

Heterosis and agronomic performance of raspberry families

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ABSTRACT

Objective: To study the heterosis and agronomic performance of raspberry (*Rubus idaeus*) F₁ families derived from open-pollinated parents, and to investigate the heterotic relationships between yield and its components.

Design/methodology/approach: A total of thirty-five genotypes, including eight open-pollinated raspberry cultivars, their 28 F₁ families and one check, were evaluated for vegetative and fruit traits. The trial was carried out under a randomized block design and under open field conditions.

Results: Mid-parent heterosis (MH) ranged from -94.83 to 311.67 %, whereas the better parent heterosis (BPH) values varied from -94.26 to 235.00%. We observed that the heterosis values for yield had a strong and positive correlation ($r=0.89$) with the heterosis values for number of fruits per plant.

Limitations on study/implications: Heterosis and performance of F₁ families in raspberry would depend on the pedigree of parents as their relatedness is a key factor to exploit the heterosis in plants.

Findings/conclusions: High values of heterosis were found in some raspberry crosses. Progeny derived from parents MU1 and TD865 showed considerable mid-parent heterosis (MH) and good performance for fruit size-related traits, soluble solids content and yield, evidencing that both parents may be utilized as donor parents in raspberry breeding program.

Keywords: Raspberry breeding, *Rubus idaeus*, heterosis, hybrid performance.

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INTRODUCTION

In Mexico, raspberry (*Rubus idaeus* L.) has growth in total annual production, harvested area, and yield per hectare particularly in the states of Michoacán and Jalisco (SIAP, 2019). In the past, the 'Autumn bliss' variety was the most widely planted in Mexico.



Recently, the raspberry industry in Mexico have invested in the developing new varieties with better fruit quality (flavor, firmness, and color) and yield (Hernández-Bautista *et al.*, 2019). The development of new raspberry varieties is carried out employing traditional breeding schemes; 1) parents heterozygous are crossed manually, 2) individual selection is worked in the new F₁ families, 3) the best plants are propagated clonally by roots or *in vitro* techniques for a second evaluation, and 4) the best selections observed in the second evaluation are evaluated in a large trial named semi-commercial evaluation (Hernández-Bautista *et al.*, 2019).

Heterosis or hybrid vigor is defined as the phenomenon where the progeny derived from the cross of two parents shows superior performance than their parents (Acquaah 2007). Three hypotheses have been proposed to explain the phenomenon of heterosis. The dominance hypothesis, which is the hypothesis accepted most widely, explains that recessive genes of each inbred parent are masked by the dominant genes when these are inherited to F₁ progeny (Davenport, 1908). The second hypothesis, proposed by East (1980), is known as true overdominance and establishes that the heterozygote genotype is superior to its both homozygous parents due to the overexpression of the genes. Epistasis is considered the third genetic model to explain heterosis. Epistasis particularly that involves dominance effects (dominance × dominance) has been reported as main factor conferring heterosis (Yu *et al.*, 1997).

Previous studies suggest that heterosis is positively related to the genetic distance observed between the two parents (Cox and Murphy, 1990). Therefore, it is common in the breeding programs to maintain two or more heterotic groups. In contrast, studies in cassava (Ceballos *et al.*, 2016), and pepper (Geleta *et al.*, 2004) reported a poor relationship between genetic distance and heterosis, suggesting heterosis is a complex phenomenon which is affected by genetic and environmental factors. The objectives of the paper were: 1) to study the degree of heterosis and agronomic performance of raspberry hybrids growth under open field conditions, and 2) to study the heterotic relationships among yield and its components.

MATERIALS AND METHODS

The plant material for this study consisted of eight open-pollinated raspberry parents, their F₁ families and one check. A total of 28 F₁ families were obtained under a diallel mating design without reciprocal crosses. The parental genotypes were CP65, CP47, TD865, MRSL, MU1, JG, JJ24 and CP57, and the check was one commercial variety named 'Autumn Bliss'. The trial was performed under open-field conditions and conducted from September 2015 to May 2016 in Ziracuaretiro, Michoacán, Mexico. Parents, F₁ hybrid families and one check were transplanted under a randomized complete blocks design with four replicates (26 plants per plot). The agronomic management for fertilization was worked following the recommendations for commercial production.

A total of nine traits quantitative traits were scored. Number of canes per plant and plant height were evaluated in each plant at 50% blooming stage. Number of berries per plant, berry weight (g), berry length (mm), berry width (mm) and total soluble solids (°Bx), were obtained from harvests that were worked two times weekly for two months.

Number of drupelets per berry was measured by counting the drupelets from 10 fruits with exportation quality. Finally, yield per plant was estimated as total weight obtained of all harvesters worked throughout the season.

Data were analyzed using the mean values of each genotype in each replication. Analysis of variance and Tukey's test were performed ($P \leq 0.05$). For each trait, components of phenotypic variance were estimated from analysis of variance using restricted maximum likelihood methods. Experimental data from field trial was analyzed using the following mixed linear model:

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

where Y_{ij} is the observed performance of the i th hybrid in the block j , μ is the overall mean, h_i is the random effect of hybrid i , b_j is the fixed effect of the block j and e_{ij} is the random residual term. The computation was performed using the PROC MIXED procedure in SAS Program version 9.3 (SAS Institute, 2012). The percentage heterosis based on mid-parent (MH) and better parent (BPH) were calculated using the following formulas:

$$\text{Mid-parent heterosis} = \frac{\left(F_1 - \left(\frac{P_1 + P_2}{2} \right) \right)}{\frac{P_1 + P_2}{2}} \times 100$$

$$\text{Better-parent heterosis} = \frac{(F_1 - (HP))}{HP} \times 100$$

where: F_1 = mean of F_1 family, P_1 = mean of female parent, P_2 = mean of male parent and HP = is the better parent value.

Finally, to know how the values of heterosis for yield are affected by the yield-components heterotic values, the Pearson's correlation coefficients were estimated using the mid-parent (MH) and better-parent heterosis (BPH) values. This analysis was performed employing PROC CORR in SAS program version 9.3 (SAS Institute, 2012).

RESULTS AND DISCUSSION

Analysis of variance detected significant differences for the factor genotypes on all studied traits (Table 1), demonstrating the presence of sufficient genetic variability among parents and families. These results were supported by estimated genetic variances. Yield per plant exhibited the highest proportion of genetic variance, whereas berry size-related traits (berry length and width) had the lowest levels of genetic variance. Number of berries per plant and plant height had a relatively high proportion of variance evidencing the wide gene pool presents in the population. Berry weight, number of canes per plant and soluble solids content had variance values < 10 , and number of drupelets > 480 . Similar results in

phenotypic variation were reported by Fotirić-Akšić *et al.* (2011) and Stephens *et al.* (2012), who found a low phenotypic variance for berry weight, berry length, solid soluble content, berry width, and high variance for height plant and number of drupelets.

Some genotypes exhibited better traits than those observed on ‘Autumn Bliss’ under open field conditions (Table 2). For berry weight, MRSL exhibited with the highest value for this trait (13.25 g), followed by TD865×MRSL and TD865. In the case of number of berries per plant, the genotypes ranged from 10 fruits to 235 fruits. Sixteen F_1 families produced a higher number of berries compared with the check, and the family TD865×MU1 was the best. For yield, the highest values in the families were found on TD865×MRSL and MRSL×MU1, which exhibited values of 740.55 and 721.45 g, respectively, followed by CP47×CP57 and CP47×MU1.

Concerning to number of canes, the family MU-1×CP57 reflected the highest value (14 canes) for this characteristic whereas lowest value was obtained for the parental CP57. The highest values for plant height were noticed in plants of the genotypes CP47, CP65×JJ24, CP47×JG and CP47×CP57. For fruit-size related traits such as berry length, berry diameter and number of drupelets per berry, the best hybrid families that reflected the highest values were determined for the hybrid combinations TD865×MRSL for berry length; MRSL×JG for berry diameter, and MRSL×MU1 for number of drupelets per fruit. Finally, for soluble solids content, more than 50% of the genotypes exhibited higher values than the check, where crosses involving TD865 tended to show high soluble solids content followed by the TD865×JJ24.

The heterosis percentages values relative to mid-parent (MH) and better parent (BPH) are presented in Table 3. Across the entire experiment, about 40% of the crosses exhibited MH and a lower percentage of families showed a positive BPH for every trait. In total yield per plant, the MH ranged from −91.83 to 122.27%, whereas the BPH from −94.26 to

Table 1. Mean squares of analysis of variance and genetic components for yield and eight yield-related characteristics of the 37 evaluated genotypes of raspberry.

Trait	Mean Squares			C. V.	Variance component		
	Genotype	Replication	Error		σ_G^2 †	σ_{REP}^2	σ_E^2
Yield per plant (g)	163435.93 **	3982.40	4942.64	17.68	39623.30	−25.95	4942.60
Number of berries per plant	11881.75 ***	387.56	456.57	20.09	2856.30	−1.87	456.57
Berry weight (g)	11.32 ***	0.27	0.21	10.24	2.78	0.00	0.21
Berry length (mm)	0.61 **	0.02	0.01	4.61	0.15	0.00	0.01
Berry width (mm)	0.60 ***	0.01	0.01	4.73	0.15	0.00	0.01
Number of drupelets per berry	1987.04 ***	69.67	41.81	7.44	486.31	0.75	41.81
Number of canes per plant	38.34 ***	1.21	0.99	14.29	9.34	0.01	0.99
Plant height (cm)	7407.27 ***	6.29	408.93	11.04	1749.60	−10.88	408.93
Total soluble solids (°Bx)	6.56 ***	1.16	0.42	6.06	1.53	0.02	0.42
d.f.	36	3	108				

† σ_G^2 = Genotypic variance; σ_{REP}^2 = Blocks variance; σ_E^2 = Environmental variance; f. = Degrees of freedom; **, *** indicate significant difference at $P < 0.01$ and < 0.001 , respectively.

Table 2. Mean performance of 8 parents, 28 F₁ families and the check ‘Autumn Bliss’ for nine characters of raspberry.

Genotype	Yield per plant (g)	Number of berries per plant	Berry weight (g)	Berry length (mm)	Berry width (mm)	Number of drupelets per berry	Number of canes per plant	Plant height (cm)	Total soluble solids (Bx°)
CP65	248.98 j-p	55.45 l-p	3.98 e-i	2.01 g-j	2.15 d-h	69.75 l-m	8.40 d-h	241.25 a-e	11.13 b-h
CP47	472.86 d-i	126.21 c-j	4.55 c-h	2.49 c	2.51 c	98.25 c-h	8.70 d-g	282.50 a	12.40 a-c
TD865	451.39 e-i	81.67 i-n	5.48 bc	2.46 cd	2.27 cd	127.50 a	3.00 m-o	241.50 a-e	13.70 a
MRSL	904.17 [†] a	124.25 c-k	13.25 a	3.16 a	2.82 b	112.75 a-d	2.00 no	174.75 f-l	9.27 i-l
MU1	560.23 b-f	103.44 e-l	4.89 c-g	2.22 c-g	2.13 d-h	104.50 b-f	7.75 e-i	183.50 f-l	12.45 a-c
JG	209.54 l-q	59.50 l-p	3.80 f-k	2.01 g-j	2.15 d-h	69.75 l-n	4.00 k-o	241.25 a-e	11.28 b-f
JJ24	210.67 l-q	58.35 l-p	3.66 g-k	2.12 e-i	1.87 hi	92.25 e-j	8.25 d-h	166.25 f-m	10.49 d-j
CP57	518.70 d-h	174.90 bc	3.28 h-k	2.02 g-j	2.07 d-i	104.50 b-f	1.32 o	112.71 mn	7.59 l
CP65×CP47	405.65 f-l	111.60 e-l	3.91 f-j	2.10 f-i	2.17 d-g	78.56 i-m	9.84 b-e	144.90 i-n	11.33 b-f
CP65×TD865	428.80 f-k	136.45 c-h	3.91 f-j	2.10 f-i	2.13 d-h	82.37 g-l	7.40 e-j	200.85 c-i	10.58 d-j
CP65×MRSL	666.26 b-d	168.10 cd	4.46 c-h	2.85 b	3.14 a	111.79 a-d	10.60 b-c	152.33 g-n	10.55 d-j
CP65×MU1	246.55 j-p	70.20 j-o	3.88 f-j	2.07 g-i	2.15 d-h	88.39 f-k	5.33 i-m	134.56 k-n	11.39 b-f
CP65×JG	432.67 f-j	97.50 f-l	3.86 f-j	1.77 jk	1.90 f-i	64.04 m-o	3.00 m-o	182.40 f-l	10.13 e-j
CP65×JJ24	454.54 e-i	127.21 c-j	3.65 g-k	1.85 i-k	1.79 ij	71.66 k-n	4.00 k-o	265.15 ab	10.65 c-j
CP65×CP57	73.51 p-q	29.68 n-p	2.66 jk	1.72 kl	1.89 f-i	34.36 q	7.75 e-i	174.75 f-l	9.38 h-l
CP47×TD865	335.10 h-n	90.30 g-m	4.60 c-g	2.03 g-j	2.03 d-i	74.35 j-n	4.00 k-n	171.79 f-l	12.05 a-d
CP47×MRSL	279.70 i-n	64.85 k-p	5.23 c-e	2.04 g-j	1.97 e-i	75.46 j-n	11.75 a-n	142.29 j-n	9.90 f-j
CP47×MU1	517.10 d-h	224.10 ab	4.46 c-h	2.29 c-g	2.16 d-h	75.74 j-n	7.00 f-j	189.25 e-k	11.51 b-f
CP47×JG	113.00 o-q	30.75 m-p	3.69 g-k	2.18 d-h	2.26 cd	82.15 g-m	5.89 h-l	249.70 a-c	11.35 b-f
CP47×JJ24	471.60 d-i	138.10 c-h	4.14 d-i	2.37 c-f	2.22 c-e	81.06 h-m	8.00 d-i	145.85 i-n	10.99 b-i
CP47×CP57	535.10 c-g	168.85 b-d	3.79 f-k	2.28 c-g	2.10 d-h	96.27 d-i	11.60 a-c	245.95 a-d	11.64 b-e
TD865×MRSL	346.95 g-n	76.05 i-o	6.55 b	3.22 a	2.82 b	107.79 b-e	4.75 j-n	130.02 l-n	11.35 b-f
TD865×MU1	740.55 ab	235.50 a	4.47 c-h	2.39 c-e	2.18 d-g	80.81 h-m	9.20 c-g	205.45 c-h	11.25 b-g
TD865×JG	352.45 g-n	132.00 c-i	3.67 g-k	2.09 f-i	2.01 d-i	82.28 g-l	9.65 b-f	172.75 f-l	10.18 e-j
TD865×JJ24	185.56 m-q	52.50 l-p	3.65 g-k	2.29 c-g	2.06 d-i	73.03 k-n	3.88 l-o	188.79 e-k	12.60 ab
TD865×CP57	235.63 k-p	62.25 l-p	3.75 f-k	2.24 c-g	2.18 d-f	115.25 a-c	2.25 no	189.44 d-k	10.15 e-j
MRSL×MU1	721.45 a-c	170.65 b-d	5.34 b-d	2.95 ab	3.12 a	126.51 a	10.00 b-e	150.03 h-n	10.50 d-j
MRSL×JG	631.10 b-e	154.40 c-f	4.68 c-g	3.03 ab	3.40 a	121.90 ab	12.35 ab	160.50 g-n	9.44 g-k
MRSL×JJ24	489.30 d-h	158.05 c-e	4.59 c-g	2.12 e-i	1.95 e-i	82.11 g-m	7.40 e-j	160.80g-n	11.81 b-e
MRSL×CP57	366.65 f-m	105.70 e-l	4.22 c-i	1.45 l	1.56 j	48.00 o-q	6.70 g-k	136.40 k-n	8.85 j-l
MU1×JG	100.26 o-q	19.91 p-o	5.35 b-d	1.70 kl	1.89 g-i	44.23 pq	5.74 h-m	206.88 c-g	11.33 b-f
MU1×JJ24	639.75 b-e	142.75 c-g	4.36 c-i	2.22 c-g	2.23 c-e	58.15 n-p	8.08 d-i	197.50 c-j	11.13 b-h
MU1×CP57	162.88 n-q	74.13 i-o	2.55 k	2.14 e-h	2.18 d-g	107.77 b-e	14.00 a	134.32 k-n	10.45 e-j
JG×JJ24	467.00 e-i	144.65 c-g	4.29 c-i	2.12 e-i	2.09 d-h	81.13 h-m	7.25 e-i	185.50 e-l	11.25 b-g
JG×CP57	29.75 q	10.05 p	3.10 i-k	1.90 h-k	2.00 d-i	85.47 g-l	7.85 d-i	219.00 b-f	9.45 g-k
JJ24×CP57	252.47 j-p	62.65 l-p	5.02 c-f	2.15 e-h	2.03 d-i	99.84 c-g	5.34 i-m	108.71 n	9.23 i-l
‘Autumn Bliss’	458.59 e-i	92.50 g-l	4.68 c-g	2.22 c-g	1.93 f-i	104.50 b-f	4.00 k-o	190.77 d-k	7.80 kl
LSD	196.96	59.86	1.28	0.29	0.29	18.12	2.79	56.65	1.82
Mean	397.74	106.36	4.47	2.23	2.20	86.87	6.97	183.25	10.72

Genotypes sharing same letter are equal according to Tukey’s test (P<0.05); [†]=Number in italics indicates the highest value for each case.

Table 3. Percentages of mid-parent (MH) and better parent (BPH) heterosis exhibited by F₁ hybrids for yield and eight yield-components.

Genotype	Yield per plant (g)		Number of berries per plant		Berry weight (g)		Berry length (mm)		Berry width (mm)		Number of drupelets per berry		Number of canes per plant		Plant height (cm)		Total soluble solids (°Bx)	
	MH	BPH	MH	BPH	MH	BPH	MH	BPH	MH	BPH	MH	BPH	MH	BPH	MH	BPH	MH	BPH
CP65×CP47	12.39	-14.21	22.87	-11.58	-8.27	-14.06	-6.94	-15.91	-6.62	-13.35	-6.48	-20.05	15.06	13.07	-44.67	-48.71	-3.68	-8.63
CP65×TD865	22.45	-5.00	99.02	67.07	-17.30	-28.63	-6.03	-14.66	-3.57	-6.22	-16.49	-35.40	29.82	-11.90	-16.79	-16.83	-14.81	-22.81
CP65×MRS1	15.56	-26.31	87.09	35.29	-48.21	-66.34	10.39	-9.67	26.44	11.35	22.51	-0.85	103.85	26.19	-26.77	-36.86	3.46	-5.17
CP65×MU1	-39.06	-55.99	-11.61	-32.11	-12.55	-20.75	-2.37	-6.93	0.26	-0.03	1.45	-15.41	-34.16	-36.51	-36.64	-44.23	-3.39	-8.53
CP65×JG	88.72	73.78	71.13	66.67	-0.76	-2.95	-12.09	-12.09	-11.33	-11.33	-8.18	-8.18	-51.61	-64.29	-24.39	-24.39	-9.60	-10.20
CP65×JJ24	97.78	82.56	123.56	118.01	-4.58	-8.36	-10.20	-12.48	-10.99	-16.65	-11.53	-22.32	-51.81	-52.38	30.13	9.91	-1.46	-4.27
CP65×CP57	-80.85	-85.83	-74.23	-83.03	-26.67	-33.12	-14.66	-14.76	-10.10	-11.77	-60.56	-67.12	59.47	-7.74	-24.84	-27.56	0.24	-15.67
CP47×TD865	-27.49	-29.13	-13.12	-28.45	-8.21	-15.97	-18.24	-18.69	-14.95	-18.96	-34.13	-41.69	-31.62	-54.02	-34.43	-39.19	-7.66	-12.04
CP47×MRS1	-59.38	-69.07	-48.22	-48.62	-41.25	-60.54	-28.02	-35.63	-26.09	-30.17	-28.48	-33.08	119.63	35.06	-37.76	-49.63	-8.63	-20.16
CP47×MU1	0.11	-7.70	95.20	77.56	-5.60	-8.90	-2.85	-8.16	-7.03	-13.97	-25.29	-27.53	-15.15	-19.54	-18.78	-33.01	-7.35	-7.54
CP47×JG	-66.88	-76.10	-66.70	-75.64	-11.73	-19.01	-3.16	-12.50	-2.85	-9.86	-2.21	-16.39	-7.24	-32.30	-4.65	-11.61	-4.12	-8.47
CP47×JJ24	37.99	-0.27	49.65	9.42	0.90	-8.97	2.52	-5.15	1.45	-11.38	-14.90	-17.50	-5.33	-8.05	-35.00	-48.37	-3.98	-11.37
CP47×CP57	7.93	3.16	12.15	-3.46	-3.17	-16.74	1.11	-8.53	-8.12	-16.21	-5.04	-7.88	131.54	33.33	-2.83	-12.94	16.41	-6.15
TD865×MRS1	-48.81	-61.63	-26.14	-38.79	-30.07	-50.59	14.64	2.02	10.68	-0.07	-10.27	-15.46	90.00	58.33	-37.53	-46.16	-1.18	-17.15
TD865×MU1	46.41	32.19	154.50	127.76	-13.87	-18.45	2.10	-2.98	-0.98	-3.98	-30.33	-36.62	70.37	17.95	-3.32	-14.93	-14.00	-17.92
TD865×JG	6.65	-21.92	88.34	61.63	-20.75	-32.87	-6.49	-15.08	-8.75	-11.26	-16.58	-35.47	175.71	141.25	-28.43	-28.47	-18.53	-25.74
TD865×JJ24	-43.94	-58.89	-25.01	-35.72	-20.03	-33.29	-0.30	-7.28	-0.60	-9.31	-33.54	-42.73	-30.80	-52.74	-7.40	-21.83	4.18	-8.03
TD865×CP57	-51.42	-54.57	-51.48	-64.41	-14.28	-31.50	0.18	-8.92	0.64	-3.90	-0.65	-9.61	4.17	-25.00	-18.57	-21.56	-4.66	-25.91
MRS1×MU1	-1.47	-20.21	49.92	37.34	-41.14	-59.70	9.83	-6.52	25.84	10.54	16.46	12.20	104.08	28.21	-16.25	-18.24	-3.31	-15.66
MRS1×JG	13.33	-30.20	68.97	24.27	-45.09	-64.67	17.16	-4.13	36.98	20.63	33.59	8.12	311.67	208.75	-22.84	-33.47	-8.10	-16.27
MRS1×JJ24	-12.22	-45.88	73.11	27.20	-45.77	-65.40	-19.55	-32.80	-16.81	-30.76	-19.89	-27.17	45.10	-9.76	-5.69	-7.98	19.56	12.61
MRS1×CP57	-48.46	-59.45	-29.33	-39.57	-48.87	-68.12	-43.84	-54.00	-36.30	-44.81	-55.81	-57.43	303.61	235.00	-31.54	-39.04	4.97	-4.53
MU1×JG	-73.95	-82.10	-75.40	-80.74	22.99	9.25	-19.46	-23.22	-11.60	-11.86	-49.23	-57.67	-2.64	-26.36	-2.59	-14.25	-4.51	-9.02
MU1×JJ24	65.97	14.19	76.51	38.06	1.86	-10.97	2.13	-0.17	11.42	4.63	-40.90	-44.36	0.99	-1.47	12.94	7.63	-2.97	-10.61
MU1×CP57	-69.81	-70.93	-46.73	-57.62	-37.54	-47.87	1.26	-3.36	3.59	1.95	3.13	3.13	206.91	79.42	-34.04	-39.97	4.28	-16.06
JG×JJ24	122.27	121.67	147.58	147.26	15.11	12.99	2.64	0.03	4.00	-2.61	0.16	-12.05	18.85	-11.59	-8.96	-23.11	3.40	-0.20
JG×CP57	-91.83	-94.26	-91.39	-94.25	-12.34	-18.39	-5.42	-5.54	-5.03	-6.80	-1.90	-18.21	195.02	96.19	-5.81	-9.22	0.17	-16.19
JJ24×CP57	-30.77	-51.33	-46.28	-64.18	44.70	37.09	3.80	1.29	2.86	-1.93	1.49	-4.46	12.04	-34.96	-44.25	-51.42	2.03	-12.06

121.67%. A total of thirteen hybrids had a positive percentage of MH and BPH. Among these hybrids, the maximum heterosis for yield was obtained by JG×JJ24, with values of 122.27 and 121.67% for MH y BPH, respectively. These results were higher than those found by Kaczmarska *et al.* (2016), who reported better-parent heterosis (BPH) of strawberry as high as 28% in crosses derived from a top-cross-mating. For number of berries per plant, positive MH was detected on 15 hybrid families with magnitudes ranging from 12.15 to 154.50%, while 14 F₁ families exhibited positive BPH. The crosses TD865×MU1 and JG×JJ24 had the highest percentage of heterosis. For berry weight, MH ranged from -48.87 to 44.70% whereas BPH varied from -68.12 to 37.09%. In both estimations of heterosis, the hybrids JJ24×CP57, MU1×JG, and JG×JJ24 exhibited the highest heterosis percentages for this trait. In terms of berry length, 12 and 3 crosses reflected the highest positive values of MH and BPH, respectively, which had values that ranged from 0.18 to 17.16 % for MH and 0.03 to 2.02% for BPH. In berry width, BPH varied from -44.81 to 20.63 and MH ranged from -36.30 to 36.98. Among the F₁ hybrids, the highest heterosis was recorded by MRSL×JG. Concerning number of drupelets per berry, few hybrid families exhibited MH and BPH positive values, specifically, seven families for MH and three families for BPH. Among the hybrids, MRSL×JG and MRSL×MU1 were the best crosses with the highest value of heterosis for both cases. In number of canes per plant, 68% of the hybrids displayed positive MH whereas 43% of hybrids exhibited positive values for BPH. For plant height, the heterosis was only found on two families (CP65×JJ24 and MU1×JJ24). In terms of soluble solids content, only one hybrid family showed a positive BPH while ten families exhibited MH positive values. Considering all hybrids, MRSL×JG was the best cross with the highest heterosis for soluble solids content with values ranged from 12.61 to 19.56%. Such results are in agreement with Harbut *et al.* (2009), who evaluated 29 genotypes including 15 cultivars and 14 hybrids. They found that some strawberry hybrids had higher values of fruit weight and others vegetative traits, that their respective parents, indicating that heterosis were present for those traits.

Significant correlations ($P < 0.05$) were observed among heterosis values of F₁ progeny for some traits (Figure 1). Almost all detected correlations were similar for both MH and BPH. 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). The yield per plant was only positively correlated ($r = 0.89$ for both heterosis estimations) to number of berries per plant. These results are consistent with Stephens *et al.* (2012), who observed a positive correlation between yield and number of berries per plant, suggesting that yield heterosis is mainly caused by the increased number of berries per plant.

The fruit weight has been considered a primary component in the archived yield in each plant. González (2016) evaluated 42 F₁ sub-families of primocane red raspberry obtained under a partial diallel design. He found that the berry weight showed a poor correlation ($r = 0.03$) with the yield per plant. In contrast, Radovich *et al.* (2013) detected a moderate correlation between berry weight and yield. In our study, we found significant correlation between berry weight and berry length ($r_{\text{BPH}} = 0.41$), and number of canes per plant ($r_{\text{MH}} = -0.59$ and $r_{\text{BPH}} = -0.56$), but a non-significant association with yield,

	Yield/ plant	Number of berries per plant	Berry weight	Berry length	Berry width	Number of drupelets per berry	Number of canes per plant	Plant height	Total soluble solids
Yield/plant	1	0.89***	0.37	0.26	0.09	0.20	-0.25	0.30	0.24
Number of berries per plant	0.89***	1	0.11	0.20	0.14	0.15	-0.09	0.31	0.19
Berry weight	0.25	-0.01	1	0.41*	0.04	-0.08	-0.56**	0.12	0.06
Berry length	0.24	0.27	0.10	1	0.81***	0.51**	-0.29	0.07	-0.24
Berry width	0.20	0.25	-0.09	0.91***	1	0.58**	-0.01	0.02	-0.32
Number of drupelets per berry	0.20	0.20	-0.12	0.69***	0.70***	1	0.06	-0.16	-0.02
Number of canes per plant	-0.28	-0.13	-0.59**	-0.03	0.12	0.19	1	-0.20	-0.21
Plant height	0.35	0.32	0.15	0.03	0.01	-0.14	-0.21	1	0.20
Total soluble solids	-0.14	-0.21	-0.11	-0.06	-0.08	0.04	0.10	0.16	1

Figure. 1. Significant correlation coefficients among mid-parent (MP, lower diagonal) and better-parent (upper diagonal) heterosis values for yield and its components. *, **, *** indicate significant difference at $P < 0.05$, 0.01 and 0.001, respectively.

suggesting the association between yield and yield-components is complex and depends on genetic diversity degree and population type (floricane or primocane).

Berry length was positively correlated to berry width ($r_{MH}=0.91$ and $r_{BPH}=0.81$) and number of drupelets per berry ($r_{MH}=0.69$ and $r_{BPH}=0.51$). Berry width also exhibited significant positive correlation with the number of drupelets per berry ($r_{MH}=0.70$ and $r_{BPH}=0.58$). All previous results suggest that the heterosis for size fruit-related traits is influenced for the level of heterosis exhibited in the number of drupelets per berry. Similarly, Radovich *et al.* (2013) found that fruit size was positively affected by number of fruiting laterals and drupelets per berry. In addition, such positive association has also been reported in blackberry (Strik *et al.*, 1996), where cultivars presenting a high number of drupelets also exhibited a large fruit. Finally, we found a significant correlation between number of drupelets per berry and number of berries per plant ($r_{BPH}=0.38$); however, such association was only detected in the better parent heterosis values.

CONCLUSION

Some raspberry families out-yielded ‘Autumn Bliss’ and simultaneously showed significant heterosis for yield and other yield components. Specifically, the progeny derived

from parents MU1 and TD865 had good agronomic performance and positive heterosis for fruit size-related traits, soluble solids content and yield. Concerning the association between yield-components and yield heterosis, the number of berries per plant was the more important yield-component affecting the yield heterosis expression.

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