47.3	1.72 ± 0.10	1.13 ± 0.03	13.6 ± 0.6	1.16 ± 0.07	23.4 ± 2.3
ECU-256 x AMS	151.1 ± 45.7	1.93 ± 0.17	1.09 ± 0.05	13.2 ± 0.4	1.26 ± 0.08	23.5 ± 2.5
Parental mean	186.2	1.81	1.10	13.8	1.16	25.7
Hybrid mean	181.0	1.89	1.11	13.7	1.16	23.7
	Glasshouse					
ECU-197	236.7 ± 49.5	1.60 ± 0.12	1.01 ± 0.02	10.6 ± 0.6	0.65 ± 0.26	78.1 ± 12.1
ECU-256	59.3 ± 55.5	1.89 ± 0.10	1.01 ± 0.02	11.1 ± 1.0	0.36 ± 0.08	85.3 ± 9.2
AMS	158.5 ± 40.9	2.23 ± 0.25	1.04 ± 0.03	11.8 ± 0.7	0.52 ± 0.11	99.6 ± 16.2
ECU-197 x ECU-256	306.2 ± 76.4	2.31 ± 0.20	1.03 ± 0.02	11.7 ± 0.6	0.46 ± 0.09	97.4 ± 4.4
ECU-197 x AMS	273.3 ± 30.9	1.85 ± 0.18	1.03 ± 0.02	11.4 ± 0.3	0.47 ± 0.08	87.8 ± 9.3
ECU-256 x AMS	223.6 ± 54.8	2.39 ± 0.25	0.98 ± 0.02	12.0 ± 0.9	0.51 ± 0.09	83.7 ± 13.0
Parental mean	151.5	1.91	1.02	11.2	0.51	87.7
Hybrid mean	267.7	2.18	1.01	11.7	0.48	89.6

TABLE 5. Estimates of parameters[x] [m], [e], [d], [h], [d x e] and [h x e] for yield and fruit quality characters with a 6-parameter model fit (SPF), and with the best fitting incomplete model (BF).

	Yield (g)		Fruit weight (g)		Fruit shape (length/width)	
	SPF	BF	SPF	BF	SPF	BF
Parameter[x]			Family ECU-197 x ECU-256			
[m]	168.1 ± 23.4	171.6 ± 23.2	1.75 ± 0.08	1.75 ± 0.08	1.04 ± 0.01	1.04 ± 0.01
[e]	20.1 ± 23.4	6.9 ± 20.5	0.00 ± 0.08	0.00 ± 0.08	0.03 ± 0.01	0.03 ± 0.01
[d]	55.3 ± 23.4	53.0 ± 23.3	-0.18 ± 0.08	-0.16 ± 0.07	0.03 ± 0.01	0.03 ± 0.01
[h]	100.5 ± 48.9	71.1 ± 42.0	0.42 ± 0.18	0.42 ± 0.18	0.03 ± 0.02	0.03 ± 0.02
[d x e]	-33.4 ± 23.4	-33.8 ± 23.4	-0.03 ± 0.08	---	0.03 ± 0.01	0.03 ± 0.01
[h x e]	-57.7 ± 48.9	---	-0.15 ± 0.18	-0.15 ± 0.18	0.03 ± 0.02	---
χ^2	---	1.392	---	0.138	---	0.347
P	---	0.238	---	0.710	---	0.556
			Family ECU-197 x AMS			
[m]	196.9 ± 23.4	195.1 ± 23.130	1.83 ± 0.09	1.81 ± 0.07	1.08 ± 0.02	1.08 ± 0.01
[e]	-0.7 ± 23.4	-0.33 ± 23.355	-0.09 ± 0.09	-0.09 ± 0.07	0.06 ± 0.02	0.05 ± 0.01
[d]	26.5 ± 23.4	27.3 ± 23.332	-0.26 ± 0.09	-0.25 ± 0.09	-0.02 ± 0.02	-0.02 ± 0.01
[h]	20.2 ± 36.7	22.0 ± 36.509	-0.05 ± 0.14	---	0.00 ± 0.03	---
[d x e]	-12.6 ± 23.4	---	0.06 ± 0.09	0.05 ± 0.09	0.00 ± 0.02	---
[h x e]	-55.5 ± 36.7	-56.0 ± 36.652	0.02 ± 0.14	---	0.00 ± 0.03	---
χ^2	---	0.289	---	0.106	---	0.015
P	---	0.591	---	0.948	---	1.000
			Family ECU-256 x AMS			
[m]	141.6 ± 23.0	159.2 ± 18.2	2.01 ± 0.09	2.04 ± 0.08	1.06 ± 0.02	1.06 ± 0.02
[e]	32.7 ± 23.0	---	-0.06 ± 0.09	-0.10 ± 0.08	0.03 ± 0.02	0.04 ± 0.02
[d]	-28.8 ± 23.0	---	-0.08 ± 0.09	-0.11 ± 0.09	-0.04 ± 0.02	-0.04 ± 0.02
[h]	45.8 ± 42.4	---	0.16 ± 0.18	---	-0.03 ± 0.03	-0.04 ± 0.02
[d x e]	20.8 ± 23.0	---	0.09 ± 0.09	0.11 ± 0.09	-0.02 ± 0.02	-0.03 ± 0.02
[h x e]	-68.9 ± 42.4	---	-0.17 ± 0.18	---	0.02 ± 0.03	---
χ^2	---	4.910	---	1.298	---	0.387
p	---	0.427	---	0.523	---	0.534

(Continued in next page)

TABLE 5. Continued.

	SSC (ºBrix)		TA (g/100 g)		AAC (mg/100 g)	
	SPF	BF	SPF	BF	SPF	BF
Parameter[x]			Family ECU-197 x ECU-256			
[m]	12.4 ± 0.4	12.4 ± 0.4	0.82 ± 0.07	0.83 ± 0.91	53.2 ± 3.8	58.9 ± 1.9
[e]	1.5 ± 0.4	1.4 ± 0.3	0.32 ± 0.07	0.30 ± 0.04	-28.5 ± 3.8	-34.4 ± 2.0
[d]	-0.7 ± 0.4	-0.7 ± 0.4	0.00 ± 0.07	0.01 ± 0.06	-3.9 ± 3.8	-3.9 ± 1.1
[h]	0.6 ± 0.5	0.6 ± 0.55	-0.07 ± 0.09	-0.09 ± 0.07	7.6 ± 4.5	---
[d x e]	-0.5 ± 0.4	-0.4 ± 0.3	-0.14 ± 0.07	-0.15 ± 0.06	-0.2 ± 3.8	---
[h x e]	-0.2 ± 0.5	---	-0.02 ± 0.09	---	-8.1 ± 4.5	---
χ^2	---	0.128	---	0.0621	---	3.491
p	---	0.720	---	0.8032	---	0.322
			Familiy ECU-197 x AMS			
[m]	12.2 ± 0.3	12.3 ± 0.2	0.70 ± 0.08	0.80 ± 0.04	56.5 ± 5.05	56.4 ± 3.5
[e]	0.9 ± 0.3	1.0 ± 0.2	0.46 ± 0.08	0.32 ± 0.04	-32.3 ± 5.05	-32.3 ± 3.5
[d]	-0.5 ± 0.3	-0.6 ± 0.1	-0.15 ± 0.08	-0.08 ± 0.05	-7.2 ± 5.05	-7.2 ± 5.0
[h]	0.3 ± 0.5	---	0.14 ± 0.09	---	-0.9 ± 6.98	-0.8 ± 2.4
[d x e]	0.1 ± 0.3	---	0.03 ± 0.08	---	3.6 ± 5.05	3.6 ± 5.0
[h x e]	0.2 ± 0.5	---	-0.21 ± 0.09	---	0.1 ± 6.98	---
χ^2	---	0.477	---	1.821	---	0.000
p	---	0.924	---	0.610	---	0.986
			Family ECU-256 x AMS			
[m]	12.8 ± 0.4	12.9 ± 0.4	0.84 ± 0.05	0.86 ± 0.04	60.4 ± 4.7	58.3 ± 3.5
[e]	1.5 ± 0.4	1.4 ± 0.4	0.40 ± 0.05	0.39 ± 0.04	-32.1 ± 4.7	-30.4 ± 3.4
[d]	0.1 ± 0.4	---	-0.02 ± 0.05	-0.02 ± 0.05	-3.3 ± 4.7	-4.4 ± 2.6
[h]	-0.2 ± 0.6	-0.3 ± 0.6	0.04 ± 0.02	---	-6.7 ± 8.1	---
[d x e]	0.7 ± 0.4	---	0.06 ± 0.05	0.06 ± 0.05	3.8 ± 4.7	---
[h x e]	-0.9 ± 0.6	-0.9 ± 0.6	-0.02 ± 0.02	---	2.0 ± 8.1	---
χ^2	---	3.061	---	0.338	---	0.745
p	---	0.216	---	0.845	---	0.863

[x] Mean parent [m], environment [e], additive [d], dominance [d] and the additive x environment [d x e] and dominance x environment [h x e] interactions effects.

TABLE 6. Broad-sense heritability ∀ SE for yield and fruit quality characters.

Environment	Yield	Fruit weight	Fruit shape (length/width)	SSC	TA	AAC
Outdoors	0.50 ± 0.53	0.76 ± 0.41	0.77 ± 0.39	0.87 ± 0.29	0.88 ± 0.27	0.90 ± 0.25
Glasshouse	0.91 ± 0.23	0.90 ± 0.24	0.81 ± 0.36	0.53 ± 0.52	0.48 ± 0.53	0.54 ± 0.51