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PARÁMETROS GENÉTICOS Y MEJORAMIENTO DE FRAMBUESA

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RESUMEN

En México, el desarrollo de variedades de frambuesa (*Rubus idaeus* L) ha tomado mucho auge debido al emergente mercado de exportación y a la importancia de las frutillas como alimento nutritivo. Sin embargo, la información sobre el potencial genético de progenitores de frambuesa evaluados en México para su uso en los programas de mejoramiento es nula. Por ello, los objetivos del presente trabajo fueron: 1) estimar la heredabilidad y el grado de dominancia de algunas características de importancia agronómica en genotipos de frambuesa; 2) identificar genotipos con alta aptitud combinatoria general (ACG), 3) generar e identificar genotipos de frambuesa con buena adaptabilidad a condiciones tropicales. Un total de ocho progenitores fueron cruzados bajo un esquema dialélico. La progenie, así como los progenitores fueron evaluados bajo condiciones de campo abierto en Ziracuaretiro, Michoacán, en los años 2015 y 2016. Posteriormente, en 2017, un total de 39 progenies fueron seleccionadas y propagadas para ser evaluadas para comportamiento agronómico. Acorde con los resultados, la heredabilidad de las características estudiadas resultó ser de baja a intermedia (0.00 - 0.62). Por otro lado, los efectos no aditivos fueron más importantes en la herencia de la mayoría de las características que los efectos aditivos. El progenitor MRLS exhibió efectos positivos para rendimiento por planta, peso de frutilla, número de frutillas por planta, largo y diámetro de frutilla. Por su parte, el genotipo C47 tuvo una buena ACG para número de cañas y altura de planta, y el progenitor TD865 para contenido de sólidos solubles.

Acorde con los resultados del estudio de las selecciones avanzadas, los genotipos S.39 y S.27 exhibieron alto rendimiento, así como una alta calidad de fruto, evidenciando que ambos genotipos tuvieron una buena adaptabilidad a un clima tropical, por lo que pudieran ser una buena opción para los productores de la región de Ziracuaretiro, Michoacán.

Palabras clave: frambuesa; mejoramiento genético, calidad de fruto, parámetros genéticos, adaptabilidad, cruzas.

GENETIC PARAMETERS AND RASPBERRY BREEDING

Aurelio Hernández Bautista, Dr.
Colegio de Postgraduados, 2019

ABSTRACT

In Mexico, the development of raspberry (*Rubus idaeus* L) varieties has taken a big boom due to the emerging export market and the importance of this fruit as a nutritive food. However, the information about the genetic potential of raspberry progenitors evaluated in Mexico for their use in raspberry breeding programs is null. Therefore, the objectives of the present work were: 1) to estimate the heritability and degree of dominance of some characteristics of agronomic importance in raspberry genotypes; 2) to identify raspberry genotypes with high general combining ability (GCA), and 3) to generate and identify raspberry genotypes with good adaptability to tropical conditions. A total of eight raspberry parents were crossed under a diallelic scheme. The parents and their progenies were evaluated under open field conditions at Ziracuaretiro, Michoacán, the 2015 and 2016 years. Subsequently, in 2017, a total of 39 progenies were selected and propagated to be evaluated for agronomic performance. According to the obtained results, the heritability of the studied characteristics ranged from low to intermediate (0.00 - 0.62). On the other hand, the non-additive effects were more important in the inheritance of most of the characteristics than the additive effects. The progenitor MRLS exhibited positive GCA effects for yield per plant, berry weight, number of berries per plant, berry length and diameter. Genotype C47 had a good GCA for number of canes and plant height, and the parent TD865 for soluble solids content.

According to the results of the advanced selections, the genotypes S.39 and S.27 exhibited high yield, as well as a high quality of fruit, showing that both genotypes had a good adaptability to tropical climate conditions and these might be a good choice for growers from Ziracuaretiro, Michoacan.

Keywords: raspberry; genetic improvement, fruit quality, genetic parameters, adaptability, crosses.

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DEDICATORIA

A mi hijo Aurelio y mis padres

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INTRODUCCIÓN GENERAL

Recientemente, el interés en la producción de frambuesa (*R. idaeus* L.) se ha incrementado en diversas partes del mundo, debido a la fuerte demanda de este producto y a su importancia como alimento nutritivo. Entre el periodo del 2012 a 2016, la producción mundial de frambuesa se incrementó un 35 % (FAOSTAT), situación que evidencia el incremento del área sembrada, así como la generación de nuevos paquetes tecnológicos.

Para el 2016, la Federación de Rusia fue el primer productor de frambuesa a nivel mundial, con un volumen de 164 602 toneladas, seguido por Estados Unidos y Polonia. México se ubicó como el cuarto mayor productor de frambuesa, con un volumen de 112 661 toneladas. La frambuesa en Mexico es producida en ocho estados: Baja California, Colima, Ciudad de México, Hidalgo, Jalisco, Estado de México, Michoacán y Puebla (SIAP, 2016). Sin embargo, los tres principales estados productores de frambuesa son Jalisco, Baja California y Michoacán, que en conjunto aportan un 99.8 por ciento de la producción nacional (SAGARPA, 2016).

La producción de frambuesa en México ha sido posible debido a las condiciones climáticas que tiene el país y que favorecen la siembra del cultivo. Por esta razón, una gran cantidad de compañías tanto extrajeras como nacionales se han establecido principalmente en Jalisco, con el propósito de exportar frutillas a países como Estados Unidos, Arabia Saudita, Reino Unido, Hong Kong, Canadá y Japón (SAGARPA, 2016).

Otro aspecto que ha favorecido al incremento del área cultivada en México, es el desarrollo de nuevas variedades con una mayor adaptabilidad. Inicialmente, la producción de frambuesa se basó en la introducción de variedades extranjeras, sin embargo, la baja adaptabilidad de dichas variedades ha obligado a las compañías exportadoras lleven a cabo sus pruebas experimentales de evaluación y mejoramiento de variedades en las regiones de producción.

A la fecha, el mejoramiento genético convencional es el método más usado para la generación de nuevas variedades de frambuesa. Diversas estrategias han sido desarrolladas para la obtención de materiales que se pueden adaptar a las diferentes condiciones ambientales de un área o región. Entre estas estrategias se puede mencionar el desarrollo de cultivares primocañas, así como la obtención de materiales con bajo requerimiento de horas frio (Hall et al., 2011).

En general, los esfuerzos del mejoramiento se enfocan principalmente en la obtención de variedades con mayor rendimiento. Sin embargo, la calidad de fruto (firmeza, vida de anaquel y tamaño de fruto) es también otro aspecto importante en los programas, ya que es uno de los diversos factores que afectan las decisiones de los consumidores (Weber 2013). Más recientemente, características vegetativas tales como hábito de crecimiento erecto, tallos sin espinas y la adaptabilidad a cosechadoras mecánicas son nuevas características favorables que los mejoradores incorporan dentro de las nuevas variedades (Hall y Sobey, 2013).

La selección del germoplasma parental es una de las decisiones clave para el éxito de cualquier programa de mejoramiento genético. De forma general en frambuesa, la selección de progenitores que participaran en la etapa de evaluación de segregantes, se lleva a cabo basado en su valor fenotípico. Sin embargo, el valor fenotípico de los progenitores no siempre es un parámetro confiable, debido a que los efectos aditivos son los únicos que se heredan a la progenie.

Actualmente, existen diversas metodologías para estimar dicho valor aditivo, sin embargo, la estimación de la aptitud combinatoria general (ACG) y el mejor predictor lineal insesgado (BLUP), son los estimadores más comúnmente usados. La ACG es el comportamiento promedio de una línea en diversas combinaciones hibridas, y su estimación es obtenida como la desviación de la progenie con respecto a la media poblacional (Acquaah 2007). Por otro lado, el BLUP es un método que estima los efectos aleatorios de un modelo mixto (Henderson 1950).

Sin embargo, a pesar de que la estimación de los valores aditivos en características de frambuesa es muy importante para su mejoramiento genético, la información de tales valores en materiales de frambuesa evaluados en México es muy limitada. Por ello, el presente trabajo se enfocó en estimar diversos parámetros genéticos de características importantes de frambuesa, con base en un esquema de cruzamiento dialélico.

Considerando que la interacción genotipo por ambiente afecta de forma significativa algunas características de interés en frambuesa, esta investigación también se enfocó en identificar selecciones avanzadas con buena adaptabilidad a las condiciones climatológicas del municipio de Ziracuaretiro, Michoacán.

CAPÍTULO I. BREEDING POTENTIAL OF RASPBERRY PRIMOCANE SELECTIONS BASED ON THEIR COMBINING ABILITIES[1]

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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 their 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 measure 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 1.1. 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):

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

$$\sigma_D^2 = \sigma_{SCA}^2 = MS_S - MS_E \tag{4}$$

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):

$$h^2 = \frac{\sigma_A^2}{\sigma_F^2} \tag{5}$$

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 1.2). 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 1.2). 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 1.3. 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 1.3). 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 1.4. 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 1.5. 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 1.6). 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 for 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 of 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 1.6 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 1.1. 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		

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 1.2. 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 diameter		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	

General combining ability (GCA); Specific combining ability (SCA); degrees of freedom (d.f.)
, * indicate s significant difference at *P* ≤ 0.01 and 0.001, respectively.

Table 1.3. 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

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 ($\sigma^2_{F)}$; Narrow-sense heritability (h^2).

Table 1.4. 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

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

Table 1.5. 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	

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

Table 1.6. 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

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

CAPÍTULO II. RELATIONSHIP OF PARENTAL GENETIC DISTANCE WITH AGRONOMIC PERFORMANCE, SPECIFIC COMBINING ABILITY, AND PREDICTED BREEDING VALUES OF RASPBERRY FAMILIES[2]

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ABSTRACT

Previous findings in some crops suggest that parental distance is correlated with heterosis and agronomic performance. However, this pattern is not always evident in the progeny. The present study aimed to assess the relationship of parental distance with the agronomic performance of raspberry families and three estimators based on non-environmental effects: specific combining ability, general combining ability, and best linear unbiased prediction. A total of 35 genotypes, including eight open-pollinated raspberry cultivars and their 28 F_1 hybrids, were scored for vegetative and fruit traits. The relationship between estimators and parental distance ranged from 0.02 to 0.66. The estimators based on purely additive effects were superior to the *per se* performance of raspberry crosses. Additionally, it was observed that the specific combining ability—as an estimator associated with the parental genetic relatedness—performed poorly, and low correlation coefficients were observed for most of the traits. It was found that the degree of association for the estimators increased when narrow-sense heritability was high. It is concluded that the estimators based on only additive effects show a better association with parental relatedness, and therefore parental distance was an effective parameter in identifying crosses with high yield and large fruit size.

Keywords: additive effect; best linear unbiased prediction; general combining ability; hybrid performance; parental genetic relatedness; *Rubus idaeus*.

INTRODUCTION

In Mexico, the raspberry (*Rubus idaeus* L.) has gained much popularity due to the high profitability obtained per hectare, a situation that has offered a great opportunity for farmers to substantially increase their incomes. During the past 5 years, this situation caused a high increase in the annual production of raspberries due to the rapid growth of the harvested area, particularly in the states of Michoacán and Jalisco (SIAP 2013). New varieties have played a significant role in this expansion and are critical to the continuing success of the raspberry industry in Mexico.

Breeding efforts in raspberry are focused primarily on yield and adaptability. However, the fruit quality is also important in breeding programs, as it is one of the several factors that stimulate the consumption of raspberry fruits. Therefore, traits related to fruit quality such as firmness, sweetness, fruit size, and fruit shelf life are considered during the selection process of the best genotypes (Weber 2013). More recently, vegetative traits like erect growth habit, thornlessness, the ability to use mechanized harvesters, and primocane fruiting are new favorable traits that breeders consider incorporating into new varieties (Hall and Sobey 2013).

The selection of parental germplasm is key to successful plant breeding programs. Genetic relatedness among parents is one of the most important criteria that breeders consider during the selection of parents for hybrid breeding (Singh et al. 2016). Genetic research describes parental genetic distance as a factor linked to the heterosis and performance of crosses (Cox and Murphy 1990; Bernardo 1992). For this reason, it is common in breeding programs to maintain a wide genetic diversity of the parental germplasm. Using morphological and molecular data-based distances, plant biologists have shown that parental genetic distances effectively play an important role in the performance of crosses (Xiao et al. 1996; Lanza et al. 1997; Betran et al. 2003). Particularly, Xiao et al. (1996) studied the relationship among genetic distances of 10 rice parents and the performance and heterosis of their F_1 progeny. Their results showed that heterosis and hybrid performance were correlated with genetic distance measures estimated by molecular markers. In fruit crops, the positive association between parental genetic distance and performance was also reported in melons (Monforte et al. 2005) and strawberry (Kaczmarska et al. 2015). In contrast to these previous findings, Ceballos et al. (2016) found that the agronomic performance and specific combining ability of cassava crosses were poorly associated with parental genetic distance by SNPs, indicating that parental distance was not effective for identifying the highest yielding crosses for fresh root and dry matter weights. In another study that focused on peppers, Geleta et al. (2004) estimated the parental relatedness using amplified fragment length polymorphism (AFLP) markers and measured the degree of correlation between the Neí's distance and hybrid performance as well as SCA. Interestingly, they reported that AFLP-based distance measurements failed to explain the hybrid performance and SCA; however, this correlation improved when genetic distance was modeled using the agronomic performance of the crosses.

The performance of a hybrid is a function of its genotype (represented by additive and non-additive effects), environment, and genotype-by-environment interaction (Molina 1992). However, the additive effects or breeding values are uniquely transmitted to the progeny. Therefore, knowing the parental breeding values is vital for a breeding program because the predicted F_1 phenotypic value depends on them. The general combining ability (GCA) and best linear unbiased prediction (BLUP) are the two estimators more commonly used for estimating the breeding value in plants and animals, respectively. GCA is the average performance of a line in hybrid combinations, and its estimation is obtained based on the deviation of its progeny mean from the population mean (Acquaah 2007). BLUP is a method for estimating the random effects of a mixed model (Henderson 1950). A major advantage of BLUP is shrinkage towards the mean, which leads to reducing the prediction error (Piepho et al. 2008).

The primary objective of this study was to examine the relationships between parental morphological distance and agronomic performance of raspberry families, specific combining ability, and the breeding values, which were derived from BLUP and GCA estimators.

MATERIAL AND METHODS

Plant material and field experiment

The plant material for this study consisted of eight raspberry primocane selections and 28 hybrid families. The parental cultivars used were CP65, CP47, TD-865, MRSL-29, MU-1, JG, JJ-24, and CP57. A brief description of the selections is presented in Table 2.1.

Evaluation of the crosses and parents was conducted at Ziracuaretiro, Michoacán, Mexico, during two seasons o years (2015 and 2016). A total of 3744 plants, including eight parents and 28 F_1 families (104 plants per genotype), were transplanted into an open field under a randomized complete block design with four replications. Each replication consisted of 26 plants per genotype.

Field plot management

Fertilization was applied according to the phenological stage of the crop; 16-9-9 kg/ha (N, P, K) for the vegetative period, 48-27-129 Kg/ha for the flowering stage, and 32-10-10 for the harvest period. Weeds were controlled using applications of diuron + gramoxone (16.7 mL/L of water). A mixture of azoxystrobin-propiconazole (1.25 mL/L of water) + captan (2 g/L of water) was applied twice monthly to combat fungal diseases. A treatment containing abamectin (1 mL/L of water) and bifenazate (1.25 mL/L of water) was used to combat mites.

Data collection

A total of two harvests per week were carried out during 2 months. The fruits were collected from each plant. The marketable yield per plant and number of fruits per plant were calculated as the total weight and number of fruits obtained from the combined harvests conducted throughout the season, respectively. However, for marketable yield per plant, only were counted the fruits exhibiting a well-shaped fruit. Fruit weight (g), fruit length (mm), fruit width (mm), and total soluble solids (°Brix) were recorded from samples of five fruits per plant, which were collected weekly during the harvest period. The number of canes per plant and plant height were recorded, on individual plant basis, for all growing plants in each plot at 50% blooming stage.

Data analysis

Estimation for general and specific combing ability

The general (GCA) and specific combining abilities (SCA) were calculated following Method 2 and Model 2 of the Griffing's diallel mating schemes (Griffing 1956). The modified program DIALLEL-SAS was employed for the estimation of both GCA and SCA effects (Zhang and Kang 2003). Statistical analysis was performed using SAS 9.3 (SAS Institute 2012) under the general linear model procedure. The statistical model was denoted by:

$$Y_{ijlr} = \mu + l_l + r(l)_{rl} + g_i + g_j + s_{ij} + gl_{il} + gl_{jl} + sl_{ijl} + e_{ijlr}$$

where Y_{ijl} is the mean from each plot; μ is the population mean; l_l is the year effect; $r(l)_{rl}$ is the replication effect nested within year *l*; 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*; gl_{il} is the GCA × year interaction effect of parent *i* with the year *l*; gl_{jl} is the GCA × year interaction effect of parent *j* with the year *l*; sl_{ijl} is the SCA × year interaction effect of hybrid ij with the year l, and e_{ijl} is the random residual effect. Additionally, genetic variance components were calculated based on the method of moments. The structure of the ANOVA used to estimate genetic variance components is included in the ANEXO, Table 2S.

Description of statistical estimators measured in the progeny

In the plant breeding is established that agronomic performance of the progeny is positively correlated with the parental distance. To evaluate the relationship between parental relatedness and agronomic performance of the progeny, we used the phenotypic value of the progeny as one estimator and after this phenotypic value was partitioned for obtaining three new estimators. Therefore, a total of four different estimators were calculated for each raspberry family. The description of the estimators is given below:

Estimator based on the familial phenotypic value (PV): PV was obtained based on the mean of each cross. The mean of a cross was estimated by the average of the phenotypic values observed in each replication. This type of estimator considered the effects of genotype, year, and the genotype-by-year interaction.

Estimator based on the breeding value derived from parental BLUP (BV_{BLUP}):The estimator based on best linear unbiased prediction , denoted as BV_{BLUP}, considered only additive effects and was calculated for each family. First, the breeding values for parents were estimated by BLUP using a mixed model (ANEXO, Table 1S). The mixed model was fitted considering the genotypes and genotype-by-year interaction as random effects, whereas the year and replications as fixed effects. When the genotype-by-year interaction was significant, the following linear mixed model was fitted as:

$$y = X\beta + Z_1 g + Z_2 w + e$$

where y is the vector of phenotypic observations; β is a vector of fixed effects due to the blocks, year, and general average; g is the random effect of genotypes; w is the vector of the random effects of the genotype-by-year interaction; X, Z_1, and Z_2 are incidence matrices for the year, genotypes, and their interaction effects, respectively, and e is the vector of random residues. On the other hand, when the genotype-by-year interaction was non-significant, the data were analyzed with the term of interaction excluded from the model.

As second step, the estimators of progeny were estimated as: $BV_{BLUP} = \mu + \frac{1}{2}\left(BLUP_j + BLUP_j\right)$, where, μ is the population mean, $BLUP_i$ is the breeding value of parent *i*, $BLUP_j$ is the breeding value of parent *j* (Hallauer et al. 2010).

Estimator based on specific combining abilities (SCA)*:* The SCA effects only account for non-additive effects. Therefore, we decided to use this type of estimator to evaluate whether both dominance and epistasis effects have stronger associations with parental genetic distance than the estimators accounting for other factors. For this estimator, we used the values of SCA obtained previously in the program DIALLEL-SAS.

Estimator based on the breeding value derived from parental GCA (BV_{GCA}): we employed the values of parental GCA to obtain another estimator based on additive effects. The estimator for each F_1 full-sib's families was calculated as:

$$BV_{ij} = \frac{1}{2}(GCA_j + GCA_j),$$

where: g_i is the GCA effect of parent *i* and g_j is the GCA effect of parent *j*.

Estimation of morphological distances between parents and association analysis

The estimations of genetic relatedness among parents were calculated using the Euclidian distance proposed by Sneath and Sokal (1973). The matrix of distances was performed based on the eight morphological traits. For the clustering analysis, we employed the criteria of unweighted pair group method with the arithmetic mean (UPGMA) for the hierarchical cluster in the NTSYS software (Rohlf 2008).

The relationships of the predicted breeding values, performance, and specific combining ability of the crosses with parental genetic distance were detected by the correlation coefficient, represented by “r”, which was calculated through the Pearson’s test. Such analyses were performed using R program (R Core Team 2013).

RESULTS

Performance of hybrid families and parents

Comparisons between means for 8 parents and 28 F_1 hybrid families are provided in Table 2.2. Some families exhibited better traits than those observed in their parents, demonstrating the presence of transgressive segregation.

The marketable fruit yield ranged from 91.63 to 924.13 g/plant, with a population mean of 445.25 g/plant. In 2017, the average yield was 26.7% higher than that obtained in 2016. According to the comparison among means, the families and parents with the significantly highest yields (compared to the average yield of 445.25 g/plant) were obtained from the families: MRSL×MU1, TD-865×MU1, CP65×MRSL, MRSL×JG, CP47×MU1, MU1×JJ-24, and CP47×CP57, and the parents MRSL and MU1.

Regarding the number of fruits per plant, the means ranged from 33.03 fruits for the hybrid combination CP65×CP57 to 286.53 fruits for the hybrid family TD865×MU1. A total of nine families produced a significantly higher number of fruits, compared to the average number of fruits produced for all evaluated families (127.25 fruits/plant). The crosses with significantly higher fruit means for both years were: TD865×MU1, CP47×MU1, MRSL×MU1, CP65×MRSL, CP47×CP57, MRSL×JG, MRSL×JJ24, CP65×TD865, MU1×JJ24, and JG×JJ24.

The soluble solids content was slightly higher in 2017 than it was in 2016. The soluble solids content varied from 13.90 °Brix/year for the parent TD865 to 7.64 °Brix/year for the parent

CP57. A total of eight families and three parents had significant averages higher than 10.90 °Brix. Among the parents, TD865, CP47, and MU1 exhibited the highest soluble solids contents. Consequently, the families including TD865, C47, and MU1 tended to show significantly high amounts of soluble solids. These high magnitudes were estimated on: TD865×JJ24, CP47×TD865, MRSL×JJ24, CP47×CP57, CP47×MU1, CP65×CP47, CP47×JG, and TD865×MRSL.

Concerning individual fruit weight, the average obtained for the first year (4.44 g) was higher than that of the second year (4.14 g). MRSL was the parental genotype with the highest value for this trait (12.27 g), followed by the families TD865×MRSL, MRSL×MU1, MU1×JG, and CP47×MRSL, with values ranging from 5.10 g to 6.43 g. Such values were found to be significantly higher than the average fruit weight obtained from all plants of the families and parents evaluated during the 2 years.

The diameter of fruits produced by both families and parents was noticeably greater in 2016 than in 2017. Fruit diameter ranged from 1.54 cm for seedlings from the family MRSL×CP57 to 3.39 cm for the hybrid family MRSL×JG. Among the observed progeny, the significantly highest values for fruit diameter were found on progeny derived of the hybrid combinations MRSL×JG, MRSL×MU1, CP65×MRSL, and TD865×MRSL, which produced fruits with equatorial distances greater than 2.70 cm.

For fruit length, the mean of the entire population was 2.19 cm. The mean per year was higher for the second season than it was for the first season. The hybrid families reflecting the significantly highest values were determined for the hybrid combinations TD865×MRSL, MRSL×JG, MRSL×MU1, CP65×MRSL, and TD865×MU1.

The number of canes for all genotypes varied from 1.38 canes to 15.67 canes, with a mean value of 8.15 for both years. Ten families had significantly higher values than the population mean.

The high values were noticed in plants of the hybrid combinations: MU1×CP57, MRSL×JG, CP47×MRSL, CP47×CP57, CP65×MRSL, MRSL×MU1, CP65×CP47, TD865×JG, and TD865×MU1.

Concerning cane length, the maximum values were observed in CP47 (277.25 cm), whereas the minimum was recorded for JJ24×CP57 (103.46 cm). The results demonstrated that the best hybrid families with significant values for this trait were: CP65×JJ24, CP47×JG, CP47×CP57, JG×CP57, MU1×JG, TD865×MU1, and CP65×TD-865, with values up of 194 cm. Among the parental selections, the significantly highest values were observed in CP47, TD865, CP65, and JG, with values ranging from 236.00 cm to 277.25 cm.

Analysis of variance

Analysis of variance revealed highly significant differences ($P < 0.01$) for the effects of genotype and year on all studied characters in the present study (Table 2.3). General and specific combining ability were also significant for all traits, revealing the importance of non-additive and additive effects in the genetic complex of the scored quantitative traits. Moreover, the mean squares due to the genotype-by-year interaction were significant for marketable yield per plant, number of fruits per plant, fruit diameter, and number of canes, indicating that their phenotypic expression is significantly influenced by the year during which they are grown. For GCA and SCA, the interaction effects were non-significant for all variables. For instance, the variables marketable fruit yield per plant and number of fruits per plant exhibited significance ($P < 0.001$) for both interactions GCA × Year and SCA × Year, indicating that the effects of combining ability differed between the years. For Number of canes per plant, only GCA × Year was statistically significant ($P < 0.001$).

Genetic variability and genetic parameters

Variance components resulting from genetic and environmental factors were estimated for each retained trait using the method of moments (Table 2.4). Marketable fruit yield per plant had the highest proportion of phenotypic variance whereas traits related to fruit size, such as fruit length and width, had the lowest levels of genetic variance. Overall, the number of fruits per plant and cane length had a relatively high proportion of variance resulting from additive and dominance effects, which evidenced the wide gene pool present in the examined population. Concerning the combining ability variances, the SCA variance values were higher than those of GCA, suggesting that non-additive effects were more predominate on the inheritance of the studied traits. A similar trend was observed for the ratio of GCA and SCA effects, where the values were greater than 1. With the exception of average fruit weight, narrow sense heritability estimates for most traits were found to be relatively low, as the heritability values were less than 0.20.

Using the phenotypic data of yield and its components, a cluster analysis revealed that there was genetic variation among the 8 raspberry parents (Figure 2.1). Euclidian distances ranged from 20.11 to 710.35 with an average of 303.95. Cultivars MRSL-29, JJ-24, and CP65 were the most distantly related parents. In contrast, the lowest genetic distance was found between CP65 and JG (20.11).

General and specific combining ability effects

A wide range of GCA effects were observed in raspberry parents for the 8 quantitative traits measured (Table 2.5). C65 and JG had a significant and positive GCA effect for cane length. Genotype C47 had good GCA for marketable fruit yield per plant, number of fruits per plant, soluble solids content, fruit length, number of canes per plant, and cane length. TD865 showed positive and significant breeding values for soluble solids content, average fruit weight, fruit length, and cane length. The parental cultivar MRSL exhibited positive GCA effects for marketable fruit yield, number of fruits per plant, average fruit weight, fruit length, and fruit diameter. MU1 presented a positive GCA for marketable fruit yield per plant, number of fruits per plant, soluble solids content, average fruit weight, fruit diameter, and number of canes per plant. The parental genotype labeled as JJ24 had good GCA for soluble solids content.

The selection for best SCA values was performed considering the positive effects for all traits, as the objective of these crosses was to obtain selections with increased phenotypic values for all traits evaluated in the present research. For marketable fruit yield per plant, a total of 13 families had significant and positive SCA values (Table 2.6). The 3 highest values were obtained from C47 × C57, TD865 × MU1, and JG × JJ24. For number of fruits per plant, most families showed significant GCA values, but only 14 combined in a positive direction. The best 3 families were TD865 × MU1, C47 × MU1, and C65 ×MRSL. For soluble solids content, 8 families (C47 × C57, MRSL × JJ24, MU1 × C57, JG × C57, TD865 × C57, C65 × C57, TD865 × JJ24, and TD865 × MRSL) combined significantly in a positive direction for increased soluble solids content. The SCA values for these families ranged from 1.71 to 0.45. With regard to average fruit weight, a total of seven families produced positive SCA values. The best hybrid combinations were MRSL × C57, MU1 × JG, and JJ24 × C57. The SCA effects for fruit diameter ranged from 0.84 to -1.05. Of 28 families, SCA effects with significantly positive values were only observed in 10 families. For both years, SCA effects for fruit length were found for 8 families. For these hybrid combinations, the 3 highest values were observed in MRSL × JG, TD865 × MRSL, and C65 × MRSL. A total of 13 families had good SCA values for the number of canes per plant. The maximum and minimum SCA effects were exhibited by MRSL × JG and JG × JJ24, respectively. Concerning cane length, a total of 11 families exhibited significantly positive SCA effects. The 3 highest positive SCA values were demonstrated by C47 × C57, C65 × JJ24, and TD865 × C57.

Analysis of correlation between parental genetic distance and estimators

Correlation values ranged from 0.02 to 0.66 (Table 2.7). The highest correlations in marketable fruit yield per plant, number of fruits per plant, average fruit weight, fruit diameter, and fruit length were obtained for the estimators BV_{BLUP} and BV_{GCA}. In contrast, the estimator based only on non-additive effects (SCA) exhibited the lowest correlations for these same traits. Concerning soluble solids content and cane length, the best estimations were obtained by estimators BV_{BLUP} and BV_{GCA} for both traits. Finally, PV was the best estimator for number of canes per plant.

In general, the estimators that accounted for additive effects (BV_{GCA} and BV_{BLUP}) improved the estimations of correlation for most of the traits (Figure 2.2). Specifically, BV_{GCA} and BV_{BLUP} improved the coefficient of correlation in the marketable yield per plant by superior percentages to 1400% and 60%, in relation to the values obtained by SCA and PV, respectively. Regarding traits like average fruit weight and fruit length, the correlation obtained by BV_{GCA} and BV_{BLUP} was superior to SCA and PV, by at least 50%. For fruit diameter and cane length, only BV_{GCA} obtained a positive increase compared to SCA and PV.

DISCUSSION

Raspberry breeding is based on the production of segregating progenies, and hybridization is an effective way to obtain new varieties. However, high levels of phenotypic variation in the population are necessary to improve certain traits (Acquaah 2007). Here, the analysis of variance revealed highly significant differences ($P < 0.01$) among genotypes for all studied characteristics, indicating the presence of sufficient genetic variability among genotypes. This genetic variability can be exploited in a raspberry breeding program to improve yields and the yield components studied. These results were supported by estimated genetic variances where marketable yield per plant exhibited the highest phenotypic variation in our study, followed by vegetative traits. Previous studies have suggested that variation in traits related to fruit and vegetative qualities exists among red raspberry cultivars. Fotirić-Akšić et al. (2011) evaluated red and yellow raspberry seedlings to estimate genetic parameters. They reported ranges of phenotypic variation from 2.29 to 3.56 g for fruit weight, 1.71 to 1.86 cm for fruit length, 0.96 to 1.75 cm for fruit width, and 11.66 to 13.67 °Brix for solid soluble content. Additionally, Stephens et al. (2012a) studied 45 raspberry parents during 3 years and found that the fruit weight varied from 2.5 to 5 g, number of canes ranged from 6 to 11 canes, and height plant varied from 129.1 to 146.5 cm. All these previous estimations are comparable to those obtained in the present study.

Although the genotype-by-environment interaction for quantitative traits has been widely studied in some fruits such as strawberries, in raspberries this information is limited. Stephens et al. (2012a) studied the performance of 90 full-sib families for yield and other yield components. They found that the expression of yield and number of canes varied annually. In the present study, the genotype-by-year interaction was significant for the marketable fruit yield, number of fruits per plant, fruit diameter, and number of canes per plant, demonstrating the strong effects of environment on the phenotypic expression of these traits. One study suggested that the soluble solids content and fruit size are significantly affected by the environment (Dossett et al. 2008). We found that the genotype-by-year interaction was non-significant for soluble solids content and average fruit weight. Similar results were also obtained in a previous study carried out by Stephens et al. (2012b). All these results suggested that the soluble solids content and fruit weight might vary yearly due to varying conditions in altitude, day length, temperature, relative humidity, and plant material type (Miranda-Filho 1985).

Across the entire experiment, some families exhibited transgressive segregation for some traits, indicating that this important phenomenon may be exploited using open-pollinated raspberry cultivars as parents. The obtained results are consistent with the findings of Harbut et al. (2009), who evaluated 29 genotypes, including 15 cultivars and 14 hybrids. In their research, they found that some strawberry hybrids had higher values of fruit weight and others vegetative traits than did their respective parents. Because raspberries are propagated vegetatively and selection is focused on individual plants, the results obtained in the present study suggest that obtaining full-sib families is more advantageous in terms of time, costs, and phenotypic diversity than developing lines for the formation of F_1 hybrids. Therefore, this type of family could give good results for developing new varieties.

In raspberry, several studies have measured the breeding potential of several genotypes based on mixed models (Stephens et al. 2012a; Stephens et al. 2012b); however, there is information limited about the identification of superior raspberry genotypes using genetic design. In the present study, traits as average fruit weight, fruit diameter and fruit length (cm), the GCA effect was positive for TD865, MRSL and MU1 but negative for C65, JJ24 and C57. This result was not surprising as TD865, MRSL and MU1 were selected for its fruit size. Specifically, MU1 was resulted of the cross between the cultivar ‘Josephine’ which exhibit a large fruit and the parent M65.

C47, TD865, MU1 and JJ24, had positive GCA effects for soluble solids content, indicating that these four parental genotypes contributed to progeny with higher soluble solids content. Such result was expected as C47, TD865, MU1 and JJ24 showed a *per se* soluble solids content over 10 °Brix.

Number of canes per plant and cane length are important yield components for developing high-yielding raspberry cultivars. C65, C47 had positive GCA effects for both traits while JJ24 and C57 exhibited negative effects. Besides, it was observed that detection of a GCA positive effects for number of canes per plant and cane length not sure a high GCA effect in the yield per plant. This was observed in the parents C65 and C47 where their GCA values were high for both vegetative traits but low or intermedium for yield.

Genotypes MRSL and MU1 had the highest significant GCA effects for yield per plant, suggesting that both parents contributed to offspring with high yield. Additionally, both parents exhibited a good agronomic performance. All these results indicate that MRSL and MU1 are well adapted to the tropical climate of the region characterized for a temperature range of 3 to 35 °C and an annual precipitation of 1 200 mm. In Mexico, most of the raspberry production is located in geographic areas with tropical climate. Therefore, it is feasible that these selections could have a significant impact on the development of new high-yielding varieties.

In general, progeny derived from parents MRSL and MU1 showed good performance for fruit length, fruit width, and yield, whereas progenies that involved TD-865 exhibited good characteristics for soluble solids and other traits related to fruit size. Therefore, MRSL, TD865, and MU1 may be utilized as donor parents in a raspberry breeding program for enhancing yield, soluble solids content, and fruit size in elite materials.

Genetic relatedness present among parental germplasm is an important parameter that plant breeders use to select vegetative materials. It is assumed that as parental genetic diversity increases, progeny hybrid performance also increases (Lee et al. 1989). Previous investigations have reported that genetic distance is a significant factor that plays an important role in the hybrid performance of several crops (Xiao et al. 1996; Lanza et al. 1997; Solomon et al. 2012). In contrast, there are reports on alfalfa (Riday et al. 2003), cassava (Ceballos et al. 2016), maize (Godshalk et al. 1990), barley (Shahnejate-bushehri et al. 2005), and wheat (Martin et al. 1995) where this relation is null. Due to these results, the phenotypic value was partitioned to obtain and evaluate different estimators.

In the present study, the estimators BV_{BLUP} and BV_{GCA}, which were composed of additive effects, had higher correlation values than the estimators considering environmental effects or only non-additive effects. For complex traits such as marketable yield per plant, the estimators BV_{BLUP} and BV_{GCA} increased the correlation coefficient value over 1000% and 50% with respect to estimators based on specific combining ability and phenotypic value, respectively. This marked increase was also observed in soluble solids content and average fruit weight, where BV_{GCA} and BV_{BLUP} increased as minimum the correlation coefficient by 50%. These results indicated that, by omitting the genotype-by-environment interaction and environmental effects on the estimator, a clearer pattern of association with parental distance could be observed in comparison with the phenotypic value. Besides, the results suggested that the additive effects are more associated with the parental distance that the non-additive effects. This was expected as the additive effects of parents are only transmitted to the progeny.

On the other hand, estimators based purely on dominance effects showed the weakest correlation values in genetic distance for most of the traits, indicating that this type of estimator has low power to associate it with parental genetic distance. Such results could be due to the fact that Euclidian distances account for phenotypic effects (additive + non-additive + genotype-by-environment interaction + environmental effects), whereas the estimations based on SCA only consider non-additive effects. This situation has also been observed in peppers (Geleta et al. 2008) and cassava (Ceballos et al. 2016), where SCA had low correlation with Nei's genetic distances. In fact, a stronger association was reported when the phenotypic value was correlated with Nei's genetic distances.

When the degree of association for estimators was plotted against heritability, a clear positive pattern was observed. However, this relationship was more evident in BV_{GCA} and BV_{BLUP}, where the coefficients of determination (R^2) were moderate ($R^2 = 0.45$) and high ($R^2 = 0.81$), respectively (Figure 2.3). These results suggest that the higher the heritability of one trait, the BV_{GCA} and BV_{BLUP} will show a stronger association with parental genetic distance.

More recently, molecular techniques were developed to elucidate the allelic richness present in natural populations (Ibrahim et al. 2010). However, genetic distances estimated by molecular markers frequently showed poor correlation with agronomic performance or heterosis (Munhoz et al. 2009). This result could be explained by genetic divergence estimated by molecular markers only considers the polymorphism present in the genome and not the effect of each genomic region (Santos et al. 2015). Estimators based on additive effects account for the gene effects. Therefore, we hypothesized that if the molecular markers are combined with the additive estimators, a stronger correlation could be observed. However, other factors such as the linkage between a molecular marker and genomic region affecting the trait of interest and the different levels of dominance degree in the F_1 progeny—should be considered as they have a strong effect on the relationship between genetic distance and performance (Bernardo 1992).

Although SCA exhibited a stronger correlation with the phenotypic value for most of the traits, BV_{GCA} and BV_{BLUP} had acceptable association values (ANEXO, Table S3). Based on BV_{GCA} and BV_{BLUP}, our results showed that genetic distance was an effective parameter in identifying crosses with high yield as well as large fruit size. Additionally, it was observed that the genetic distance was effective in discriminating crosses with high soluble solids content and cane length. These results support the hypothesis that genetic distance plays an important role in hybrid performance.

CONCLUSION

Here, we presented proofs about why the *per se* performance and specific combining ability of the raspberry families showed a low of correlation with parental genetic distance estimated by morphological traits. It was observed that by calculating estimators based on gene effects exclusively additive, the correlation coefficient exhibited a higher value. In addition, we also detected that the heritability of one trait is linked with the correlation degree between the additive estimators and parental genetic distance. Finally, our results showed that parental distance based on morphological traits was an effective parameter in identifying crosses with high yield as well as large fruit size.

Conflicts of interest

The authors declare no conflict of interest.

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CUADROS

Table 2.1 Description of raspberry parents used in the diallel mating design

Parent	Habit	Color fruit	Production type	Fruit size	Fruit shape	Fruit firmness	Density of spines in stem
C65	Upright	Medium red	Primocane	Medium	Conical	Soft	Dense
C47	Semi-upright	Light red	Primocane	Medium	Broad conical	Medium	Dense
TD865	Semi-upright	Light red	Primocane	Medium	Conical	Firm	Medium
MRSL	Upright	Medium red	Primocane	Large	Conical	Very firm	Sparse
MU1	Upright	Dark red	Primocane	Medium	Conical	Soft	Dense
JG	Upright	Yellow	Primocane	Medium	Conical	Medium	Dense
JJ24	Upright	Medium red	Primocane	Medium	Trapezoidal	Medium	Dense
C57	Upright	Dark red	Primocane	Small	Circular	Firm	Medium

Table 2.2 Phenotypic means obtained for parents and families for yield and others seven yield-components scored during the years 2015-2016 and 2016-2017

Parent or family	Marketable fruit yield/plant (g)	Number of fruits/plant	Soluble solids content (°Bx)	Average fruit weight (g)	Fruit diameter (cm)	Fruit length (cm)	Number of canes/plant	Cane length (cm)
CP65	233.64 **	53.29 ***	11.38	3.90	2.15	2.01 *	9.67	236.00 ***
CP47	493.26	150.00	12.15 ***	4.46	2.42 **	2.40 *	10.37 **	277.25 ***
TD-865	502.62	100.47	13.90 ***	5.06 *	2.26	2.43 **	3.66 ***	236.25 ***
MRSL	924.13 ***	150.03	9.02 ***	12.27 ***	2.66 ***	3.00 ***	2.40 ***	169.50
MU1	610.08 *	124.27	12.70 ***	4.72	2.11	2.18	9.23	178.25
JG	244.70 **	69.12 ***	11.41	3.68 *	2.13	1.98 **	4.61 ***	236.00 ***
JJ-24	219.25 **	63.19 ***	11.16	3.59 *	1.86 ***	2.11	8.86	161.00
CP57	541.79	183.78 ***	7.64 ***	3.30 **	1.98 **	1.93 **	1.38 ***	116.00 ***
CP65×CP47	392.78	116.64	11.58 *	3.79	2.29	2.22	11.52 ***	139.65 ***
CP65×TD-865	436.42	162.13 **	10.83	3.79	2.00 *	1.97 **	8.77	195.60 *
CP65×MRSL	748.52 ***	198.98 ***	10.63	4.35	3.11 ***	2.83 ***	12.45 ***	147.08 ***
CP65×MU1	346.48	98.84	11.31	3.75	2.03 *	1.95 **	6.25 *	129.31 ***
CP65×JG	110.76 ***	136.12	10.33	3.74	1.88 ***	1.75 ***	3.45 ***	177.15
CP65×JJ-24	448.70	116.87	10.90	3.52 *	1.79 ***	1.86 ***	4.45 ***	259.90 ***
CP65×CP57	91.63 ***	33.03 ***	9.58 ***	2.53 ***	1.91 ***	1.71 ***	8.53	169.50
CP47×TD-865	433.84	109.16	12.25 ***	4.48	2.03 *	2.02 *	4.82 ***	166.54
CP47×MRSL	355.78	77.66 **	10.10 *	5.10 **	1.96 **	2.03 *	14.02 ***	137.04 ***
CP47×MU1	736.87 ***	267.90 ***	11.71 *	4.33	2.17	2.30	8.34	184.00
CP47×JG	99.28 ***	36.43 ***	11.55 *	3.56 *	2.27	2.19	6.90	244.45 ***
CP47×JJ-24	546.60	156.65	10.79	4.02	2.15	2.29	9.06	140.60 ***
CP47×CP57	606.10 *	189.34 ***	11.84 **	3.67 *	2.08	2.26	12.99 ***	240.70 ***

TD-865×MRSL	513.72		92.27	*	11.55	*	6.43	***	2.82	***	3.22	***	5.75	**	124.77	***
TD-865×MU1	788.63	***	286.53	***	11.50		4.34		2.18		2.39	*	11.10	***	200.20	*
TD-865×JG	476.14		156.92		10.43		3.55	*	1.97	**	2.06		11.45	***	167.50	
TD-865×JJ-24	209.09	***	60.35	***	12.40	***	3.53	*	2.06		2.27		4.45	***	183.54	
TD-865×CP57	259.03	**	71.03	***	9.95	**	3.63	*	2.15		2.20		2.56	***	184.19	
MRSL×MU1	891.62	***	205.62	***	10.75		5.23	**	3.14	***	2.88	***	11.94	***	144.78	***
MRSL×JG	748.45	***	181.68	***	9.69	***	4.56		3.39	***	3.02	***	14.50	***	155.25	*
MRSL×JJ-24	579.58		179.90	**	12.06	***	4.46		1.97	**	2.12		8.41		155.55	*
MRSL×CP57	408.95		119.03		8.65	***	4.10		1.54	***	1.43	***	7.53		131.15	***
MU1×JG	103.63	***	50.25	***	11.08		5.22	**	1.90	***	1.67	***	6.73		201.63	**
MU1×JJ-24	694.51	***	161.99	*	11.38		4.23		2.24		2.19		9.15		192.25	
MU1×CP57	174.71	***	71.41	***	10.70		2.44	***	2.09		2.06		15.67	***	129.07	***
JG×JJ-24	515.10		161.29	*	10.63		4.17		2.08		2.09		8.07		180.25	
JG×CP57	280.23	*	122.16		9.70	***	2.98	***	1.99	**	1.87	***	8.63		213.75	***
JJ-24×CP57	262.54	**	66.64	***	9.03	***	4.14		2.05		2.12		5.66	**	103.46	***
Standard error	64.86		15.35		0.3		0.3		0.08		0.08		0.81		8.74	
Combined Mean	445.3		127.3		10.9		4.29		2.19		2.19		8.15		178.03	
Mean for 2016	392.8		109.3		10.8		4.44		2.21		2.22		7.06		183.28	
Mean for 2017	497.7		145.2		10.99		4.14		2.17		2.16		9.24		172.78	

*, **, *** indicate significant difference at $P \le 0.05$, 0.01 and 0.001, respectively. This significant difference is based on the comparison between BLUP and population mean.

Table 2.3 Mean squares of eight quantitative characteristics evaluated in 2015 and 2016 in Michoacán, Mexico

Source of variation	d.f.	Marketable fruit yield/plant	Number of fruits /plant	Soluble solids content	Average fruit weight	Fruit diameter	Fruit length	Number of canes/plant	Cane length
Year	1	792296.06 ***	92328.57 ***	2.77 *	6.37 ***	0.12 **	0.28 ***	343.22 ***	2048.00 **
Replications (Year)	6	2155.06	304.76	1.07 *	0.24	0.01	0.02	1.86	110.55
Genotype	35	420584.94 ***	30161.45 ***	12.14 ***	19.70 ***	1.20 ***	1.21 ***	103.57 ***	15072.74 ***
General Combining Ability	7	963724.45 ***	62618.54 ***	15.42 ***	60.91 ***	2.20 ***	2.82 ***	203.26 ***	25640.20 ***
Specific Combining Ability	28	284800.06 ***	32047.18 ***	4.57 ***	9.39 ***	0.95 ***	0.81 ***	103.65 ***	12430.87 ***
Genotype× Year	35	24759.98 ***	1153.59 ***	0.48	0.19	0.02 *	0.02	2.60 **	8.69
General Combining Ability × Year	7	39713.94 ***	1838.30 ***	0.17	0.34	0.01	0.01	5.41 ***	10.57
Specific Combining Ability × Year	28	21021.50 ***	982.42 ***	0.55	0.15	0.02 *	0.02	1.89	8.21
Error	210	3501.42	383.82	0.42	0.20	0.01	0.02	1.37	246.01

d.f. degrees of freedom

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

Table 2.4 Genetic variance components calculated by moments methods for yield and seven of its components

Parameters	Marketable fruit yield/plant	Number of fruits/plant	Soluble solids content	Average fruit weight	Fruit diameter	Fruit length	Number of canes/plant	Cane length
σ^2_E	3501.4200	383.8180	0.4182	0.1956	0.0135	0.0151	1.3675	246.0121
σ^2_{GxL}	5314.6400	192.4438	0.0143	-0.0016	0.0018	0.0008	0.3072	-59.3316
σ^2_{SCAxL}	4380.0188	149.6494	0.0334	-0.0108	0.0026	0.0012	0.1317	-59.4495
σ^2_{GCAxL}	905.3130	36.3621	-0.0062	0.0035	-0.0002	-0.0001	0.1009	-5.8860
σ^2_{SCA}	32972.3206	3883.0952	0.5019	1.1553	0.1153	0.0987	12.7190	1552.8320
σ^2_{GCA}	8033.8983	363.9609	0.1388	0.6422	0.0158	0.0252	1.1947	168.0596
$\sigma^2_{SCA}/ \sigma^2_{GCA}$	4.1041	10.6690	3.6153	1.7989	7.2988	3.9115	10.6463	9.2398
σ^2_A	32135.5933	1455.8437	0.5553	2.5689	0.0632	0.1009	4.7788	672.2384
σ^2_D	131889.2825	15532.3809	2.0074	4.6211	0.4612	0.3946	50.8761	6211.3281
σ^2_P	172811.6276	17558.0541	3.0081	7.3783	0.5403	0.5117	57.2550	7064.2432
h^2	0.19	0.08	0.18	0.35	0.12	0.20	0.08	0.10

σ^2_E environmental variance, σ^2_{GxL} genotype-by-year interaction variance, σ^2_{SCAxL} specific combining ability-by-year interaction variance, σ^2_{GCAxL} general combining ability-by-year interaction variance, σ^2_{SCA} specific combining ability variance, σ^2_{GCA} general combining ability variance, σ^2_A additive genetic variance, σ^2_D non-additive genetic variance, σ^2_P phenotypic genetic variance, h^2 narrow-sense heritability

Table 2.5 Estimates of GCA effects for yield and seven yield-components for 8 parental genotypes evaluated in 2015 and 2016 in Michoacán, Mexico

Parent	Marketable fruit yield/plant (g)	Number of fruits/plant	Soluble solids content (°Bx)	Average fruit weight (g)	Fruit diameter (cm)	Fruit length (cm)	Number of canes/plant	Cane length (cm)
C65	-96.47 ***	-17.61 ***	-0.02	-0.54 ***	-0.04 **	-0.14 ***	0.14	8.94 **
C47	15.05 *	10.85 ***	0.61 ***	-0.08	0.01	0.03 **	1.51 ***	20.37 **
TD865	11.48	-0.59	0.86 ***	0.12 **	0	0.12 ***	-1.71 ***	9.41 ***
MRSL	208.76 ***	20.99 ***	-0.66 ***	2.01 ***	0.36 ***	0.38 ***	0.61 ***	-26.52 **
MU1	94.93 ***	24.58 ***	0.58 ***	0.03	0.03 *	0	1.43 ***	-6.85 ***
JG	-118.43 ***	-16.22 ***	-0.18 **	-0.35 ***	0	-0.11 ***	-0.44 ***	21.27 ***
JJ24	-31.27 ***	-11.52 ***	0.14 *	-0.34 ***	-0.16 ***	-0.06 ***	-0.64 ***	-6.12 ***
C57	-84.05 ***	-10.5 ***	-1.33 ***	-0.86 ***	-0.19 ***	-0.22 ***	-0.9 ***	-20.5 ***
Standard error	6.19	2.05	0.07	0.05	0.01	0.01	0.12	1.64

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

Table 2.6 Estimates of SCA for yield and 7 yield-related characteristics evaluated on 28 full-sibs' families during the years 2015 and 2016 in Michoacán, Mexico

Hybrid family	Marketable fruit yield/plant (g)	Number of fruits/plant	Soluble solids content (°Bx)	Average fruit weight (g)	Fruit diameter (cm)	Fruit length (cm)	Number of canes/plant	Cane length (cm)
C65 × C47	28.95	-3.86	0.09	0.11	0.13 ***	0.13 **	1.72 ***	-68.86 ***
C65 × TD865	76.15 ***	53.08 ***	-0.92 ***	-0.09	-0.15 ***	-0.20 ***	2.19 ***	0.56
C65 ×MRSL	190.98 ***	68.34 ***	0.40	-1.42 ***	0.60 ***	0.40 ***	3.55 ***	-13.55 **
C65 × MU1	-97.23 ***	-35.39 ***	-0.14	-0.04	-0.15 ***	-0.11 **	-3.47 ***	-51.98 ***
C65 × JG	-119.60 ***	42.69 ***	-0.37	0.33 *	-0.27 ***	-0.19 ***	-4.40 ***	-29.76 ***
C65 × JJ24	131.18 ***	18.74 **	-0.12	0.10	-0.20 ***	-0.13 ***	-3.20 ***	78.88 ***
C65 × C57	-191.76 ***	-104.85 ***	0.55 *	0.32	-0.01	-0.01	2.37 ***	43.28 ***
C47 × TD865	-37.94 *	-28.35 ***	-0.12	0.14	-0.17 ***	-0.33 ***	-3.12 ***	-39.93 ***
C47 × MRSL	-313.29 ***	-81.44 ***	-0.74 ***	-1.12 ***	-0.59 ***	-0.58 ***	3.76 ***	-35.01 ***
C47 × MU1	181.63 ***	105.21 ***	-0.37	0.08	-0.05	0.07	-2.74 ***	-8.71
C47 × JG	-242.59 ***	-85.45 ***	0.23	-0.30 *	0.07	0.07	-2.32 ***	26.11 ***
C47 × JJ24	117.56 ***	30.06 ***	-0.86 ***	0.14	0.12 **	0.12 **	0.04	-51.85 ***
C47 × C57	247.76 ***	62.79 ***	1.71 ***	0.63 ***	0.28 ***	0.38 ***	3.44 ***	119.94 ***
TD865 × MRSL	-151.77 ***	-55.38 ***	0.45 *	0.00	0.27 ***	0.52 ***	-1.29 ***	-34.82 ***
TD865 × MU1	236.96 ***	135.29 ***	-0.84 ***	-0.11	-0.03	0.06	3.23 ***	19.45 **
TD865 × JG	137.83 ***	46.47 ***	-1.15 ***	-0.51 ***	-0.23 ***	-0.14 ***	5.45 ***	-42.37 ***
TD865 × JJ24	-216.38 ***	-54.79 ***	0.50 *	-0.55 ***	0.03	0.01	-1.35 ***	3.56
TD865 × C57	-79.25 ***	-70.72 ***	0.80 ***	0.59 ***	0.21 ***	0.09	-4.04 ***	55.32 ***
MRSL × MU1	142.67 ***	32.79 ***	-0.06	-1.11 ***	0.57 ***	0.31 ***	1.76 ***	-1.05
MRSL × JG	212.86 ***	49.65 ***	-0.36	-1.39 ***	0.84 ***	0.56 ***	6.19 ***	-16.20 **

MRSL × JJ24	-43.16	*	43.17	***	1.68	***	-1.51	***	-0.41	***	-0.39	***	0.29		9.99	*
MRSL × C57	-99.65	***	-37.92	***	-0.81	***	2.60	***	-1.05	***	-0.87	***	-7.29	***	44.80	***
MU1 × JG	-318.12	***	-85.36	***	-0.21		1.25	***	-0.32	***	-0.42	***	-2.41	***	10.52	**
MU1 × JJ24	185.59	***	21.68	**	-0.24		0.24		0.19	***	0.05		0.21		27.03	***
MU1 × C57	-306.46	***	-122.07	***	1.21	***	-0.67	***	-0.07		0.06		5.21	***	-9.02	
JG × JJ24	219.54	***	61.77	***	-0.23		0.57	***	0.05		0.07		0.99	**	-11.60	*
JG × C57	73.76	***	-4.07		1.21	***	-0.02		-0.08		0.03		-0.84		49.04	**
JJ24 × C57	-230.87	***	-79.61	***	-0.71	**	1.02	***	0.21	***	0.24	***	1.03	*	-52.57	***
Standard error	18.97		6.28		0.21		0.14		0.04		0.04		0.37		5.03	

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

Table 2.7 Correlation values (r) of genetic distance (GD) with agronomic performance (PV), specific combining ability (SCA), breeding values (BV_{BLUP} and BV_{GCA}), estimated on the raspberry families

Trait	PV	SCA	BV_{BLUP}	BV_{GCA}
Marketable fruit yield/plant	0.26	0.03	0.42	0.47
Number of fruits/plant	0.02	0.03	0.10	0.25
Soluble solids content	0.15	0.12	0.38	0.34
Average fruit weight	0.34	0.41	0.66	0.61
Fruit diameter	0.47	0.20	0.42	0.56
Fruit length	0.37	0.10	0.52	0.50
Number of canes/plant	0.32	0.27	0.25	0.15
Cane length	0.38	0.15	0.24	0.46

FIGURAS

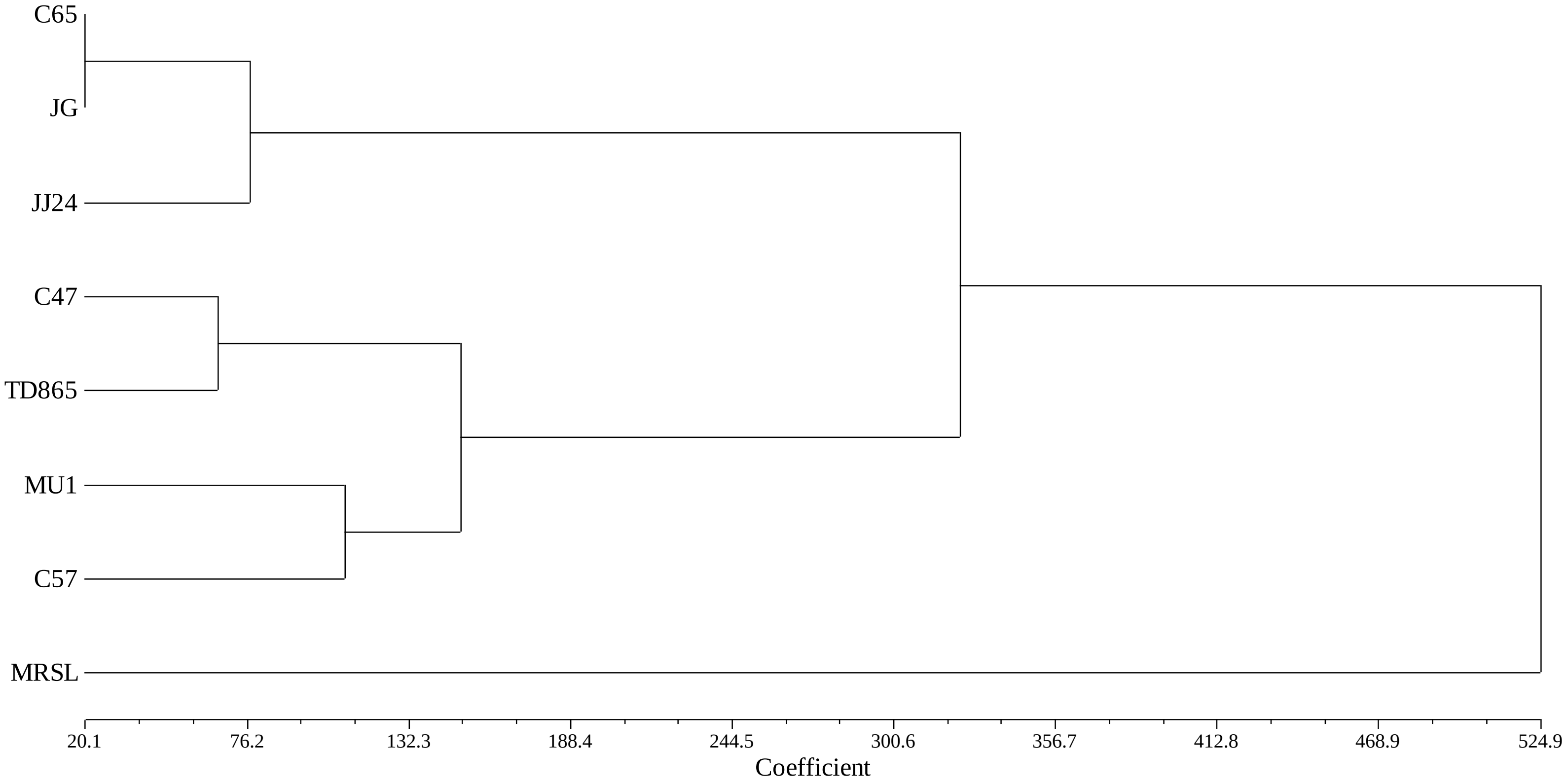

Figure 2.1. Dendogram estimating Euclidian genetic distance among 8 raspberry parents based on yield and seven of its components.

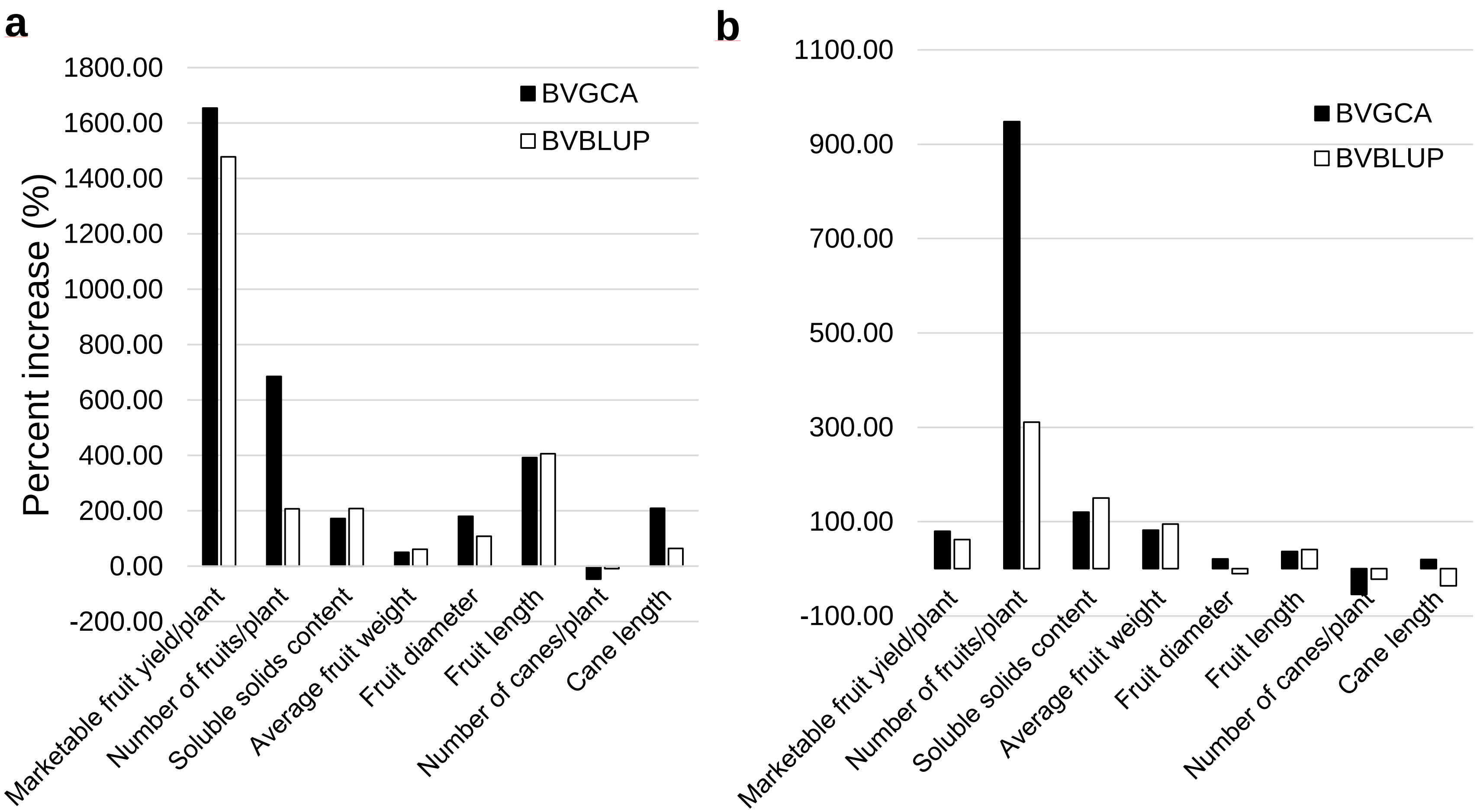

Figure 2.2. Percentage increase in the Pearson's correlation coefficient obtained by additive estimators BV_{BLUP} and BV_{GCA} with respect to: a) specific combing ability (SCA) and b) agronomic performance (PV).

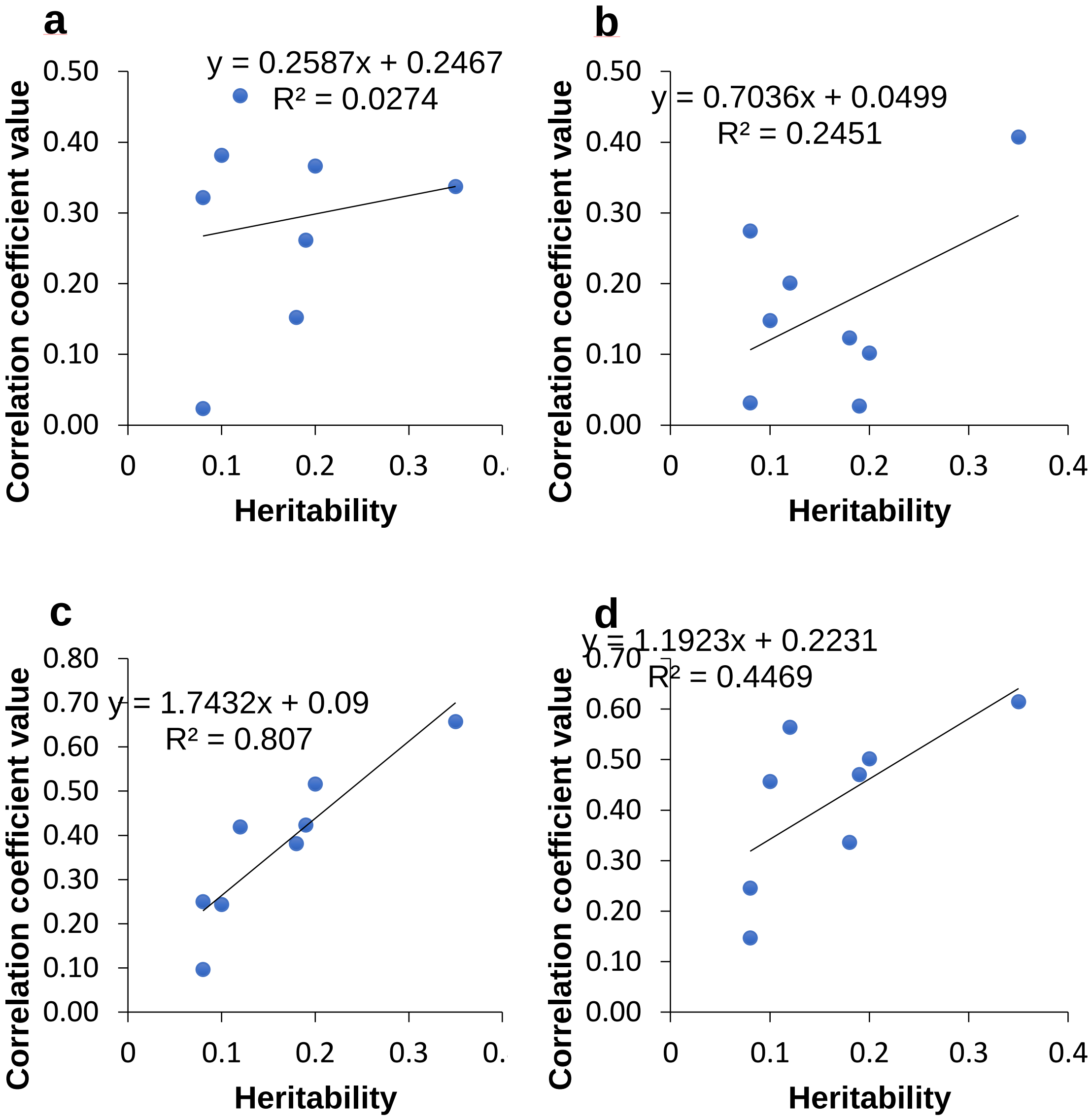

Figure 2.3 Relationship of parental genetic distance with association level of estimators: a) agronomic performance, b) specific combining ability, c) BV_{BLUP} and d) BV_{GCA}.

CAPÍTULO III. ADAPTABILITY OF RASPBERRY PRIMOCANE GENOTYPES IN A TROPICAL ENVIRONMENT AND ITS IMPLICATION IN THE RASPBERRY PRODUCTION IN MEXICO[3]

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Short title: phenology of primocane raspberry genotypes

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ABSTRACT

BACKGROUND: The worldwide tendency for growing raspberries in different climatic environments demands the need of development new cultivars with good adaptability.

OBJECTIVE: The aim of the present study was to study the adaptability of red raspberry selections for tropical conditions.

RESULTS: Days to flowering, days from flowering to first pick, days to first pick, and days from transplanting to last pick were from 135 to 183 days, 22 to 49 days, 163 to 222.3 days, and 250.0 to 299.5 days, respectively. Harvest period varied among genotypes, and the genotypes S.39 and S.27 had the longest harvest period and the highest marketable yields, evidencing their good adaptability to tropical conditions. Berry weight varied from 2.74 to 5.37 g, suggesting that the studied selections produced fruits with small and intermedium size. In addition, these results indicated that such genotypes might be suitable for fruit exportation to different international markets.

CONCLUSION: The present study demonstrated the adaptability of certain genotypes such as S.39 and S.27 at a tropical environment, which might be a good option for raspberry growers producing for fresh consumption.

Keywords: *Rubus idaeus*, agronomic performance, berry size, raspberry breeding.

INTRODUCTION

Raspberry (*Rubus idaeus* L.) production increased by 35% worldwide during 2012 to 2016 [1]. Mexico has favorable climatic conditions for growing raspberries. Therefore, several foreign and national companies are established in the municipalities of Jalisco, Mexico, such as Sayula, Ciudad Guzmán, and Jocotepec. These companies currently export raspberries mainly to the United States, Saudi Arabia, United Kingdom, Hong Kong, Canada, and Japan, the United States being the main country for exporting [2].

Initially, raspberry production in Mexico was based on the introduced varieties from United kingdom and United States. However, the lack of adaptability of the varieties to new production areas and the new demands of consumers have forced the companies to develop new cultivars. In raspberries, conventional genetic improvement is the main method used to develop new cultivars. Several strategies have been used to obtain materials that can be adapted to the different environmental conditions. Among these strategies, the development of primocane-fruiting cultivars, as well as, obtaining cultivars that require low chilling conditions are most important [3]. Another important aspect is the efficiency in fruit harvesting, with an emphasis on plant structure and cultivars without thorns [4]. Since raspberries are more susceptible to certain diseases than blackberry, breeders have focused on seeking genotypes that may be resistant to fungal diseases and more recently to several viral diseases [3].

In raspberry plants, the genotype-by-environment interaction affects some quantitative traits with different magnitudes. Previous studies have shown that berry weight, lateral length, and number of fruit per lateral interacted in a low degree with the environment, whereas, a strong genotype-by-environment interaction was observed for cane length, number of canes, and cane diameter [5]. Hernández-Bautista [6] studied the breeding potential of primocane genotypes and genotype-by-environment interaction for some important agronomic traits, and reported a significant effect of the genotype-by-environment interaction for the marketable yield, number of canes, berry diameter, and number of fruits per plant across seasons. Therefore, due to these results combined with the high variability of geographic and climatic conditions in Mexico, raspberry breeding programs evaluate several geographic sites to identify the selections with good adaptation to a wide number of sites.

Unlike in blackberry, where the ‘Tupy’ cultivar shows a wide adaptability to different production zones in Mexico, there is no known raspberry cultivar that exhibits a similar degree of adaptation. Therefore, there is a need to develop new cultivars adapted specifically to the tropical conditions of the production areas. The objective of the present study was to evaluate the adaptability of primocane raspberry genotypes on the basis of their phenology and yield under the effect of tropical conditions in regions with "off-season" production windows, such as the Central Mexico and other areas in the world where daylengths remain below 13.5 hours/day (low latitude) and high-elevation (highlands).

MATERIALS AND METHODS

The experiment included evaluation of 39 raspberry selections and two checks (‘Josephine’ as check 1, and ‘Autumn Bliss’ as check 2). ‘Autumn Bliss’ is considered a cultivar with good adaptability to a tropical climate, producing high yields and fruits with good quality [7]. The 39 selections were obtained from evaluations performed in previous years [6]. The trial was carried out from 2017 to 2018 at Ziracuaretiro, Michoacan State, Mexico. Based on the Köppen classification, the climate of the region is tropical with rain in the summer (Aw = equatorial savannah with dry winter, with precipitation less than 60 mm in winter) [8]. Ziracuaretiro is located within the coordinates 19°26′N and 101°55′W, and approximate elevation of 1,380 m, with an annual pluvial precipitation of 1,496.5 mm and temperatures that oscillate between 9.3 and 30.2 °C (Figure 1) [9].

Genotypes were grown under a randomized complete block design with four replicates. The plot row was 3 m and consisted of 10 plants spaced 0.3 m apart. The plants were obtained through *in vitro* culture using axillary buds and were transplanted to the field during May 2017. The agronomic management of the trial was performed according to the commercial recommendations.

For data collection, a total of 15 phenotypic and agronomic traits were studied. The phenology of genotypes was evaluated at the stages of: days to flowering, days to first pick, days from flowering to first pick, harvest period, and days from transplanting to last pick. Days to flowering were calculated as the number of days elapsed from transplanting to the opening of the first flower in 50% of the plot plants. The days to first pick were obtained by counting the days elapsed from the date of transplanting to the beginning of production in 50% of the plot plants. The harvest period was obtained by counting days that the genotypes produced berries. Days from transplanting to last pick were obtained as the number of days elapsed from transplanting to the last pick. Measurements of plant height, number of flowers per cane, and number of laterals per cane were recorded from a total of five plants per plot, on an individual plant basis.

Fruit samples were harvested on each plot two times per week. During the harvest period, a total of seven traits were evaluated: 1) total number of berries and 2) yield per plot (g) were evaluated by counting and weighting the final number of produced berries per plot throughout the season. Marketable number of berries, or marketable yield, was determined by the final number of berries that were selected according to the exportation standards required by the companies. The percentage of loss in harvest was calculated as the difference between the initial yield per plot and estimated marketable yield per plot. Average berry weight (g) was estimated by dividing marketable yield by marketable number of berries. The soluble solids content of berries was measured 10 times across the cycle using a sample comprising 10 fruits.

Data were analyzed using the mean values of each genotype in each plot. The assumptions of normality and homogeneous variances were verified using the Shapiro-Wilk and Levene tests, respectively, considering a significance of 0.05. Thereafter, an analysis of variance (ANOVA) was performed using the PROC ANOVA in the statistical package SAS® version 9.3 [10]. ANOVA was performed considering the following statistical model:

$$Y_{ij} = \mu + h_i + b_j + e_{ij}$$

where Y_{ij}, is the observed performance of the *i*th genotype in the block j, μ is the overall mean, h_i is the fixed effect of hybrid i, b_j is the fixed effect of the block j and e_{ij} is the random residual term with $\sim N(0, \sigma_e^2)$. Finally, the comparison of the means was performed by Tukey's test at $P < 0.05$ using SAS® Program version 9.3.

RESULTS AND DISCUSSION

Phenology of Raspberry Selections

Significant differences were observed in the periods comprising the days to flowering, days to first pick, days from flowering to first pick, harvest period, and days from transplanting to last pick (Table 3.1). The studied selections exhibited a different phenology across time. For days to flowering, the selections showed an average floral opening of 159.4 days after transplanting. The highest value in days to flowering was exhibited by S.22 (183 days), while the lowest value was for the ‘Autumn Bliss’ (check 2) (135 days). These results are in agreement with the previous findings of Sønsteby and Heide [11], who found that ‘Autumn Bliss’ was the earliest commercial annual-fruiting cultivar.

For the period between flowering and the first pick, the maximum found was S.2 with 49.3 days, while the minimum was S.25 with 22.0 days. For days to first pick, the selections with early flowering also exhibited early production. The check 2 and S.27 were the genotypes with the earliest producing period (163 days), whereas S.2 and S.22 were the latest (222.3 days). Such variation in harvest time suggested that the genotypes interacted in a different manner with the environment. In this sense, previous studies have reported that the interaction between factors such as temperature, photoperiod, and genotype affect the harvest time [11, 12]. Regarding the harvest period, genotypes S.39 and check 2 exhibited a harvest period of almost four months (119 days), which was the longest harvest period found in this study. In contrast, S.2 and S.34 showed the shortest harvest period with 58 and 53.8 days, respectively. These results were consistent with the findings of Parra-Quezada [13], who reported that cultivar ‘Autumn Bliss’ had an average harvest period of 90 days under climatic conditions of highlands. In contrast, Moura [14] and Curi [15] reported a harvest period > 280 days in primocane cultivars, which were evaluated under tropical climatic conditions. Such difference in results suggests an environmental effect on the harvest period in the raspberry cultivars.

In the present study, interestingly, it was noticed that there was not a clear relationship between the earliness for flowering and duration of the harvest. This result indicated that it is possible to obtain raspberry cultivars flowering early with a long harvest period. In Mexico, October, December, and January have the highest prices for selling raspberries and therefore are frequently considered the best months for producing raspberries. For this reason, farmers offer most of their total production in those months. In our study, we identified that selections such as S.27, S.39, S.19, and S.11 had long harvest periods (3–4 months) and high marketable yields. Therefore, those selections might lead to the growers to a harvest period with production during the months with a high price.

Vegetative and Fruit Traits

The results of the comparison of means are presented in Table 3.2. Statistical significance ($P < 0.05$) in cane length, number of laterals per cane, number of flowers per cane, average berry weight, and soluble solids content was observed between genotypes. In floricane cultivars, the plant height is a strong component affecting yield [16]. On the other hand, in primocane cultivars, plant height plays an important role in the type of trellis system; high cultivars (>1.8 m, e.g., Himbo-Top® or Ambrosia®) require a larger trellis system than dwarf cultivars (<1.5 m, e.g., Caroline®). In the present study, the length of cane varied significantly among genotypes. The population ranged from 0.94 to 2.12 m and had a mean of 1.51 m. Selections with a low and high plant height as well as with high yields were observed in the study. These results identified no relationship between the marketable yield and plant height. Interestingly, the selection S.39 had a low height (1.29 m) and high yield (4273.92 g/plot), which suggested that this selection could help growers to reduce costs in the trellis system while obtaining good yields in field.

Previous studies have shown that the number of flowers and number of laterals per cane are indirect parameters of adaptability of raspberry genotypes to climatic conditions of evaluation. Sønsteby and Heide [11] studied the effect of temperature and day length on ‘Polka’ cultivar. They found that the number of flowers increased with increasing temperature and day length. On the other hand, Sønsteby and Heide [11] also reported that number of dormant buds is affected by temperature, suggesting that to have a high number of non-dormant buds, primocane cultivars should be grown under 25 °C. In the present study, the number of laterals per cane varied from 4.67 to 16.75 laterals and number of flowers per cane from 9.67 to 169.25 flowers. Such results suggested that selections such as S.1 had a better adaptability than S.9 and S.36. The low values for number of flowers per cane were due to the high susceptibility of the selections to *Botrytis cinerea*. This fungus frequently affects the flowers in raspberry [17] [18]. Our results are in agreement with those found by Fotirić-Akšić [19], who studied 100 seedlings and reported a range from 8.6 to 19.8 laterals per cane.

Currently, certain fresh fruit sizes are demanded by the different export destinations. For example, large or intermedium fruits are better appreciated by the consumers of raspberry fruits in the United States market, whereas small fruits are preferred in the Japanese market.

For this reason, the fruit size is considered as one of the primary goals of breeding programs [4]. During evaluation of raspberry segregates, fruit size is ranked according to the following classification: small (<4.50 g), intermedium (4.51–5.59 g), and large (>6.0 g). In the present study, the berry weight varied from 2.74 to 5.37 g, thereby selections had fruits with small and intermedium size. Similar results for berry weight were obtained by Stephens [20] and Radovich [21]. In the present study, the fruit weight as well as their high yield observed in S.27 (4.91 g) and S.39 (5.37 g), indicated that these selections are candidates for American marketing. On the other hand, high-yielding selections such as S.19, S.38, and S.11 had berry weights <4.5, which indicated that such genotypes might be suitable for fruit exportation to Japan.

Another aspect of relevant importance that every berry breeder pursues is the berry quality [3]. The quality of fruit is constituted by several variables such as: firmness, soluble solids content, titratable acidity, and long shelf life. Soluble solids content is an important trait influencing the flavor of raspberry fruits [4] as well as the decision of consumers. In Mexico, the exportation market for fresh consumption requires that farmers produce raspberry fruits with a minimum range from 8-10 °Brix. In the present study, with exception of S.13, the studied genotypes had higher values than 8, suggesting that the selections meet the requirement of brix degrees for exportation. Similar results under tropical conditions were published by Maro [22], who on their study on primocane cultivars found that the cultivars exhibited a high soluble solids concentration (>9 °Brix). All previous results indicate that soluble solids concentration is favored by warm environments.

Yield of Raspberry Selections

The number of berries and yield obtained for the ten best and worst raspberry genotypes are presented in Table 3.3. According to the results, the Tukey's test detected statistical significance ($P < 0.05$) in number of berries per plot, yield per plot, number of marketable berries per plot, marketable yield per plot, and losses in yield. The estimated marketable yield in 'Autumn Bliss' was 1165.33 g/m, which was higher than that reported by Knight [23], who reported that 'Autumn Bliss' yielded ~450 g/m in southern Florida, U.S.A. Therefore, the region of Ziracuaretiro is suitable for the production of raspberries.

In general, for yield/plot and number of fruit/plot, the values ranged from 513.58 to 4940.22 g/plot and from 102.30 to 1264.34 fruit/plot, respectively. The selection S.10 and check 2 had the highest values for yield/plot and number of fruit/plot. However, for the number of marketable fruits and yield, S.10 resulted in a loss of yield up to 50% because of the low quality of berries due to a poor firmness. In contrast, selections S.27 and S.39 had a higher marketable yield (> 3900 g/plot) than the cultivar 'Autumn Bliss', suggesting that both selections had a good adaptability to tropical conditions. Furthermore, both genotypes grown in tropical conditions might be a good option for growers to produce raspberry fruits for fresh consumption.

Environmental factors, such as temperature and light intensity, cause earliness and delay initiation of raspberry production [24, 11]; however, such factors affect the cultivars to different magnitudes. In blackberry, Hussain [25] observed that low temperatures caused that 'Tupy' blackberry began its production later than 'Xavante', evidenced that the cultivars responded differently to the temperature effect. Similarly, we observed that selections produced raspberry fruits at different times. Based on the cumulative yield of the 10 selections with the highest yields (Figure 2), selection S.19 began its production later in the season than the two highest-yielding selections (S.27 and S.39), but S.19 had a higher cumulative yield in a shorter production time (41 days). In Mexico, some growers prefer to grow varieties with a short harvest period to reduce labor costs during the harvest period. Therefore, the selection S.19 might be a good option for growers to produce higher yields in fewer months, reducing the labor cost. At the end of the harvest period, selections S.27 and S.39 had higher substantial increases in the cumulative yield, compared with the rest of studied selections. These results indicated that both selections have the potential to produce raspberry during a long period. According to Hussain [25], this advantage has a significant impact for exportation, because it makes possible the commercialization of fruits during periods of low supply.

CONCLUSIONS

On the basis of the results of our study, the raspberry selections evaluated varied in phenology as well as yield. Interestingly, high-yielding genotypes had long and short harvest periods allowing the growers to have production in periods of low supply. Additionally, these results indicated that some evaluated selections had a good adaptability to tropical and high-elevation (highlands) conditions. For berry weight and soluble solids content, the best genotypes had superior values than the requirements demanded by the international market. Selections as S.27 and S.39 might be suitable for the exportation market.

Conflicts of interest

The authors declare no conflict of interest.

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Table 3.1. Phenology of the ten genotypes with the highest and lowest values obtained in the grow season 2017-2018.

Ranking	Days to flowering			Days from flowering to first pick			Days to first pick			Harvest period			Days from transplanting to last pick		
Highest values	S.22	183.0	a	S.2	49.3	a	S.2	222.3	a	S.39	119.0	a	S.22	299.5	a
	S.8	174.3	b	S.1	46.3	ab	S.22	222.3	a	Check2	119.0	a	S.39	297.3	a
	S.2	173.0	bc	S.23	45.3	a-c	S.30	215.3	b	S.27	115.5	a	S.30	295.0	ab
	S.20	173.0	bc	S.36	45.3	a-c	S.33	213.8	b	S.12	103.0	b	S.32	294.8	a-c
	S.26	173.0	bc	S.28	44.3	a-c	S.20	206.3	c	S.32	103.0	b	S.7	289.5	a-d
	S.30	173.0	bc	S.5	42.3	b-d	S.23	206.3	c	S.19	98.3	bc	S.12	289.3	a-d
	S.33	173.0	bc	S.6	42.3	b-d	Check1	206.3	c	S.17	98.0	bc	S.6	283.3	b-e
	S.13	171.0	c	S.30	42.3	b-d	S.8	205.8	c	S.25	98.0	bc	Check1	283.0	c-e
	S.7	165.0	d	S.34	42.3	b-d	S.26	205.3	cd	S.35	98.0	bc	S.8	282.8	de
	S.15	165.0	d	Check1	42.3	b-d	S.31	204.8	cd	S.10	93.0	b-d	Check2	282.3	de
Lowest values	S.1	153.0	i	S.13	29.0	h-m	S.29	185.5	i-l	S.3	72.3	h-l	S.9	275.0	e-i
	S.10	153.0	i	S.19	28.8	h-m	S.9	184.0	j-m	S.20	70.3	i-l	S.24	275.0	e-i
	S.14	153.0	i	Check2	28.3	h-m	S.10	183.3	j-m	S.23	70.3	i-l	S.4	269.8	f-j
	S.28	153.0	i	S.27	28.0	i-n	S.19	182.8	k-m	S.36	67.0	j-m	S.5	268.0	g-k
	S.39	148.0	j	S.18	27.5	j-n	S.17	180.8	lm	S.21	66.5	k-m	S.31	267.0	g-k
	S.5	144.0	k	S.16	27.0	k-n	S.25	179.0	mn	S.33	63.0	k-n	S.29	266.5	h-k
	S.9	144.0	k	S.39	25.3	l-n	S.35	178.5	mn	S.28	62.3	l-n	S.21	264.8	i-k
	S.36	144.0	k	S.17	24.8	mn	S.39	173.3	n	S.31	62.3	l-n	S.28	259.5	j-l
	S.27	135.0	l	S.35	24.5	mn	Check2	163.3	o	S.2	58.0	mn	S.36	256.3	kl
	Check2	135.0	l	S.25	22.0	n	S.27	163.0	o	S.34	53.8	n	S.34	250.0	l
Mean		159.4			35.0			194.5			83.1			277.6	

Means sharing the same letters within the same column are not significantly different by the Tukey's test (P ≤0.05)

Table 3.2. Means of ten best and worst genotypes for vegetative and fruit traits.

Ranking	Cane length (m)			Number of laterals/cane			Number of flowers/cane			Average berry weight (g)			Soluble solid content		
Highest values	S.27	2.12	a	S.1	16.75	a	S.1	169.25	a	S.39	5.37	a	S.32	13.60	a
	S.21	2.08	ab	S.19	16.50	ab	S.18	150.50	ab	S.36	5.35	a	S.39	13.55	a
	S.26	1.99	a-c	S.2	15.25	a-c	S.12	146.25	a-c	S.21	5.31	a	S.28	13.10	a
	S.22	1.93	a-d	S.11	15.25	a-c	Check 2	134.00	a-d	S.27	4.91	ab	S.29	13.10	a
	Check 1	1.87	a-e	S.27	15.25	a-c	S.24	131.75	a-d	Check 1	4.85	ab	Check 1	12.95	a
	S.9	1.84	a-e	S.17	15.00	a-c	S.20	120.50	a-e	S.35	4.68	bc	S.27	12.93	a
	S.2	1.84	a-e	S.20	14.75	a-c	S.14	108.25	a-f	S.33	4.55	b-d	S.16	12.70	a
	S.11	1.78	a-e	S.29	14.75	a-c	S.19	106.25	a-g	S.9	4.51	b-e	S.33	12.70	a
	S.20	1.74	a-e	S.16	14.50	a-d	S.17	103.50	a-g	S.5	4.33	b-f	S.35	12.70	a
	S.14	1.73	a-f	S.37	14.50	a-d	S.39	102.00	a-g	S.4	4.30	b-g	S.24	12.45	a
Lowest values	S.3	1.33	e-h	S.25	11.00	c-f	S.26	49.50	e-h	S.3	3.32	k-p	S.12	10.70	ab
	S.35	1.30	e-h	S.26	11.00	c-f	S.21	49.25	e-h	S.11	3.23	l-p	S.7	10.65	ab
	S.39	1.29	e-h	S.38	10.50	c-f	S.33	47.00	e-h	S.24	3.21	m-p	S.30	10.65	ab
	S.25	1.27	e-h	S.7	9.75	d-g	Check 1	45.50	e-h	S.12	3.21	m-p	S.25	10.45	ab
	S.7	1.21	f-h	S.8	9.75	d-g	S.34	42.50	e-h	S.2	3.14	m-p	S.20	10.35	ab
	S.19	1.13	gh	S.15	9.75	d-g	S.35	40.75	f-h	S.25	3.02	n-p	S.17	9.80	ab
	S.33	1.10	gh	S.28	9.50	e-g	S.8	34.75	f-h	S.13	3.00	n-p	S.21	9.80	ab
	Check 2	1.10	gh	S.34	9.50	e-g	S.28	33.25	gh	S.28	2.90	op	S.6	9.00	ab
	S.28	1.08	gh	S.9	6.50	fg	S.9	10.00	h	S.22	2.88	op	S.23	8.55	ab
	S.30	0.94	h	S.36	4.67	g	S.36	9.67	h	S.1	2.74	p	S.13	6.20	b
Mean		1.51			12.66			76.63			3.84			11.48	

Means sharing the same letters within the same column are not significantly different by the Tukey's test (P ≤ 0.05)

Table 3.3. Means obtained for best and worst ten genotypes for number of fruits, yield and losses in yield.

Ranking	Num. of berries /plot			Yield/plot (g)			Num. of marketable berries/plot			Marketable yield/plot (g)			Losses in yield (%)		
Highest values	S.10	1264.34	a	S.10	4940.22	a	S.22	983.78	a	S.27	4088.22	a	S.10	57.79	a
	Check 2	1166.93	ab	Check 2	4679.50	b	S.11	969.06	ab	S.39	3998.87	a	S.25	33.36	b
	S.22	1154.68	a-c	S.27	4633.33	b	S.38	928.37	bc	Check 2	3496.00	b	S.34	32.67	b
	S.12	1090.53	b-d	S.39	4273.92	c	S.24	904.47	cd	S.19	3443.38	b	S.6	27.18	bc
	S.24	1074.93	b-d	S.19	4021.79	d	Check 2	900.68	cd	S.38	3223.75	c	S.17	27.00	b-d
	S.19	1046.08	c-e	S.38	3915.49	d	S.19	896.99	cd	S.11	3129.27	c	S.28	25.68	b-d
	S.38	1017.12	de	S.16	3563.47	e	S.12	858.73	de	S.14	2940.57	d	Check 2	25.29	b-e
	S.11	1016.18	de	S.14	3469.83	ef	S.2	841.33	e	S.24	2907.81	de	S.15	24.51	b-f
	S.16	1014.50	de	S.12	3342.16	fg	S.27	833.14	e	S.22	2831.04	de	S.16	21.96	c-g
	S.25	1005.65	de	S.22	3259.25	g	S.1	805.12	ef	S.16	2780.54	ef	S.9	19.60	c-h
Lowest values	S.32	430.06	n	S.32	1476.23	q	S.32	345.32	rs	S.32	1272.25	q	S.24	10.56	h-l
	S.33	414.53	no	S.28	1440.03	q	S.3	318.92	s	S.28	1057.92	r	Check 1	10.03	h-l
	S.3	380.21	n-p	S.3	1238.21	r	S.28	309.66	s	S.3	1056.83	r	S.4	9.57	h-l
	S.30	308.97	o-q	S.31	1030.45	s	S.8	223.55	t	S.4	892.57	s	S.29	9.53	h-l
	S.8	284.02	pq	S.30	997.71	st	S.31	208.87	t	S.31	853.83	st	S.2	9.16	i-l
	S.31	266.82	pq	S.4	986.96	s-u	S.30	207.84	t	S.30	852.11	st	S.20	7.79	j-l
	S.23	246.21	q	S.8	969.26	s-u	S.23	199.98	tu	S.8	836.96	st	S.39	6.43	kl
	S.4	235.47	q	S.23	852.86	tu	S.4	198.49	tu	S.23	707.98	tu	S.33	6.32	kl
	S.9	191.05	qr	S.9	842.33	u	S.9	150.57	u	S.9	677.34	u	S.5	5.92	kl
	S.36	102.30	r	S.36	513.58	v	S.36	84.35	v	S.36	440.88	v	S.11	2.71	l
Mean		698.88			2512.51			559.09			2072.84			16.38	

Means sharing the same letters within the same column are not significantly different by the Tukey's test (P ≤ 0.05)

FIGURAS

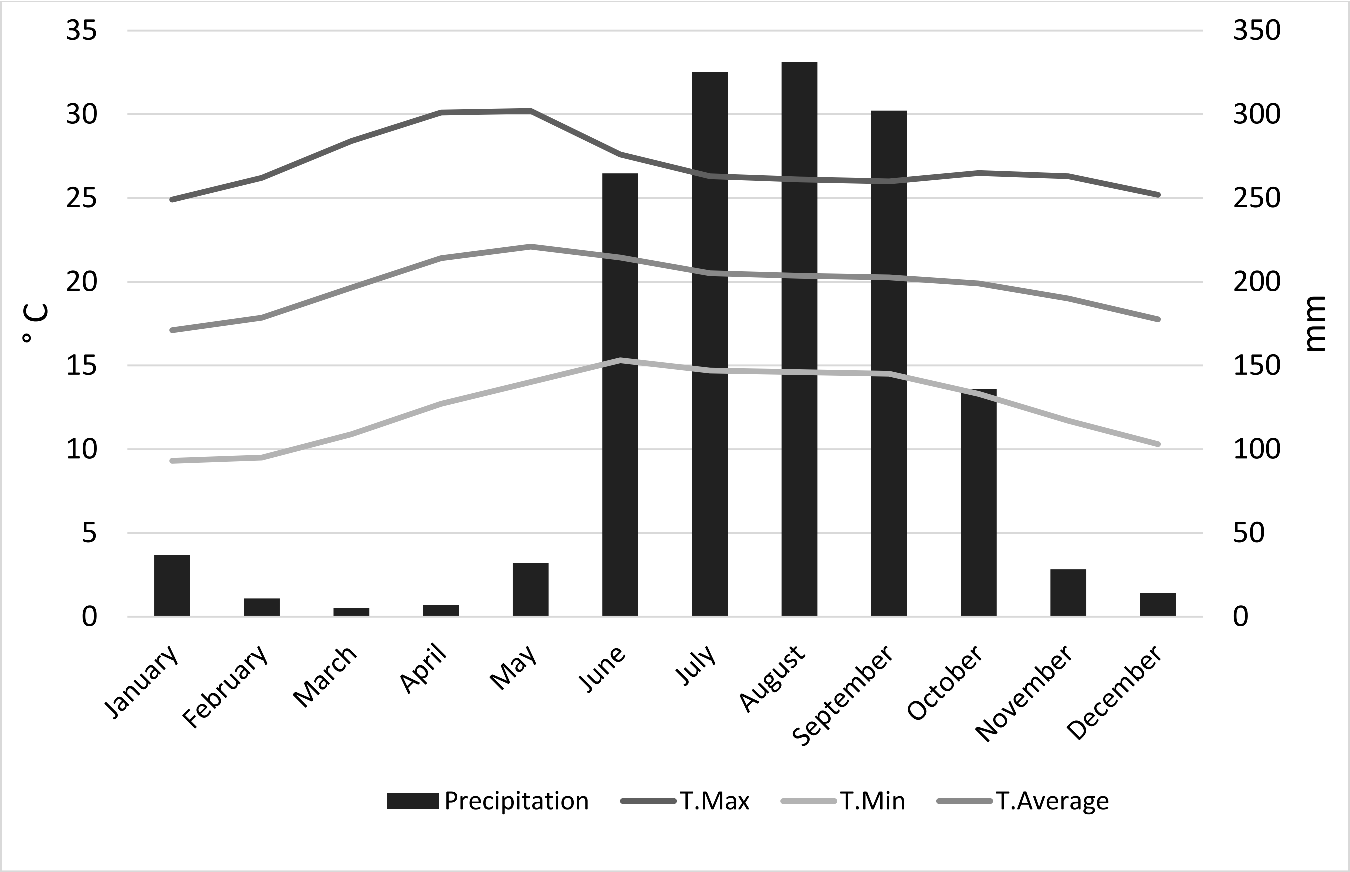

Figure 3.1. Monthly temperature and precipitation over the Ziracuaretiro, Michoacan, Mexico for a 35-yr (1963–99) period. Data from the INIFAP-Mexico [8].

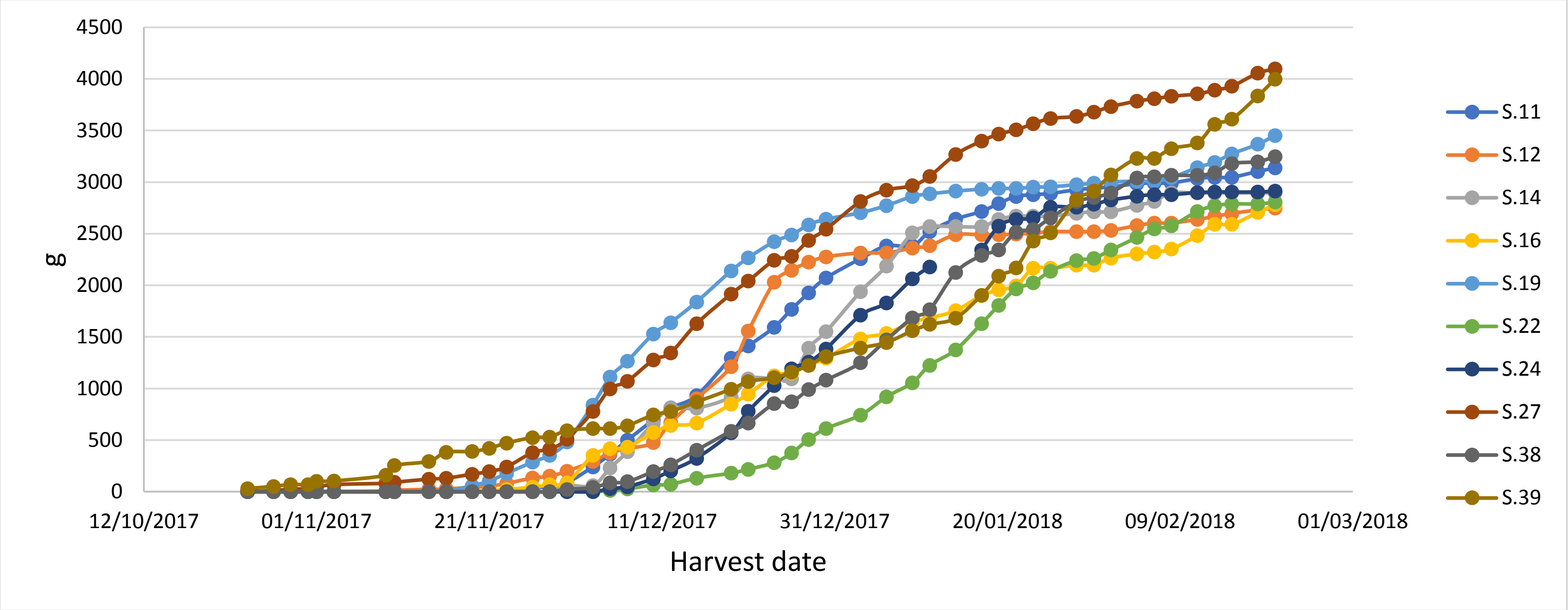

Figure 3.2. Cumulative marketable yield of the best ten raspberry selections evaluated in the grow season of 2017-2018.

ANEXOS

Table 1S Values of best linear unbiased prediction (BLUP) estimated by mixed model for parents and families.

Genotype	Marketable fruit yield/plant (g)	Number of fruits/plant	Soluble solids content (°Bx)	Average fruit weight (g)	Fruit diameter (cm)	Fruit length (cm)	Number of canes/plant	Cane length (cm)
CP65	-199.15 **	-71.13 ***	0.46	-0.39	-0.03	-0.18 *	1.48	57.16 ***
CP47	45.18	21.88	1.21 ***	0.17	0.22 **	0.2 *	2.16 **	97.83 ***
TD-865	53.99	-25.75	2.9 ***	0.76 *	0.07	0.23 **	-4.37 ***	57.4 ***
MRSL	450.69 ***	21.91	-1.81 ***	7.9 ***	0.47 ***	0.8 ***	-5.61 ***	-8.41
MU1	155.12 *	-2.87	1.74 ***	0.42	-0.08	-0.01	1.05	0.22
JG	-188.75 **	-55.91 ***	0.5	-0.61 *	-0.06	-0.21 **	-3.45 ***	57.16 ***
JJ-24	-212.7 **	-61.6 ***	0.25	-0.69 *	-0.33 ***	-0.09	0.69	-16.79
CP57	90.85	54.37 ***	-3.13 ***	-0.98 **	-0.2 **	-0.26 **	-6.59 ***	-61.16 ***
CP65×CP47	-49.39	-10.2	0.66 *	-0.5	0.1	0.02	3.29 ***	-37.84 ***
CP65×TD-865	-8.32	33.55 **	-0.07	-0.5	-0.19 *	-0.22 **	0.61	17.32 *
CP65×MRSL	285.41 ***	68.99 ***	-0.26	0.05	0.91 ***	0.62 ***	4.19 ***	-30.52 ***
CP65×MU1	-92.96	-27.33	0.4	-0.54	-0.16 *	-0.24 **	-1.85 *	-48.04 ***
CP65×JG	-314.81 ***	8.53	-0.55	-0.55	-0.3 ***	-0.44 ***	-4.58 ***	-0.87
CP65×JJ-24	3.24	-9.98	0	-0.77 *	-0.39 ***	-0.33 ***	-3.6 ***	80.72 ***
CP65×CP57	-332.8 ***	-90.61 ***	-1.26 ***	-1.74 ***	-0.28 ***	-0.47 ***	0.37	-8.41
CP47×TD-865	-10.74	-17.4	1.31 ***	0.18	-0.16 *	-0.17 *	-3.24 ***	-11.33
CP47×MRSL	-84.21	-47.69 **	-0.77 *	0.8 **	-0.22 **	-0.16 *	5.73 ***	-40.41 ***
CP47×MU1	274.45 ***	135.27 ***	0.79 *	0.04	-0.02	0.11	0.19	5.89
CP47×JG	-325.6 ***	-87.34 ***	0.63 *	-0.73 *	0.08	-0.01	-1.22	65.49 ***
CP47×JJ-24	95.38	28.28	-0.1	-0.27	-0.04	0.09	0.89	-36.91 ***
CP47×CP57	151.38 *	59.72 ***	0.91 **	-0.62 *	-0.11	0.06	4.72 ***	61.79 ***

TD-865×MRSL	64.44		-33.64	*	0.63	*	2.11	***	0.62	***	1.01	***	-2.33	**	-52.51	***
TD-865×MU1	323.16	***	153.19	***	0.58		0.05		-0.01		0.19	*	2.88	***	21.86	*
TD-865×JG	29.07		28.53		-0.45		-0.74	*	-0.22	**	-0.13		3.22	***	-10.38	
TD-865×JJ-24	-222.26	***	-64.34	***	1.45	***	-0.76	*	-0.13		0.07		-3.61	***	5.43	
TD-865×CP57	-175.26	**	-54.07	***	-0.91	**	-0.66	*	-0.04		0		-5.45	***	6.07	
MRSL×MU1	420.08	***	75.37	***	-0.14		0.92	**	0.94	***	0.68	***	3.7	***	-32.79	***
MRSL×JG	285.34	***	52.35	***	-1.16	***	0.26		1.19	***	0.81	***	6.2	***	-22.46	*
MRSL×JJ-24	126.42		50.63	**	1.12	***	0.16		-0.22	**	-0.07		0.25		-22.17	*
MRSL×CP57	-34.17		-7.91		-2.16	***	-0.19		-0.64	***	-0.75	***	-0.6		-46.22	***
MU1×JG	-321.51	***	-74.05	***	0.18		0.92	**	-0.29	***	-0.52	***	-1.38		23.27	**
MU1×JJ-24	234.58	***	33.41	*	0.47		-0.06		0.05		-0.01		0.98		14.02	
MU1×CP57	-254.61	***	-53.71	***	-0.19		-1.84	***	-0.09		-0.13		7.34	***	-48.28	***
JG×JJ-24	65.73		32.74	*	-0.26		-0.12		-0.1		-0.1		-0.08		2.19	
JG×CP57	-155.31	*	-4.9		-1.15	***	-1.31	***	-0.2	**	-0.32	***	0.47		35.22	***
JJ-24×CP57	-171.95	**	-58.29	***	-1.8	***	-0.15		-0.14		-0.07		-2.43	**	-73.53	***

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

Table 2S Analysis of variance for method II diallel design.

Source of variation	Degrees of freedom	Mean squares	Expected mean squares
Year [Y]	l-1	MS_E	$\sigma^2_E + r\sigma^2_{GxL} + g\sigma^2_{R(L)} + rg\sigma^2_L$
Replications (Y)	l(r-1)	$MS_{R(L)}$	$\sigma^2_E + g\sigma^2_{R(L)}$
Genotype	g-1	MS_G	$\sigma^2_E + r\sigma^2_{GxL} + rl\sigma^2_G$
General Combining Ability	p-1	MS_{GCA}	$\sigma^2_E + r\sigma^2_{SCAxL} + rl\sigma^2_{SCA} + r(p+2)\ \sigma^2_{GCAxL} + rl(p+2)\sigma^2_{GCA}$
Specific Combining Ability	[p(p-1)]/2	MS_{SCA}	$\sigma^2_E + r\sigma^2_{SCAxL} + rl\sigma^2_{SCA}$
Genotype× Env	(g-1)(l-1)	MS_{GxL}	$\sigma^2_E + r\sigma^2_{GxL}$
General Combining Ability × Env	(p-1) (l-1)	MS_{GCAxL}	$\sigma^2_E + r(p+2)\sigma^2_{GCAxL}$
Specific Combining Ability × Env	{[p(p-1)]/2}(l-1)	MS_{SCAxL}	$\sigma^2_E + r\sigma^2_{SCAxL}$
Error	Difference	MS_E	σ^2_E

l number of year, *r* number of replications or blocks, *g* number of genotypes, *p* number of parents, MS_E mean square of error; $MS_{R(L)}$ mean square of replications neaded within year, MS_G mean square of genotypes, MS_{GCA} mean square of general combining ability, MS_{SCA} mean square of specific combining ability, MS_{GCAxL} mean square of general combining ability-year interaction, MS_{SCAxL} mean square of specific combining ability-year interaction, MS_E mean square of error

Table 3S. Correlation of the different estimators on eight quantitative traits evaluated on the population.

Pairs	Marketable fruit yield/plant	Number of fruits/plant	Soluble solids content	Average fruit weight	Fruit diameter	Fruit length	Number of canes/plant	Cane length
SCA VS PV	0.81	0.94	0.28	-0.09	0.84	0.79	0.82	0.72
SCA vs BV_{BLUP}	-0.07	-0.28	-0.38	-0.40	0.05	0.00	-0.08	-0.35
SCA vs BV_{GCA}	0.05	0.10	-0.37	-0.45	0.09	0.01	0.05	-0.23
PV vs BV_{BLUP}	0.43	-0.01	0.68	0.67	0.49	0.59	-0.05	0.28
PV vs BV_{GCA}	0.61	0.37	0.74	0.75	0.60	0.61	0.43	0.45
BV_{BLUP} vs BV_{GCA}	0.87	0.54	0.97	0.98	0.90	0.98	0.57	0.89

CONCLUSIONES GENERALES

En general, los efectos no aditivos fueron más importantes que los efectos aditivos en la mayoría de las características evaluadas de los genotipos de frambuesa considerados. Progenitores como MRSL y MU-1 tuvieron altos valores de aptitud combinatoria general, evidenciando que tales genotipos pueden servir como donadores potenciales en un programa de mejoramiento para incrementar el rendimiento y la calidad de fruta.

Por otro lado, se observó que el valor fenotípico, así como la aptitud combinatoria específica exhibieron una baja correlación con las distancias genéticas parentales. En contraste, los estimadores basados en efectos aditivos tuvieron una mejor correlación. También se observó que la heredabilidad juega un papel importante en la relación entre distancia genética parental y los estimadores aditivos.

Con base en los resultados de las selecciones avanzadas, se encontró que las selecciones con los mayores rendimientos exhibieron variación en cuanto al periodo de cosecha. Tal resultado permite que los productores puedan tener un programa de cosechas más flexible y acorde a sus necesidades. Los rendimientos y la alta calidad de fruta encontrada en selecciones como S.27 y S.39, evidenciaron su buena adaptabilidad a climas tropicales. Adicionalmente, se observó que ambas selecciones cumplieron con los requerimientos mínimos para el mercado de exportación, sugiriendo que S.27 y S.39 pudieran ser materiales óptimos para producción de fruta.