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Heritability and Combining Ability Studies in Strawberry Population

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Abstract

The most efficient breeding strategies in crop improvement is the selection based on heritability and combing ability estimates for the traits of economic importance or commercial value. Therefore, the present study was to obtain estimates of heritability and to estimate the phenotypic and genotypic correlations among the characteristics of interest. The commercial cultivars ‘Aromas’, ‘Camarosa’, ‘Dover’, ‘Festival Flórida’, ‘Oso Grande’, ‘Sweet Charlie’ and ‘Milsei-Tudla’, and 103 F_1 hybrids from the crossbreeding experiments were evaluated for four traits of commercial fruit yield and 13 traits of fruit physical and chemical quality. The estimated genetic parameters were general combining ability, specific combining ability, genotypic correlation among traits, estimates of heritability, genetic and phenotypic variance. The ‘Camarosa’ and ‘Aromas’ cultivars were the most promising cultivars for use as parents in the commercial fruit production, while ‘Dover’ and ‘Sweet Charlie’ cultivars were selected for taste of fruit in strawberry breeding, as they showed higher concentrations of favorable alleles in the F_1 hybrid population. It was also verified some strong genetic correlations for some pairs of characteristics in the present study that may allow indirect selection. The estimation of these parameters is an important basis for decision making on the genetic engineering of strawberry.

Keywords: *Fragaria* × *ananassa* Duch., diallel analysis, heritability, genetic correlations

1. Introduction

The strawberry (*Fragaria* × *ananassa* Duch.) a fruit crop that belongs to the family *Rosaeceae* and the genus *Fragaria*, presenting 35 described and 11 natural species. In Brazil, seven cultivars and 103 hybrids of strawberry were evaluated for fruit mass and commercial fruit value for selections in crop's breeding programs (Vieira et al., 2017). With the provision of advanced genetic engineering tools for development of populations with improved traits of economic value, it is important to estimate genetic parameters for the application of appropriate selection methods and greater genetic gains.

In genetic improvement programs, the selection of superior individuals has been mostly based on the phenotypic evaluation of individuals from a given generation. The success in selection is associated with the degree of genetic variance in subsequent generations (Falconer, 1987). The genetic-additive variance estimators were described in Falconer (1987), and Cruz and Carneiro (2003), $\delta^2A = 4\delta^2M$ when we consider absence of epistasis and inbreeding population (F = 0). From the values of the mean squares, obtained by the analysis of variance of the data of Miracema and Viçosa, the variance component associated with the male effect was estimated (δ^2M), as described in Falconer (1987), Cruz and Carneiro (2003), and Gonçalves (2005).

The estimation of genetic variance components of a population is of fundamental importance for the selection, evaluation and improvement of genotypes and their potential for use in a breeding program. The genetic gain depends on heritability of the trait under selection, the proposed selection method, intensity of selection, and the environment. The higher the expression level of genetic variability in relation to the environment, the greater the estimated genetic gains for the next generation (Hallauer & Filho, 1981). These gains can be computed based on the heritability values of the trait.

The estimation of genetic components of variance allows understanding the nature of action of genes involved in controlling the quantitative traits and evaluating the cultivar efficiency. The most important parameters are genotypic and phenotypic variances, correlation coefficients and narrow sense heritability (Cruz et al., 2012).

The knowledge on the correlation among vegetative growth parameters, productivity and fruit quality traits allows the indirect selection of correlated traits, and the selection of complex traits through less complex components (Nogueira et al., 2012). Variance component analysis is to identify and determine the genetic and environmental components by the phenotypic expression of correlated traits (Coimbra et al., 2004).

Few studies were conducted in strawberry populations of Brazil by estimation of these genetic parameters, although were so much research was done in other countries (Vieira, 2016). Fort and Shaw (2000) studied strawberry populations of the University of California and observed heritability, in the restricted sense for plant growth and diameter traits, was considered from low to moderate, with little contribution of the additive genetic variance. Quantitative characteristics such as yield and fruit size showed significant values for additive genetic variance. The genetic parameters of strawberry related to its growth are influenced by different growing environments and types of propagules (Shaw & Larson, 2005).

Bourdon (1997), states that heritability can be classified as low, moderate or high magnitude. In general, a low magnitude (less than or equal to 20%) can be explained when the environmental effect is important for the genotype and the phenotype is small, which in practice means that the performance presented by the animal is associated with the environment provided. The moderate herdability coefficient varies between 20% and 40%, when high or equal to 40%, in which case a landfill between the phenotype and the individual's genotype is high. This coefficient ranges from 0 to 1 (0 to 100%).

The heritability and genetic correlations studies for strawberry populations desirable to develop strategies for improvement and selection of superior hybrids adapted to Brazilian conditions is still a research need. Thus, the present study was to obtain estimates of heritability and to estimate the phenotypic and genotypic correlations among the characteristics of interest.

2. Material and Methods

2.1 Experimental Location

The experiment was conducted in the experimental area of the Olericulture Sector of the Department of Agriculture of the Federal University of Lavras (UFLA) in Lavras, south of the State of Minas Gerais, Brazil, (21º14' S, 40º17' W and 918.80 m altitude). The climate of the region, according to the climatic classification of Köppen, is Cwa (mesothermal) with dry winters and rainy summers (Álvares et al., 2013). The *in vivo* experiment was conducted in growth media and experimental trays in a sterile location of the greenhouse while the field experiments were conducted on prepared raised seed beds inside the experimental area.

2.2 Experimental Design

Augmented block design-ABD as proposed by Federer (1956), with segregating F_1 population in 12 blocks and a single plant per treatment due to lack of genotype replicates. It should be noted that this design was chosen due to the lack of repeatability of the genotypes, because the object under study is the F_1 generation with few seeds at each crossing.

Treatments were applied to parents and 103 F_1 hybrids in each block (Table 1).

Table 1. Description of 12 hybrid populations generated from seven cultivars of strawberries

Population	Parents		Population	Parents	
	♀	♂		♀	♂
1	'Dover'	'Aromas'	7	'Sweet Charlie'	'Aromas'
2	'Oso Grande'	'Aromas'	8	'Milsei-Tudla'.	'Aromas'
3	'Camarosa'	'Aromas'	9	'Milsei-Tudla'.	'Sweet Charlie'
4	'Dover'	'Sweet Charlie'	10	'Camarosa'	'Sweet Charlie'
5	'Oso Grande'	'Milsei-Tudla'.	11	'Festival Flórida'	'Aromas'
6	'Festival Flórida'	'Sweet Charlie'	12	'Oso Grande'	'Sweet Charlie'

Note. ♀: Female parent; ♂: Male parent.

2.3 Defining Treatments and Variables

2.3.1 Parents and Populations of Strawberry

The parents were previously selected among cultivars introduced and planted in Brazil based on the favorable phenotypes for the characteristics of agronomic interest (Galvão, 2014; Vieira, 2016; Souza et al., 2017). The parental cultivars are ‘Aromas’, ‘Camarosa’, ‘Dover’, ‘Festival Flórida’, ‘Oso Grande’, ‘Sweet Charlie’ and ‘Milsei-Tudla’. Among seven cultivars, only ‘Aromas’ is classified as day-neutral cultivar, and all other cultivars being short days (Table 1).

2.3.2 Mating Design and Number of Crosses

The hybridization was performed with the aid of pincers, emasculating the flowers of the female parents and then pollinated and isolated with paper bags to avoid varietal contamination, according to Chandler et al. (2012). Twelve hybrid populations were obtained from crossing seven commercial cultivars following diallel partial, according to Table 1.

2.4 Collection of Seed Material for Raising Transplants

After harvesting the false fruits, the achenes were removed with the aid of a blender adapted for seed extraction (Osterizer, model 4655). The seeds were then dried at room temperature, and to overcome the integumentary dormancy was used the method described by Ito et al. (2011) adapted by Galvão et al. (2014). After this treatment, the achenes were transferred to culture *in vitro* in MS culture medium (Murashige & Skoog, 1962), solidified with agar (0.6%) and supplemented with sucrose (3%).

Sixty-days old seedlings were transplanted to tray of seventy-two cells with commercial substrate Biomix (Plantmax ®) and irrigated daily for acclimatization. Approximately 120 days after germination of seeds, the seedlings were transplanted on beds in the field.

2.5 Preparation of Raised Seed Beds and Transplanting

The beds of 0.20 m of height and 1.20 m of width were prepared with the aid of power tiller. For liming, 2.50 t ha^{-1} limestone (PRNT 92%) was used, based on soil chemical analysis. Base fertilization was done three days before transplanting with the equivalents of 1,650 kg ha^{-1} of simple superphosphate, 250 kg ha^{-1} of potassium chloride and 295 kg ha^{-1} of urea.

Seedlings were transplanted in two rows on the beds in greenhouse provided with drip irrigation at spacing of 0.30 m x 0.40 m. The beds were mulched with black polyethylene film, with a thickness of 30 µm. Seven topdressing fertilizations at 30 days interval were applied to the growing seedlings based on soil chemical analysis and according to the recommendations for the crop (Dias et al., 2007).

2.6 Collection of Data for Experimental Variables

Genotypic differences in maturity and development lead to different harvesting dates for each experimental genotype (Table 1). Fruits showing 75% dark red staining were collected and measure (Galvão, 2014; Vieira, 2016).

2.6.1 Agronomic Characteristics

The harvested fruits were weighed on a precision analytical scale and classified as non-commercial (≤ 35 mm) and commercial (> 35 mm), according to Galvão (2014). The end of the commercial production period was considered when the evaluated plant produced more than 70 % of non-commercial fruits. The data were collected and computed to have the total mass of fruits (TMF) expressed in g plant^{-1}, number of commercial fruits (NCF), number of non-commercial fruits (NNCF), and average fruit mass (AFM) expressed in g fruit^{-1} (Galvão, 2014; Vieira et al., 2017).

2.6.2 Physico-Chemical Characteristics

The firmness (Fi) of ten representative fruits of each genotype were sampled, using a manual penetrometer (Instrutherm tip, model PTR-300) and the results expressed in Newton (N). The external and internal staining (ES and IS), according to Souza (2015).

The average width (AW) and the average length (AL) were measured using a digital caliper (Universal 150mm, model MTX-316119) and the results were expressed in millimeters (mm). The fruit shape (Sh) of representative (tagged) five fruits of each genotype were sampled by two examiners and were classified by grade according to Souza (2015).

The quality of fruit was assessed following methods described in AOAC (2012). The pH was measured using pHmeter (Tec-3MP, Tecnal). Total soluble solids (TSS) in the fruits were measured by direct reading in a digital bench-top refractometer (Reichert, model AR 200,) at room temperature, and the results expressed as % TSS or ^{o}Birx. Titratable acidity (TA) was determined and expressed as percentage of citric acid 100 g^{-1} of pulp. The TSS/TA ratio was obtained by dividing the TSS readings by the percentage of TA. The TSS/TA was calculated as an indicator of fruit flavor, especially when strawberry was consumed as fresh fruit.

The total sugars (TS) were estimated by the methods of Antrona (Dische, 1962) using spectrophotometry to a length of wave of 620 nanometers (nm) and the results expressed in % of sugars total. Total pectin (TP) and soluble pectin (SP) were extracted with ethyl alcohol (95%), according to methodology described by Bitter & Muir (1962).

2.7 Statistical Analysis

The data was subjected to statistical data analysis software (SAS, 2009) to estimate the general combining ability (GCA), specific combining ability (SCA), genotypic and phenotypic correlations among traits, heritability estimation, accuracy, and genetic variance.

The data from all measured traits were tested regarding their distribution using the PROC UNIVARIATE procedure of the SAS software. The traits that deviated from the normal distribution according to the Shapiro-Wilk test were transformed. The analysis of variance was performed following the statistical model:

$$Yijk = \mu + bj + Ck + gi(k) + \xi ijk \qquad (1)$$

Where, Yijk = is the observation generated for the plot of block j that received the treatment (genotype) i originated from the crossbreed k; μ = is the overall average under zero-sum constraints for every other effects; gi(k) = is the effect of the genotype (progeny or control) i, originated from the crossbreed k (i = 1, 2, ... p_k; p_k is the number of genotypes in the crossbreed k), assuming fixed and null if i is a control or random if it is progeny.

F_1 with distribution N (0, σ_{gk}^2); bj = is the effect of block j (j = 1, 2, ... b), assumed as fixed; Ck = is the fixed effect of the crossbreed k, including control (k = 1, 2, ... c, c+1, c+2, ... c+t, where, c is the number of crossbreeds originating progenies and t is the number of controls); and ξijk = is the random experimental error associated to the ijk-th parcel, assumed to be independent and identically distributed, under N (0, σ_e^2).

It is therefore a mixed model in which the n observations yik expressed by the vector $y_{(n\times1)}$ can be matrically described by the general linear mixed model (Henderson, 1984):

$$y = X\beta + Z\gamma + \varepsilon \qquad (2)$$

with,

ε-N (φ, R); γ-N (φ, G); E(y) = Xβ; and Var(y) = V(n) = ZGZ’ + R.

These analyses were performed using the PROC MIXED procedure of the SAS software (2009).

Genetic correlations were obtained following the methodology described by Holland (2006). Estimates of genetic variance (σ^2p), phenotypic variance (σ^2F), accuracy (|r|), and heritability (h^2) in the broad sense were obtained similarly to that presented by Cruz et al. (2012). The lower and upper limits of h^2 were obtained from the expressions of Knapp et al. (1985). With the estimated averages, the diallelic analysis was performed using the methodology two of Griffing (1956), in which the genitor cultivars and the set of hybrids F_1 are included. GCA and SCA, as well as the variance components associated with these effects were predicted using the REML-BLUP (residual maximum likelihood-best linear unbiased prediction) approach using the Proc IML of software SAS 9.0 (SAS Institute, 2009). It was also estimated the coefficient of determination (R^2) obtained by the ratio between the sum of squares of the combining capacities and the sum of squares of the GCA + SCA.

The statistical model of diallelic analysis based on the average of replicates was as follows:

$$Yij = m + gi + gj + sij + \varepsilon ij \qquad (3)$$

where, Yij = average value of hybrid (i ≠ j) or parent (i = j) combination; m = mean effect of all treatments; gi = random effect of GCA of the parent i, corresponds to the deviation of its average performance in hybrid combinations; gj = random effect of the GCA of the parent j; sij = random effect of SCA for crossbreeds between parents i and j; being sij = sji; and εij = mean experimental error associated to the diallelic table averages.

For the estimation of effects and square sums of effects, the following constraints were adopted: $\sum$ gi = 0 and Sij + $\sum$ Sij = 0.

Considering these constraints, the effect estimators were described as follows (Cruz et al., 2012):

$$m = \frac{2}{p(p+1)} y \tag{4}$$

$$gi = \frac{1}{p+2}\left[Yii + Yi - \frac{2}{p} y..\right] \tag{5}$$

$$Sij = Yij - \frac{1}{p+2}[Yii + Yij + Yi + Yj] + \frac{2}{(p+1)(p+2)} Y \tag{6}$$

3. Results and Discussion

There was a significant difference for most of the evaluated characteristics, indicating that there is variability among the populations studied except for the traits TS and Sh. For most of the evaluated characteristics, the accuracy values were higher than 0.70, except for some physical and chemical characteristics (TA, TS, SP, AW, and Sh) (Table 2). According to Resende and Duarte (2007), accuracy values between 0.70 and 0.90 determine a high accuracy class, and values above 0.90, determine as very high class. In general, the greater accuracy of the selection, the greater will be the heritability of a characteristic and the greater the response to the selection.

Table 1. Average, average standard deviation (ASD), genetic variance (GV), phenotypic variance (PV), heritability, heritability (h^2), lower limit of heritability (LL h^2), upper limit of heritability (UL h^2) and accuracy (r) (the symbol of accuracy shall be: $\hat{r}_{gg}$) for all evaluated characteristics

Agronomic Characteristics

	TM	**NCF**	**NNCF**	**AFM**
	----------- g plant^{-1} -----------			---------- g fruit^{-1} -----------
Average	897.68	38.83	74.79	8.26
ASD	119.220	6.435	14.288	0.903
QMt	116485**	1.834**	2120.7**	0.108**
QMe	14213.39	0.329	204.14	0.024
GV	63700.9	0.93	1193.8	0.05
PV	69751.7	1.09	1269.8	0.06
h^2	0.878	0.82	0.904	0.779
LL h^2	0.814	0.726	0.853	0.663
UL h^2	0.922	0.885	0.938	0.859
|r|	0.937	0.906	0.951	0.883

Chemical and Physical Characteristics

	pH	**TSS**	**TA**	**TSS/TA**	**TS**	**OS**	**TP**	**Fi**	**CM**	**AW**	**Sh**	**ES**	**IS**
								-- N --	--------- cm	---------			
Average	3.92	6.91	0.94	7.61	6.91	65.53	405.41	2.12	35.42	28.26	3.92	5.41	4.10
ASD	0.082	0.748	0.122	1.267	3.526	22.006	88.899	0.286	3.925	3.399	1.123	0.677	0.52
QMt	0.01**	1.71**	0.007**	0.012**	0.01^{NS}	0.052**	17064.5**	0.003**	33.06**	19.428**	0.09^{NS}	154**	39**
QMe	0.007	0.56	0.004	0.005	0.007	0.029	1902.947	0.002	15.403	11.556	0.082	54.87	18.9
GV	0.006	0.717	0.002	0.005	0.002	0.014	5706.4	0.001	10.99	4.90	0.008	61.76	12.9
PV	0.01	1.025	0.004	0.007	0.006	0.031	10218.2	0.002	19.79	11.6	0.057	92.23	23.7
h^2	0.585	0.673	0.429	0.59	0.259	0.44	0.537	0.534	0.534	0.405	0.141	0.644	0.52
LL h^2	0.366	0.50	0.128	0.373	-0.132	0.145	0.293	0.289	0.288	0.091	-0.31	0.456	0.27
UL h^2	0.735	0.791	0.635	0.738	0.526	0.642	0.704	0.702	0.702	0.62	0.451	0.772	0.69
|r|	0.765	0.82	0.655	0.768	0.509	0.664	0.733	0.731	0.731	0.636	0.371	0.803	0.72

Note. ^{NS}, *, **, not significant, significant at 5% and 1%, respectively, by F test. Total mass (TM), number of commercial fruits (NCF), number of non-commercial fruits (NNCF) and average fruit mass (AFM), pH, total soluble solids (TSS), titratable acidity (TA), total soluble solids/titratable acidity ratio (TSS/TA), total sugars (TS), soluble pectin (SP), total pectin (TP), firmness (Fi), average length (AL), average width (AW), fruit shape (Sh), external staining (ES), internal staining (CI).

With regard to heritability estimates, the values ranged from 0.141 (Sh) to 0.904 (NNCF) (Table 2), with heritability values above 0.5 being considered high, between 0.3 and 0.5 are medium and below 0.3 are low (Falconer, 1987). Heritability values are useful to indicate the reliability of the phenotypic value to predict the genetic value, since high values indicate greater possibility of gain with the selection. In the present study, the agronomic traits showed the highest values, with high NCF, however, in a strawberry's improvement program, the selection should be made for commercial fruits, which also had a high heritability value. Additionally, we verified that most of the characteristics showed positive values for the lower and upper limits, except for TS and Sh, which showed negative values for the lower limit. The positive values for the lower limits indicate the possibility of gain with the selection, while lower limits with negative values indicate that the heritability can be zero and there may be no gain. The NCF and CF values were with high heritability values, an uncommon data outcome that was observed for imposing selection pressure on strawberry populations. We observed negative values with lower limit heritability for TS and Sh traits indicating no genetic gain. Remaining traits have positive values with low and high limits for heritability indicating the possibility of selection with genetic gain for the traits having positive values with lower limit of heritability.

Whitaker et al. (2012) when studying 15 experimental hybrids and two parents (‘Radiance’ and ‘Elyana’) in two locations (Balm and Dover, in Florida) observed the heritability in the broad sense for Sh with low (h^2 = 0.18±0.03), for average fruit weight with medium to high (h^2 = 0.53±0.04) and for the other analyzed traits with a median value (h^2 = 0.30 to 0.41) supporting themedium to high heritability values of some traits in the present study.

Murti et al. (2012) reported that estimates of heritability (h^2) for F_1 populations and 8 parents used as parents (‘Akihime’, ‘Sachinoka’, ‘Keumhyang’, ‘Seolhyang’, ‘Maehyang’, ‘Soogyeong’, ‘DNKW001’ and DNKW002 ‘) was 0.498 for fruit firmness and 0.678 for soluble solids content, in a study conducted at the National University of Gangneung-Wonju, Korea, values close to those found in the present study.

Knowledge on inheritable genetic correlations among genotypes for the traits has great impact on selection of genotypes with an improved trait in a plant population improvement program. Though phenotypic correlations may be useful to determine the relationship among phenotypic values from different traits, these correlations may not reflect the expected correlated changes, since there is a genetic and an environmental component within this correlation.

Table 2. Estimates of genotypic correlation coefficients between physical-chemical and agronomic traits

	TSS	**TA**	**TSS/TA**	**TS**	**SP**	**TP**	**Fi**	**AL**	**AW**	**Sh**	**ES**	**IS**	**TM**	**NCF**	**NNCF**	**AFM**
pH	0.249	**-0.75***	**0.877***	0.182	**0.535***	**0.554***	0.029	**-0.70***	**0.325***	**-0.38***	**-0.39***	-0.163	-0.231	-0.004	**-0.33***	-0.003
TSS		0.093	**0.818***	**0.421***	**0.403***	**-0.35***	-0.297	-0.176	-0.254	0.134	-0.099	0.193	0.213	0.101	0.266	-0.161
TA			**-0.50***	**0.547***	**0.031***	**0.716***	0.028	-0.022	-0.030	-0.025	**-0.35***	-0.022	**-0.33***	**-0.39***	0.078	0.123
TSS/TA				0.155	**0.384***	-0.153	**-0.29***	-0.148	0.144	-0.279	0.145	0.194	**0.330***	0.258	**0.333***	-0.238
TS					-0.015	-0.270	0.173	-0.042	-0.051	0.079	**-0.37***	-0.036	-0.098	0.026	-0.096	-0.103
SP						0.207	**-0.52***	-0.070	-0.081	-0.104	0.212	-0.047	**0.430***	0.309	**0.385***	0.012
TP							**0.393***	-0.196	0.205	-0.108	-0.209	-0.160	-0.196	-0.247	-0.026	-0.143
Fi								**0.748***	**0.648***	0.238	-0.043	-0.194	**-0.32***	0.004	0.220	**-0.36***
AL									0.079	**0.407***	0.302	-0.097	0.251	**0.413***	**-0.28***	**0.484***
AW										**-0.58***	0.023	-0.801	0.079	**0.296***	**-0.44***	**0.456***
Sh											0.059	0.291	0.249	-0.054	0.152	-0.244
ES												**0.472***	0.169	0.135	0.219	-0.231
IS													-0.138	-0.289	0.121	-0.250
TM														**0.739***	**0.562***	-0.026
NCF															0.020	0.271
NNCF																**-0.80***

Note. TSS: total soluble solids, TA: titratable acidity, TS: total sugars, SP: soluble pectin, TP: total pectin, Fi: firmness, AL: average length, AW: average width, Sh: shape, ES: external staining, IS: internal staining, TM: total mass, NCF: number of commercial fruits, NNCF: number of non-commercial fruits, AFM: average fruit mass. * significant at 5% by the Mantel test.

Estimates of genotypic correlation coefficients are presented in Table 3. Correlations among traits TM and NCF, AFM and NNCF were high, which was expected, since the commercial fruits are bigger, hence the bigger the number of this fruit type, the greater the TM, whereas a high NNCF, which are generally smaller, tends to reduce the average mass of fruits.

The correlations between other fruit traits, such as pH, TSS, TA with TSS/TA, and pH with TA, were considered strong. However, the reason might be the direct dependence of values of one of the correlated traits on the other.

The pH depends on the fruit acidity and the TSS/TA ratio depends on TA and TSS. Thus, these strong correlations were already expected.

Another strong genotypic correlation was observed between pH and AL, which may have occurred due to the presence of linked genes or pleiotropic loci participating in these traits (Table 3). TM showed positive correlation for TSS, TSS/TA ratio, SP, AL, AW, Sh, and ES. However, these values were ranging from low to medium. The correlation analysis between internal and external staining was moderate and positive, however, being considered as low by Shaw (2005), indicating that these characteristics may be conditioned by different linked genes or may be several genes including pleiotropic loci for internal and external staining. The trait "Sh" correlated positively with the trait "AL" and negatively with "AW", showing median values. According to Chitarra and Chitarra (2005), fruit size and shape are correlated, physical attributes with a market value.

For Taiz et al. (2017), pectin is one of the major polysaccharides with the function of promoting cell wall resistance to pathogen infection. The genotypic correlation between Fi and TP was positive, while correlation between SP and Fi was negative with medium values. Filho et al. (2014), observed no correlation between these traits. For SP, we observed a moderate and negative correlation with Fi.

According to Chitarra and Chitarra (2005), with the pectin depolymerization in the cell wall, which culminates the solubilization of pectins by the action of hydrolytic enzymes, a reduction of Fi occurs along with the ripening of the fruits, *i.e.*, with the increase of SP, a reduction in Fi is expected, as observed in this study. A moderate and positive correlation was observed by Filho et al. (2014) between TSS and SP because SP is one of the TSS components of fruit.

Masny et al. (2016) studied the correlations between agronomic and fruit quality characteristics of 13 commercial strawberry cultivars and presented significantly similar results as observed in the present study for the traits, AW and TSS content (0.69), Fi and fruit shape (-0.47), TSS content and NCF (-0.50), TSS content and Fi (-0.26), as well as Fi and AW (-0.55).

The GCA effects refer to the additive and epistatic gene action, and the SCA effects refer to the non-additive gene action (Cruz et al., 2012). Significance was verified for the four agronomic traits (AFM, TM, NCF, and NNCF) evaluated to study GCA and SCA effects, indicating the presence of genes with additive and non-additive effects in the determination of superiority of these traits. The coefficients of determination (R^2) were estimated for GCA and SCA, which allowed the determination of distribution of variation contributed by components of GCA and SCA (Table 4). The predominance of additive gene effects (GCA) for AFM and NNCF traits was observed which confirmed the finding of Falconer (1987) who reported that when GCA predominates, the progeny performance can be predicted based on the performance *per se* of the parents (Falconer, 1987).

Table 3. Estimates of the general combining ability effects for the agronomic traits evaluated in seven strawberry parents

Effects	**Agronomic traits**			
	TM	**NCF**	**AFM**	**NNCF**
Aromas	54.598	4.532	0.074	2.984
Oso Grande	-87.454	-0.089	0.935	-24.701
Dover	20.277	-9.193	-1.978	38.196
Sweet Ch.	-29.447	-2.226	-0.027	0.5971
Tudla	-55.55	-1.053	0.820	-16.837
Festival	-37.270	3.682	1.550	-33.796
Camarosa	66.932	4.830	0.136	0.302
MS_{GCA}	211028.69**	1164.32**	72.55**	26534.66**
MS_{SCA}	290719.3**	713.19**	6.59**	1658.568**
R^2-GCA	0.283	0.471	0.857	0.897
R^2-SCA	0.716	0.528	0.142	0.102

Note. TM: total mass, NCF: number of commercial fruits, AFM: average fruit mass, NNCF: number of non-commercial fruits. MS_{GCA}: Middle Square of general combining ability, MS_{SCA}: Middle Square of specific combining ability, R^2-GCA: Determination coefficient of general combining ability, R^2-SCA: Determination coefficient of specific combining ability. ** significant at 1% by the F test.

The non-additive gene effects (SCA) were predominant for TM and NCF traits confirming the findings of Cruz et al. (2012), when most of the variation is attributed to SCA, it is not reliable to predict the performance of progenies without evaluation of crossbreeds. However, the significant GCA effects may help in the selection of parents with higher GCA values because it allows selecting parents with a higher proportion of favorable alleles.

Thus, parents with high and positive GCA estimates are those that most contribute to the increase in the expression of the genetically inherited characteristic, while those with high and negative GCA values contribute to the reduction of their manifestation. Thus, parents with the highest GCA values could be included in genetic improvement programs of strawberry to meet the objectives of new cultivar selection for adaptation to climatic conditions of Brazil.

The cultivars 'Aromas', 'Camarosa', and 'Dover' were the only ones that provided positive estimates for the variable "TM" with values of 54,598; 66,932, and 20,277, respectively, showing that these parents tend to contribute an increases in fruit production in the crossbreeds if they are present. The cultivars 'Oso Grande', 'Sweet Charlie', 'Tudla', and 'Festival' tend to contribute a reduction in fruit production due to observed negative estimates for variable "TM" (Table 4).

Similar results with positive GCA values were reported by Masny et al. (2016) for the cultivars 'Aromas', 'Charlote' and 'Camarosa' under climatic conditions of the Central Region of Poland, when 13 cultivars were studied for genetic parameters in relation to their commercial production.

The cultivars 'Aromas', 'Camarosa' and 'Festival', expressed a positive GCA value for trait NFC, indicating their utility in production of hybrids with large fruit size (Table 4). The cultivars 'Dover' and 'Sweet Charlie' were observed with negative values of GCA and thus excluded its inclusion in hybrid production for large fruit size. The other cultivars showed positive values were included. The traits AFM and NCF has great importance being the main agronomic attributes integrated with the quality of the fruit destined for *in natura* consumption.

If parents have high GCA values and complement each other well with high SCA values, the probability of genetic gain with superior progeny selection from this pair of crossbreed populations will be higher. The SCA effects of each crossbreed were estimated and presented in Table 5.

Table 5. Estimates of the specific combining ability effects for the agronomic traits evaluated in seven strawberry parents

Effects	**Agronomic Traits**			
	TM	**NCF**	**AFM**	**NNCF**
Aromas × Aromas	-628.397	-29.382	0.855	-48.278
Aromas × Oso Grande	-130.094	-5.117	-0.646	-9.738
Aromas × Dover	7.924	-0.114	-0.078	25.173
Aromas × Sweet Charlie	3.816	-3.373	0.191	20.111
Aromas × Festival	63.842	3.874	0.392	-0.556
Aromas × Camarosa	110.475	5.438	0.377	13.288
Oso Grande × Oso Grande	-190.041	-13.554	-0.234	-21.835
Oso Grande × Dover	-5.464	-0.250	-0.078	4.768
Oso Grande × Sweet Charlie	142.825	7.189	0.670	-1.932
Oso Grande × Milsei Tudla	32.458	-2.852	0.267	28.738
Dover × Dover	-153.844	5.862	2.992	-29.942
Sweet Charlie × Sweet Charlie	-417.303	-18.280	-1.048	-18.177
Sweet Charlie × Milsei Tudla	57.951	5.962	-0.054	-1.166
Sweet Charlie × Festival	-79.550	-4.475	-0.458	-3.488
Sweet Charlie × Camarosa	-354.184	-18.290	-1.536	4.654
Milsei Tudla × Milsei Tudla	-329.182	-15.293	-0.584	-27.571
Festival × Festival	-161.118	-11.890	-1.174	4.045
Camarosa × Camarosa	-263.154	-10.394	0.083	-17.942

Note. TM: total mass, NCF: number of commercial fruits, AFM: average fruit mass, NNCF: number of non-commercial fruits.

For the trait TM, the greatest SCA effects were observed in hybrids from 'Aromas' × 'Camarosa' and 'Oso Grande' × 'Sweet Charlie' crossbreeds (Table 5). It should be noted that the 'Aromas' × 'Camarosa' crossbreed had parents with the best positive GCA estimates (Table 4). In addition, this combination has the cultivar 'Aromas' as a parent, which is known for high productivity in the field (Gecer et al., 2013). Even parents with low GCA may have high SCA values, such as 'Oso Grande' × 'Sweet Charlie'. Probably such parents complement each other well due to most favorable alleles in different gene locations, and when such parents crossed, progenies arise with combinations of these complementary favorable alleles (epistatic gene effects). Although it did not present positive GCA values for TM, 'Oso Grande' cultivar contributes with a lower percentage of non-commercial fruits (Cruz et al., 2012).

The SCA estimates for NCF indicate that hybrids with the greatest positive effects were 'Aromas' × 'Festival', 'Aromas' × 'Camarosa', 'Oso Grande' × 'Sweet Charlie', and 'Sweet Charlie' × 'Milsei Tudla' (Table 5). The parents 'Aromas', 'Camarosa' and 'Festival' expressed positive GCA estimates (Table 4). In this respect, NCF is one of the most desired traits by producers and breeders for the in natura (fresh) fruit market. The cultivars 'Aromas', 'Camarosa' and 'Festival' showed positive GCA values for NCF in these hybrid combinations should be prioritized in improvement programs.

Regarding trait AFM, the best hybrid combinations were observed in crossbreds, 'Festival' × 'Aromas', 'Aromas' × 'Camarosa', 'Oso Grande' × 'Sweet Charlie' and 'Dover' × 'Dover'. The parents 'Aromas', 'Oso Grande', 'Festival' and 'Camarosa' are considered as good parents, with positive GCA estimates. The hybrids produced from these parents represented better than expected based on the GCA of their parents. According to Masny et al. (2016), crossbreeds involving the use of parents characterized by high GCA estimates for a given characteristic considerably increase the probability of obtaining hybrid progenies with the desired values of the given characteristic.

Regarding the trait NNCF, the highest estimated values of SCA occurred for the crossbreeds between 'Oso Grande' × 'Tudla', 'Aromas' ×'Dover', Aromas' × 'Sweet Charlie 'and' Aromas' × 'Camarosa'. These combinations were expected as the best, because of their parents with the highest positive values of GCA for NNCF ('Dover', 'Aromas', 'Sweet Charlie' and 'Camarosa).

Considering all the agronomic traits for commercial fruit production, the 'Camarosa' and 'Aromas' cultivars stand out indicating a higher concentration of favorable alleles. In addition, they complement each other well because they have positive SCA, which makes these cultivars promising for the continuity of improvement programs (Tables 4 and 5).

Masny et al. (2016) studied genetic parameters of strawberry and observed superior performance of progenies obtained from the 'Camarosa' cultivar, and included the 'Camarosa' × 'Aromas' among the promising crossbreeds. Masny et al., (2016) also reported that, among the crossbreeds obtained from 13 parents, those with the highest average annual yield were 'Camarosa' × 'Aromas', 'Camarosa' × 'Albion', 'Camarosa' × 'Figaro', 'Camarosa' × 'Salsa'.

The GCA and SCA effects of the parents are helpful to provide important information on the genetic value of the parents for the characteristics of interest, and determining their usefulness in crop improvement programs for commercial fruit values in gooseberry (Pluta et al., 2014).

The strawberry improvement programs aim to improve both fruit production and quality, because these characteristics have great importance in the acceptance of the fruit by the consumers and commercial markets. For this set of variables as presented in Table 6, GCA was significant for all the traits pH, AL, AW and ES predominated with additive effects, while and SCA was significant for TSS, TA, TSS/TA ratio, SP, TP, Fi and IS showed a predominance of non-additive effects. The traits TS and Sh did not significant differ for GCA.

Table 6. Estimates of the general combining ability effects for the physical and chemical characteristics evaluated in seven strawberry parents

Effect	**Physical And Chemical Characteristics**												
	pH	**TSS**	**TA**	**TSS/TA**	**TS**	**SP**	**TP**	**Fi**	**AL**	**AW**	**Sh**	**ES**	**IS**
Aromas	-0.039	-0.06	-0.017	-0.064	-0.592	1.273	13.837	0.172	-1.458	-0.900	-0.025	0.423	-0.19
Oso Grande	0.121	0.031	0.019	-0.197	-0.986	-0.437	8.657	-0.120	1.198	1.452	-0.533	-0.25	-0.03
Dover	-0.086	0.096	0.031	0.044	0.049	-1.298	-45.331	-0.148	-2.041	-1.933	0.382	-0.15	0.298
Sweet Charlie	0.016	0.591	-0.033	0.857	1.054	-5.359	14.370	0.045	-2.063	-0.878	-0.572	-0.32	-0.36
Milsei-Tudla	-0.025	-0.86	-0.033	-0.695	1.025	-5.355	-29.939	-0.003	4.200	-0.118	1.321	-0.38	0.205
Festival	0.037	-0.16	0.049	-0.461	1.646	-6.600	30.717	0.033	5.423	4.271	0.427	0.205	0.265
Camarosa	0.015	-0.45	-0.024	-0.043	0.359	18.421	-9.463	-0.153	3.322	1.720	0.311	-0.12	0.401
MS_{GCA}	0.253^{**}	4.872^{**}	0.035^{*}	5.997^{**}	41.510^{**}	2472.35^{**}	29678^{**}	0.537^{**}	278.06^{**}	149.3^{**}	11.03^{**}	5.34^{**}	2.02^{**}
MS_{SCA}	0.024^{**}	4.070^{**}	0.044^{**}	8.547^{**}	16.41^{NS}	3530.0^{**}	17314^{*}	0.306^{**}	76.27^{**}	74.69^{**}	2.071^{NS}	1.81^{**}	1.69^{**}
R^2-GCA	0.848	0.395	0.301	0.276	0.579	0.276	0.498	0.488	0.665	0.521	0.744	0.616	0.394
R^2-SCA	0.151	0.60	0.698	0.723	0.420	0.723	0.50	0.511	0.334	0.478	0.255	0.383	0.605

Note. TSS: total soluble solids, TA: titratable acidity, TS: total sugars, SP: soluble pectin, TP: total pectin, Fi: firmness, AL: average length, AW: average width, Sh: shape, ES: external staining, IS: internal staining, MS_{GCA}: Middle Square of general combining ability, MS_{SCA}: Middle Square of specific combining ability, R^2-GCA: Determination coefficient of general combining ability, R^2-SCA: Determination coefficient of specific combining ability. ** significant at 1% by the F test.

The 'Dover' and 'Sweet Charlie' cultivars were the only ones that provided a positive effect for the TSS/TA variable indicating the sugar/acid balance of the fruit contributingto the sweet taste, making it one of the most important aspects of quality.

For the ES variable, only the cultivars 'Aromas' and 'Festival' obtained positive effects. This result corroborates to that obtained by Souza et al. (2017), in which the cultivars 'Aromas', 'Dover' and other 38 hybrids were similar to each other and showed a more intense red staining. Staining is the first characteristic observed in strawberries intended for in natura consumption and often predetermines the consumer's expectation of taste and quality (Moura et al., 2012).

The cultivars 'Aromas' and 'Camarosa' showed positive effects for SP, that the higher the SP content, the lesser the Fi of fruits. When it aims at in natura consumption, one of the quality attributes sought by the market is the high firmness of fruits, because it influences the commercialization and is directly related to better visual appearance, storability for long-term and long distance marketing (Brackmann et al., 2011). Thus, fruits that show less firmness can cause low resistance to damage during transport, handling and storage (Fagundes & Yamanishi, 2001), besides shortening the shelf life and quality.

SCA estimates for the crossbreed between 'Aromas' × 'Sweet Charlie' had positive effects for all traits, except for TS and Fi. This crossbreed had the best positive effects for pH, SP, AL and AW (Table 7).

For the TP variable, the highest positive SCA estimate was found in the crossbreed between 'Dover' × 'Dover', while the crossbreed between 'Camarosa' and 'Camarosa' had the highest negative effect. The F_1 hybrid between 'Oso Grande' and 'Sweet Charlie' showed the best positive effect for TSS/TA ratio.

The results of the genetic parameters estimated in this study by evaluating a huge number of commercial fruit yield and quality traits, will allow a better direction for selection of promising F_1 hybrids in the sequence of the strawberry improvement program for the southern region of the Minas Gerais state in Brazil.

Table 7. Estimate of the specific combining ability effects for the physical and chemical characteristics evaluated in seven strawberry parents

Effects	**Physical And Chemical Characteristics**												
	pH	**TSS**	**TA**	**TSS/TA**	**TS**	**SP**	**TP**	**Fi**	**AL**	**AW**	**Sh**	**ES**	**IS**
Aromas × Aromas	0.084	-1.086	0.0701	-1.540	1.226	-23.109	32.021	-0.119	3.326	1.516	-0.789	-0.717	0.201
Aromas × Oso Gr.	0.022	-0.407	0.056	-1.014	0.1001	-11.303	18.798	0.015	-1.133	-2.040	0.328	0.013	0.419
Aromas × Dover	-0.022	0.206	-0.0007	0.222	0.212	-6.051	-4.054	0.044	-1.230	-1.102	-0.048	-0.165	-0.067
Aromas × Sweet C.	0.101	0.133	0.025	0.023	-0.961	55.633	20.974	-0.318	7.571	6.957	0.138	0.948	0.23
Aromas × Festival	-0.014	0.077	-0.036	0.383	0.105	4.216	-37.628	0.083	0.428	2.386	-0.041	0.140	-0.297
Aromas × Camar.	0.007	-0.065	-0.036	0.315	-0.527	9.423	13.769	-0.095	1.375	0.667	-0.153	0.063	-0.093
Oso G. × Oso Gr.	-0.158	0.029	-0.054	0.685	7.544	-6.327	95.221	0.377	-2.197	0.551	0.546	-0.042	-0.079
Oso G. × Dover	0.047	-0.378	0.002	-0.372	-0.479	17.448	-4.160	-0.130	2.433	2.465	0.188	0.346	0.207
Oso G. × Sweet C.	-0.045	0.540	-0.059	1.081	-0.190	-4.878	-28.904	0.108	-1.180	-0.264	-0.503	-0.127	-0.548
Oso G. × Tudla	-0.027	0.845	0.018	0.866	-0.394	2.860	23.938	-0.142	1.063	-0.004	-0.174	-0.80	-0.219
Dover × Dover	0.088	-1.419	-0.008	-1.918	-0.458	-28.535	155.239	0.241	6.472	2.653	-0.765	0.644	-0.453
Sweet C. × Sweet C.	0.042	-0.379	0.031	-0.566	-3.018	10.236	87.894	-0.175	2.035	1.781	0.695	-0.044	0.913
Sweet C. × Tudla	0.019	-1.149	-0.061	-0.877	0.213	-6.102	-12.557	0.093	0.249	0.617	0.621	0.537	0.138
Sweet C. × Festival	0.034	-0.153	0.088	-0.818	0.538	-6.219	54.337	-0.213	-0.282	-2.975	0.149	-0.270	0.511
Sweet C. × Camar.	-0.026	-0.331	0.105	-1.355	1.369	-18.954	-26.587	0.247	-3.297	-1.366	0.517	-0.602	0.449
Tudla × Tudla	0.006	2.061	0.191	0.911	0.330	15.828	-21.584	0.056	-4.191	-2.456	-1.962	0.250	0.103
Festival × Festival	-0.060	0.142	-0.163	1.072	-4.281	-4.851	50.260	0.448	-2.587	-6.006	-0.474	0.218	-0.087
Camaro. × Camaro.	-0.014	1.780	0.123	0.275	2.220	-56.215	-85.475	0.403	-6.616	-3.914	0.286	1.042	-0.228

Note. TSS: soluble solids, TA: titratable acidity, TS: total sugars, SP: soluble pectin, TP: total pectin, Fi: firmness, AL: average length, AW: average width, Sh: shape, ES: external staining, IS: internal staining. ** significant at 1% by the F test.

4. Conclusions

For most traits, the broad sense heritability values were medium to high. It is expected higher genetic gains in the selection of traits TM, and NCF related to fruit production, TSS/TA for fruit flavor, IS and ES for fruit marketability, where high heritability values were observed.

The analysis of GCA and SCA of the studied cultivars indicates the potential of the hybrids developed from them. For the traits related to production, the cultivars ‘Camarosa’ and ‘Aromas’ stood out as promising in the improvement program. For flavor, the cultivars ‘Dover’ and ‘Sweet Charlie’ were the most promising.

There are strong and favorable genetic correlations for some pairs of characteristics that may allow indirect selection.

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