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Breeding potential of raspberry primocane selections based on their combining abilities

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ABSTRACT

Information on the genetic potential of raspberry genotypes for their use in breeding programs is currently limited. We used a diallel mating design to study the breeding values of raspberry primocane fruiting cultivars in terms of their combining ability. The objectives of this study were: to identify raspberry genotypes with high general combining ability (GCA) for use in cultivar development, to detect the best crosses in terms of their specific combining ability (SCA), and to determine the gene-action type and heritability of yield and eight of its components. The obtained results showed that the parent cultivar MRSL exhibited the highest GCA effects for the total yield per plant, fruit weight, number of fruit per plant, fruit length, fruit diameter, and number of drupelets per fruit. Genotype C47 had good GCA for the number of canes per plant and plant height, and TD-865 had high GCA for high soluble solids content. The narrow-sense heritability estimates were low to moderate (0.00 to 0.62) for most of the traits, with the soluble solids content exhibiting the highest heritability value.

Keywords: Heritability; GCA; SCA; *Rubus idaeus*; Raspberry breeding.

Abbreviations: GCA, general combining ability; SCA, specific combining ability (SCA); σ^2_D, dominance genetic variance; σ^2_A, additive genetic variance; h^2, Narrow-sense heritability.

INTRODUCTION

Raspberry (*Rubus idaeus* L.) is one of the most important berries grown in Mexico, because of the high levels of production and export. In 2013, it was cultivated in over 2078 ha of land, producing a total of 30 410.94 t of fruit [Servicio de Información Agroalimentaria y Pesquera (SIAP) 2013]. Mexico is ranked as the sixth largest raspberry producer in the world and is one of the leading exporters of raspberry to Europe and the USA [Food and Agriculture Organization (FAO) 2012]. The international raspberry trade consists of two distinct supply chains: one for fresh raspberries, and the other for processed raspberries. The vast majority of Mexico's raspberry production is exported to the USA for fresh consumption and only a small proportion is destined for the national market (SIAP 2013). Between 2000 and 2012, the raspberry productivity of Mexico increased dramatically by 100% because of the introduction of high-yielding varieties (Weber 2013), better field production practices and substantial growth in the land area dedicated to raspberry production (SIAP 2013).

Raspberry breeders largely focus on improving fruit quality and achieving higher yields. However, disease resistance and adaptation to particular growing conditions are also important targets in developing new cultivars. Selection of appropriate parents to be used in a plant breeding program is one of the most important decisions a breeder has to make (Acquaah 2007). However, the performance of the parents is not always a reliable parameter for selection (Hallauer 1990). Therefore, to obtain progeny with desirable genes, it is necessary to know the combining ability of the candidate parents which will be used into the improvement program.

The terms general combining ability (GCA) and specific combining ability (SCA) were introduced by Sprague and Tatum (1942). GCA is estimated as the average performance of a line in hybrid combinations, while SCA measures the performance of a cross of two parents in a specific combination in comparison with other cross combinations (Acquaah 2007). Information on the relative importance of GCA and SCA is of great value in a breeding program, since GCA estimates the magnitude of the additive portion of the genetic effect, while SCA is a metric for the contribution of non-additive gene effects to the total genetic variance (Falconer and Mackay 1996). Several techniques have been developed for estimating combining ability effects, e.g., diallel, partial diallel, and line × tester analysis. Diallel analysis is conducted to estimate various genetic parameters, such as the GCA of lines, SCA of crosses, dominance variance (σ^2_D), additive variance (σ^2_A), epitasis variance (σ^2_I), dominance degree, and heritability for the trait of interest (Griffing 1956).

The aim of this study was to assess the GCA of eight raspberry parents crossed in a diallel mating scheme, assessing the parents and one set of F1s in one direction, on the basis of yield and eight of its components. An additional aim was to understand the inheritance and gene action of the measured traits.

MATERIALS AND METHODS

Plant Materials and Field Experiment

Eight raspberry primocane selections labeled as C65, C47, TD865, MRSL, MU1, JG, JJ24, and C57, were crossed manually in an 8 x 8 diallel mating design to produce 28 non-reciprocal F1 sibling families. The parental selections were selected on the basis of their yield and fruit quality during previous evaluations carried out in 2013 and 2014.

Following scarification and stratification performed following the methodology described by Clark et al. (2007), a total of 104 seedlings per family were planted in field to represent the range of phenotypic diversity present in each biparental cross. Because of their high light requirements, the seeds were initially sown on the surface of pots with minimal covering on Jun 31, 2015, and the seedlings were subsequently transplanted on Sep 20, 2015.

Evaluation of the crosses and parents was conducted at Ziracuaretiro, Michoacán, Mexico, during the 2015 season. The parents and their F1 families were transplanted to the open field in a randomized complete blocks design with four replications. Each replication consisted of 26 plants in one 25-m-long row, with 1 m plant-to-plant distance and 2.5 m between the replication rows. All maintenance procedures during the vegetative period were carried out in accordance with the standard recommendations for the commercial plantations of raspberries.

Data Collection

At the end of the growing season, each plant was scored on nine characteristics over a period of two months. Characteristics related to vegetative vigor, i.e., plant height (cm) and number of canes, were scored during the flowering stage. Fruit weight (g), fruit diameter (mm), and fruit length (mm) were determined from a sample of five berries per plant, which were collected once a week during the harvest period. The number of drupelets was measured 10 times during the season by counting the drupelets from 10 berries per plant in each plot. Number of fruit per plant and total yield per plant (g) were measured by counting and weighing the total number of ripe fruit every four days throughout the season. Using the same sample of fruits used for berry weight, the mixed fresh juice from this sample was used to determine the soluble solids content (°Bx), which was measured once a week during the harvest period..

Statistical Analysis

Prior to the assessment of GCA and SCA effects, the mean of each plot consisting of 26 plants was computed and used to check the assumptions of normality and homogeneity of variance. The distributions of the data collected, as well as the homogeneity of variances, were assessed using Shapiro–Wilk and Levene's tests, respectively. The tests were performed on the SAS program [Statistical Analysis System (SAS) Institute 2012] and R program [R Core Team 2013].

Analysis of variance was conducted under a mixed model, where the genotypes were considered as fixed effects and replications as random effects. Calculations of GCA and SCA were carried out as outlined by Griffing (1956) for a diallel mating scheme with parents and F1s in one direction (Method 2, Model 2). The modified program DIALLEL-SAS was employed for the estimation of both GCA and SCA effects (Zhang and Kang 2003). This last statistical analysis was performed with SAS 9.3 (SAS 2012) under the general linear model procedure. Thus, the following statistical model was used for data analysis:

$$Y_{ijl} = \mu + b_l + g_i + g_j + s_{ij} + e_{ijl} \quad (1)$$

where Y_{ijl} is the mean from each plot, μ is the population mean, b_l is the replication effect, g_i is the GCA effect of parent i, g_j is the GCA effect of parent j, s_{ij} is the SCA effect of the hybrid ij, and e_{ijl} is the random residual effect.

Genetic variance components were calculated based on the appropriate mean square terms given in Table 1. Mean squares were estimated using the means for each plot and considering four replications per entry.

$$\sigma_E^2 = MS_E \quad (2)$$

where σ_E^2 is the environmental variance, and MS_E is the mean squares of error.

Additive and dominance genetic variances ($\sigma^2{}_A$ and $\sigma^2{}_D$) were calculated according to Griffing (1956):

$$\sigma_A^2 = 2(\sigma_{GCA}^2) = 2\frac{(MS_G - MS_S)}{(n+2)} \quad (3)$$

$$\sigma_D^2 = \sigma_{SCA}^2 = MS_S - MS_E \quad (4)$$

where MS_G is the mean squares of GCA effects, MS_S is the mean squares of SCA effects, MS_E is the mean squares of error, and n is the number of parents.

Considering to individual plant as the reference unit, heritability values were computed according to Holland et al. (2003):

$$h^2 = \frac{\sigma_A^2}{\sigma_F^2} \quad (5)$$

where h^2 is the narrow sense heritability, σ_A^2 is the additive variance, and σ_F^2 is calculated as $\sigma_A^2 + \sigma_D^2 + \sigma_E^2$.

Finally, Pearson's correlation coefficients were estimated employing the plot means. Estimations were computed using SAS 9.3 (SAS 2012).

RESULTS

Analysis of Variance, Gene Action, and Heritability

The analysis of variance detected significant differences among genotypes for all traits. The GCA and SCA were also significant for all characteristics studied (Table 2). The significance of the mean squares among genotypes for all the traits studied indicated the presence of a wide range of genetic variability among the parents and crosses. The significance of both GCA and SCA effects indicated the equal importance of additive and non-additive gene actions (Table 2). Moreover, it was noticed that the mean squares due to replications were not significant for any of the traits, indicating that the blocks effect was homogeneous among the plots.

The estimated variances of the nine traits measured in the population of eight parents and their F1 hybrids are presented in Table 3. Non-additive gene effects were found to be were more pronounced in the inheritance of traits than the additive gene effects, since the values for the variance due to SCA (σ^2_{SCA}) were higher than those due to GCA (σ^2_{GCA}). These results are supported by the ratio of GCA to SCA, which was smaller than 1. In general, dominance genetic variance (σ^2_D) had higher values than additive genetic variance (σ^2_A) for most of the characters, i.e., total yield per plant, fruit weight, number of fruit per plant, number of canes, fruit length, fruit diameter, number of drupelets per fruit, and plant height. The σ^2_A of soluble solids content exhibited a higher value than that detected for σ^2_D.

To determine the phenotypic variation due to genetic factors, narrow-sense heritability was estimated for all studied characteristics. Heritability estimates were moderate or low, ranging from 0.00 to 0.62 (Table 3). Soluble solids content had the highest heritability value (0.62) of all the traits. Heritability estimates for total yield per plant, fruit weight, fruit length and fruit diameter were found to be moderate, with values of 0.22, 0.48, 0.34, and 0.23, respectively, while traits such as the number of fruit per plant, number of canes, number of drupelets per fruit and plant height exhibited low heritability values.

General and Specific Combining Ability Effects

The values of GCA for the studied traits are presented in Table 4. C65 was observed to have a high GCA effect in the desirable direction for the number of canes and plant height, while C47 was a good combiner for total yield per plant, number of fruit per plant, number of canes, fruit length, soluble solids content, and plant height. Selection TD865 combined well for fruit weight, fruit length, fruit diameter, soluble solids content, number of drupelets per fruit and plant height. MRSL was a good combiner for total yield per plant, fruit weight, number of fruit per plant, number of canes, fruit length, fruit diameter, and number of drupelets per fruit. MU1 combined well for total yield per plant, number of fruit per plant, number of canes, fruit length, fruit diameter, soluble solids content, and number of drupelets. JG combined well only for plant height, and JJ24 for soluble solids content, while C57 was a good combiner only for number of drupelets.

The SCA is an indication of the mean performance for a specific cross and represents dominance and epistatic gene effects. The SCA effects of the 28 sibling families for all the traits investigated are shown in Table 5. The estimated SCA effects revealed that the best hybrid combinations were: C47 × C57 for yield per plant, MRSL × C57 for fruit weight, TD865 × MU1 for number of fruit per plant, MRSL × JG for number of canes, C47 × C57 for fruit length, MRSL × JG for fruit diameter, C47 × C57 for soluble solids content, TD865 × C57 for number of drupelets, and MU1 × C57 for plant height.

Correlation among Quantitative Traits

Significant correlations ($P \leq 0.05$) were observed among the nine traits (Table 6). For yield per plant, strong positive correlations were found with number of fruits per plant (r = 0.92), fruit length (r = 0.52) and fruit diameter (r = 0.50), whereas those with fruit weight, number of canes per plant and number of drupelets per fruit were significantly moderate. Notable positive correlations were found between fruit weight and number of fruits per plant (r = 0.22), fruit length (r = 0.49) and fruit diameter (r = 0.38). In addition, fruit weight was also negatively correlated with plant height (r = -0.27). We also found positive correlations with magnitudes from high to low between number of fruits per plant, number of canes per plant, fruit length, fruit diameter and number of drupelets per fruit.

DISCUSSION

This work is very important for the genetic improvement of the raspberry stock, since information about the genetic potential of raspberry genotypes for their use in breeding programs based on diallel crosses is currently scarce. The obtained results indicate that in the diallel crosses among eight raspberry parents, the non-additive gene action had a predominant role in the expression of the most of studied characteristics, since the estimated SCA variance was found to be larger than the GCA variance for total yield per plant, fruit weight, number of fruit per plant, number of canes, fruit length, fruit diameter, total soluble solids, number of drupelets per fruit, and plant height. This may suggest that hybridization by crossing selections followed by recurrent selection of superior segregants is the procedure that must be chosen by the plant breeder to obtain superior raspberry varieties. However, the mean squares for SCA and GCA were also found to be statistically significant via analysis of variance, indicating the occurrence of both non-additive and additive gene action in the studied traits. Such importance of non-additive and additive gene action was also reported by Dosset et al. (2008), who found that dominance, epistasis, and additive gene action played important roles in the inheritance of phenological, vegetative, and fruit chemistry traits in black raspberry.

Heritability is an important genetic parameter for calculating the expected gain per selection. In this study, narrow-sense heritability estimates varied from low to moderate, indicating that non-additive gene action appeared to govern the inheritance of yield and its components. Such results were in agreement with the findings of Stephens et al. (2012*a*), who obtained moderate or low heritability values for total yield per plant (0.25), number of fruit per cane (0.39), plant height (0.23), and number of canes per plant (0.20). In another study, Stephens et al. (2012*b*) also reported that narrow-sense heritability was moderately high for soluble solids content (0.73). For fruit size, Dosset et al. (2008) found low heritability (-0.10), while Connor et al. (2005) reported high heritability for fruit weight (0.63), in contrast to the moderate value we found (0.48). The genetic advance achieved through selection depends on three factors: total phenotypic variation into the population in which selection will be conducted, heritability of a trait of interest and the selection pressure (Molina 1992). In the present study, large amounts of phenotypic variance were observed for yield per plant, number of fruits per plant, number of drupelets per fruit and plant height, however, their heritability values were low. Such results obtained suggest that the breeder should impose a low selection pressure in order to archive a significant genetic advance in such traits. In contrast, in berry weight and soluble solids content, a considerable amount phenotypic variance as well as a moderate heritability, were observed for both traits, indicating selecting for improved berry weight and soluble solids content will likely produce a greater genetic advance than in yield.

A relationship between the genetic variance and heritability was observed in this study. Characteristics with low heritability values were found to have large dominance variance, while for traits with moderate heritability, such as soluble solids content, additive variance was larger than dominance variance. Similar results have been reported in other major crops, such as tomato (El-Gabry et al. 2014) and maize (Ketthaisong et al. 2014), where traits that had low heritability also exhibited dominance variance that was higher than additive variance.

Although each program has specific goals depending on the agricultural modernization and climate of the region, yield and fruit quality are common goals that breeders have identified as a primary focus. The yield is a complex trait which is highly influenced by the environment and hence indirect selection through component traits would be an advisable strategy to increase the efficiency of selection (Acquaah, 2007). Table 6 shows that yield per plant positively correlated with six yield components, indicating selection for number of fruits per plant, fruit weight, number of canes per plant, fruit length, fruit diameter and number of drupelets per fruit will aid selection for higher yield. These results are consistent with the results of Stephens et al. (2012*a*), who found that yield was associated with fruits number per plant and number of canes.

We found that number of drupelets per berry was associated with berry size-related traits such as fruit weigh, length and diameter. This result suggests that the number of drupelets per fruit present during previous stages to the fruit maturation may be a good predictor of fruit size. Similar positive associations has also been reported in blackberry (Strik et al., 1996), and raspberry (Milivojević et al., 2011), where cultivars presenting a high number of drupelets also exhibited a large fruit.

Previous studies reported a weak positive correlation between soluble solid content and yield. Stephens et al. (2012*a*), in raspberry, reported a positive and low correlation (r = 0.14), whereas Whitaker et al. (2012) detected a moderate negative correlation (r = -0.21) for both traits. In our study, the yield had a low non-significant correlation with soluble solid content; thus, directional breeding will not affect one trait favorably and the other adversely.

The estimation of GCA effects on parental genotypes for specific characteristics of agricultural importance can guide the plant breeder in the selection of raspberry parental genotypes. Multiple studies have reported significant GCA effects in some economically important berries such as black raspberry (Dosset et al. 2008), strawberry (Kaczmarska et al. 2016) and red raspberry (González 2016). In the present study, yield per plant exhibited a broader magnitude of GCA effects that the rest of traits, with values ranging 22.80 % lower and 39.04 % higher than the mean. In contrast, traits as fruit length (9.09 - 17.32 %), fruit diameter (8.04 – 16.52 %), soluble solids content (11.59 – 7.51 %), number of drupelets per fruit (-10.96 – 12.48 %) and plant height (12.92 – 10.31 %) had a low magnitude of GCA effects. Furthermore, the combining ability analysis also revealed that none of the parental genotypes exhibited GCA effects in the desirable direction for all of the traits studied. However, some parents showed strong GCA effects simultaneously for a majority of the traits, suggesting that parental genotypes such as MRSL and MU-1 may be utilized as important donor parents in a selective breeding program for enhancing raspberry fruit size and yield in elite materials. MRSL was found to be a particularly valuable parent because of its positive GCA effect for the number of fruit per plant, total yield per plant, fruit weight, and fruit size. However, its progeny exhibited intermediate to low soluble solids content, as well as low plant height. Even though flavor in raspberries is one of the most important traits for the fresh fruit market, MRSL could still contribute to improving the yield and fruit size of cultivars, since large fruit and high yields are preferred by both consumers and growers. Genotype MU-1 had a good GCA for most traits, i.e. total yield per plant, number of fruit per plant, number of canes per plant, fruit length, fruit diameter, soluble solids content, and number of drupelets per fruit. However, its progeny had an intermediate fruit size. Nevertheless, the high positive GCA effect for soluble solids content exhibited by this genotype could be utilized for developing highly desirable progeny with an enhanced expression of sweetness.

The parents C47 and C57 were involved in crosses with the highest SCA values for total yield per plant, fruit weight, number of canes, fruit length, fruit diameter, total soluble content, number of drupelets, and plant height. Consequently, these parents could be used as donors for breeding programs seeking to develop some of the traits studied in the present investigation. In contrast with the findings of Kumari et al. (2015), who found that none of the F1 hybrids had all of the desirable traits, our results showed that the F1 progeny C47 × C57 had positive SCA effects for all characters. This indicates that it is possible to obtain raspberry hybrids exhibiting only positive SCA effects. In addition, such results suggest that this cross could be used to produce new cultivars or a source population for hybridization, followed by recurrent selection, since dominance genetic effects were more pronounced in the inheritance of the vegetative and fruit traits investigated in this study.

Based on the SCA results, we can conclude that some of the best hybrid combinations resulted in crossing a parent with a high GCA effect with another parent with a low GCA effect in the desirable direction. This implies that the best hybrid combinations can be obtained not only from the combination of 'good' × 'good' GCA combiners, but also from the combinations of 'bad' × 'bad' and 'good' × 'bad' GCA combiners. Therefore, the predicted performance of F1 progeny, estimated on the basis of the GCA effects of the parents, is not a reliable parameter. The results obtained in crosses with significant positive SCA effects involving 'bad' × 'bad', or 'good' × 'bad' general combiners as parents may be attributed to the presence of non-allelic interactions (Singh et al. 2014) and to the genetic diversity in the form of a number of heterozygous loci of the parents involved in the cross combinations with a high positive GCA effect (Kumar et al. 2006). On the other hand, the low SCA effects showed by hybrids derived from parents with high GCA effects can be attributed to complementary gene action (Kumari et al. 2015).

In conclusion, this study elucidated the genetic potential of eight primocane raspberry parents. It also shed some light on the type of gene action controlling the inheritance of yield and some of its characteristics in raspberries. Non-additive gene action was more important than additive gene action in all characteristics studied, suggesting that hybridization may be utilized to create F1 raspberry cultivars from which the breeder can make superior selections. Genotypes MRSL and MU-1 had a good GCA for most traits, and these genotypes could serve as potential donors in a raspberry breeding program to enhance yield-related traits and yield in elite genotypes**.** The best hybrid combination was found to be C47 × C57, which showed positive SCA effects for all traits. Our results also indicate that superior crosses with good SCA are not necessarily derived from parents with good GCA.

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Table 1. Analysis of variance for method II diallel design.

Source of variation	Degrees of freedom	Mean squares	Expected mean squares
Replications	r-1	MS_R	$\sigma^2_E + n\sigma^2_B$
Genotypes	(n+s)-1	MS_H	$\sigma^2_E + r\sigma^2_H$
General combining ability	n-1	MS_G	$\sigma^2_E + r\sigma^2_{SCA} + r[(n+2)\sigma^2_{GCA}]$
Specific combining ability	[n(n-1)]/2	MS_S	$\sigma^2_E + r\sigma^2_{SCA}$
Error	Difference	MS_E	σ^2_E
Total	[(s+n) x r]-1		

Note: Number of replications or blocks (r); Number of parents (n); Number of families (s); Mean square of replications (MS_R); Mean square of genotypes (MS_H)Mean square of general combining ability (MS_G); Mean square of specific combining ability (MS_S); Mean square of error (MS_E); Environmental variance (σ^2_E); Replication variance (σ^2_B); Specific combining ability variance (σ^2_{SCA}); General combining ability variance (σ^2_{GCA}).

Table 2. Mean squares of nine quantitative characteristics evaluated in diallel analysis.

Source	d.f.	Yield/plant		Fruit weight		Number. of fruits per plant		Number of canes per plant		Fruit length		Fruit diame ter		Soluble solids content		Number of drupelets per fruit		Plant height	
Replication	3	3291.05		0.33		438.24		1.21		0.02		0.00		0.88		67.32		12.39	
Genotypes	35	167670.63	***	11.64	***	12198.67	**	38.39	**	0.63	***	0.61	***	5.74	***	2007.30	**	7612.26	***
GCA	7	312966.14	***	33.96	***	9610.18	***	34.91	**	1.49	**	1.16	***	19.88	***	2499.38	***	13074.44	***
SCA	28	131346.76	***	6.06	***	12845.79	***	39.27	***	0.42	***	0.47	***	2.21	***	1884.28	***	6246.72	***
Error	105	5029.17		0.21		462.43		1.00		0.01		0.01		0.41		42.36		418.01	

Note: General combining ability (GCA); Specific combining ability (SCA); degrees of freedom (d.f.)

, * indicate s significant difference at $P \leq 0.01$ and 0.001, respectively.

Table 3. Estimation of genetic variance components for yield and 8 yield-related characteristics evaluated on eight parental genotypes of raspberry and their F_1 progeny.

Parameters	Yield per plant	Fruit weight	Number of fruits per plant	Number of canes per plant	Fruit length	fruit diameter	Soluble solids content	Number of drupelets per fruit	Plant height
σ^2_E	5 029.17	0.21	462.43	1.00	0.01	0.01	0.41	42.36	418.01
σ^2_{SCA}	126 317.59	5.85	12 383.37	38.26	0.41	0.46	1.79	1 841.92	5 828.70
σ^2_{GCA}	18 161.94	2.79	-323.56	-0.44	0.11	0.07	1.77	61.51	682.77
σ^2_D	126 317.59	5.85	12 383.37	38.26	0.41	0.46	1.79	1 841.92	5 828.70
σ^2_A	36 323.88	5.58	-647.12	-0.87	0.22	0.14	3.54	123.02	1 365.55
σ^2_F	167 670.63	11.64	12 198.67	38.39	0.63	0.61	5.74	2 007.30	7 612.26
h^2	0.22	0.48	0.00	0.00	0.34	0.23	0.62	0.06	0.18
$\sigma^2_{GCA}/\sigma^2_{SCA}$	0.14	0.48	-0.03	-0.01	0.26	0.15	0.99	0.03	0.12

Note: Environmental variance (σ^2_E); Specific combining ability variance (σ_{SCA}); General combining ability variance (σ^2_{GCA}); Dominance genetic variance (σ^2_D); Additive genetic variance (σ^2_A); Phenotypic genetic variance (σ^2_F); Narrow-sense heritability (h^2).

Table 4. Values of GCA for eight parental genotypes of raspberry.

Selection	Yield per plant (g)	Fruit weight (g)	Number of fruits per plant	Number of canes per plant	Fruit length (mm)	Fruit diameter (mm)	Soluble solids content (°Bx)	Number of drupelets per fruit	Plant height (cm)
C65	-35.85 ***	-0.59 ***	-10.90 ***	0.12	-0.16 ***	-0.04 **	-0.09	-10.68 ***	9.00 **
C47	3.85	-0.13	12.03 ***	1.20 ***	0.02	0.00	0.64 ***	-1.74	20.73 ***
TD865	-3.67	0.14 *	-1.23	-1.64 ***	0.13 ***	0.01	0.84 ***	9.34 ***	9.47 **
MRSL	174.53 ***	2.14 ***	18.56 ***	0.40 **	0.40 ***	0.37 ***	-0.62 ***	12.16 ***	-26.55 ***
MU1	68.45 ***	0.00	18.34 ***	1.13 ***	0.02	0.03	0.53 ***	1.32	-6.24 *
JG	-101.92 ***	-0.39 ***	-25.24 ***	-0.38 *	-0.12 ***	0.00	-0.15	-7.67 ***	21.18 ***
JJ24	-18.29	-0.32 ***	-1.81	-0.31 *	-0.07 ***	-0.18 ***	0.15	-4.59 ***	-6.26 *
C57	-87.11 ***	-0.85 ***	-9.76 **	-0.54 ***	-0.21 ***	-0.18 ***	-1.28 ***	1.85	-21.34 ***
Mean	447.07	5.36	97.70	5.43	2.31	2.24	11.04	97.41	205.46
SE	10.49	0.07	3.18	0.15	0.01	0.02	0.09	0.96	3.02

Note: *, **, *** indicate significant difference at $P \leq 0.05$, 0.01 and 0.001, respectively.

Table 5. Values of SCA for twenty-eight F_1 hybrids of raspberry.

F_1 hybrid	Yield per plant (g)		Fruit weight (g)		Number of fruits per plant		Number of canes per plant		Fruit length (mm)		Fruit diameter (mm)		Soluble solids content (°Bx)		Number of drupelets per fruit		Plant height (cm)	
C65 × C47	41.60		0.16		3.73		1.46	**	0.00		0.00		-0.01		4.59		-67.88	***
C65 × TD865	72.27	*	-0.10		41.84	***	1.86	***	-0.09	*	-0.05		-0.96	**	-2.68		-0.67	
C65 ×MRSL	131.53	***	-1.55	***	53.70	***	3.02	***	0.39	***	0.60	***	0.47		23.92	***	-13.17	
C65 × MU1	-182.10	***	0.00		-43.98	***	-2.98	***	-0.02		-0.05		0.15		11.37	***	-51.25	***
C65 × JG	174.38	***	0.38		26.90	**	-3.80	***	-0.18	***	-0.26	***	-0.43		-3.99		-30.83	**
C65 × JJ24	112.63	***	0.09		33.18	***	-2.87	***	-0.15	**	-0.20	***	-0.20		0.55		79.36	***
C65 × C57	-274.95	***	0.33		-85.89	***	2.21	***	-0.04		-0.07		0.47		-38.48	***	57.99	***
C47 × TD865	-61.14		0.12		-27.24	**	-2.62	***	-0.35	***	-0.19	***	-0.22		-19.64	***	-34.93	***
C47 × MRSL	-294.73	***	-1.25	***	-72.48	***	3.09	***	-0.61	***	-0.61	***	-0.91	**	-21.35	***	-8.29	
C47 × MU1	48.74		0.12		86.98	***	-2.39	***	0.02		-0.09		-0.45		-10.23	***	24.74	**
C47 × JG	-184.99	***	-0.26		-62.78	***	-1.99	***	0.05		0.05		0.06		5.17		-51.67	***
C47 × JJ24	89.99	**	0.12		21.13	*	0.05		0.19	***	0.19	***	-0.59	*	1.01		39.52	***
C47 × C57	291.42	***	0.64	**	55.25	***	3.13	***	0.46	***	0.36	***	1.81	***	25.11	***	-35.94	***
TD865 × MRSL	-219.97	***	-0.19		-48.03	***	-1.07	*	0.48	***	0.23	***	0.34		-0.10		-40.95	***
TD865 × MU1	279.71	***	-0.14		111.64	***	2.65	***	0.02		-0.06		-0.92	**	-16.23	***	2.54	
TD865 × JG	61.98		-0.54	**	51.73	***	4.61	***	-0.14	**	-0.20	***	-1.31	***	-5.78		44.81	***
TD865 × JJ24	-188.53	***	-0.63	**	-51.21	***	-1.24	**	0.00		0.02		0.82	**	-18.10	***	-0.22	
TD865 × C57	-6.98		0.74	***	-56.12	***	-3.41	***	0.09		0.20	***	1.03	**	40.10	***	-17.17	
MRSL × MU1	82.42	**	-1.26	***	27.00	**	1.40	**	0.32	***	0.51	***	-0.20		26.65	***	12.94	

MRSL × JG	162.43 ***	-1.53 ***	54.34 ***	5.27 ***	0.53 ***	0.83 ***	-0.58 *	31.03 ***	8.90
MRSL × JJ24	-62.99	-1.70 ***	34.55 ***	0.25	-0.43 ***	-0.45 ***	1.49 ***	-11.84 ***	26.96 **
MRSL × C57	42.24	2.98 ***	-29.46 **	-6.09 ***	-0.81 ***	-0.97 ***	-0.32	-50.36 ***	15.84
MU1 × JG	-262.33 ***	1.28 ***	-79.93 ***	-2.07 ***	-0.42 ***	-0.34 ***	0.15	-35.79 ***	-4.28
MU1 × JJ24	193.54 ***	0.21	19.47 *	0.20	0.04	0.17 ***	-0.34	-24.96 ***	44.24 ***
MU1 × C57	-187.25 ***	-0.63 **	-81.20 ***	4.77 ***	0.07	-0.01	1.01 **	33.70 ***	121.50 ***
JG × JJ24	191.15 ***	0.54 **	64.96 ***	0.88	0.08	0.06	0.46	7.02 **	46.06 ***
JG × C57	-159.96 ***	0.01	-58.45 ***	-0.59	0.04	-0.08	0.87 *	3.63	-8.21
JJ24 × C57	-186.98 ***	1.55 ***	-77.31 ***	0.93	0.23 ***	0.19 ***	-1.03 **	31.26 ***	-51.01 ***
Mean	381.48	4.21	109.25	7.52	2.20	2.20	10.73	83.23	176.64
SE	32.15	0.21	9.75	0.45	0.05	0.05	0.29	2.95	9.27

Note: *, **, *** indicate significant difference at $P \leq 0.05$, 0.01 and 0.001, respectively.

Table 6. Phenotypic correlations among nine fruit and vegetative traits.

Trait	Yield/plant	Fruit weight	Number of fruits per plant	Number of canes per plant	Fruit length	Fruit diameter	Soluble solids content	Number of drupelets per fruit	Plant height
Yield/plant	1	0.35 ***	0.92 ***	0.33 ***	0.52 ***	0.50 ***	0.15 ns	0.35 ***	0.01 ns
Fruit weight		1	0.22 *	-0.05 ns	0.49 ***	0.38 ***	0.13 ns	0.24 *	-0.27 **
Number of fruits per plant			1	0.36 ***	0.40 ***	0.34 ***	0.22 ns	0.28 ***	0.08 ns
Number of canes per plant				1	0.30 **	0.39 ***	-0.10 ns	0.31 ***	-0.13 ns
Fruit length					1	0.92 ***	0.17 ns	0.78 ***	-0.20 ns
Fruit diameter						1	0.02 ns	0.74 ***	-0.19 ns
Soluble solids content							1	0.00 ns	0.24 ns
Number of drupelets per fruit								1	-0.20 *
Plant height									1

Note: *, **, *** indicate significant difference at $P \leq 0.05$, 0.01 and 0.001, respectively.