

## GENETIC PARAMETERS AND ESTIMATED BREEDING VALUES OF BLACKBERRY PARENTS UNDER A WARM ENVIRONMENT

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In blackberry, the identification of the best plants is usually based on the phenotypic value. However, the phenotypic value of complex traits is not always a reliable parameter that allows the maximum genetic gain per cycle of selection. The present study aimed to explore the breeding potential of thirteen blackberry parents based on their breeding values, and estimate genetic parameters of important traits in blackberry breeding. A total of fourteen crosses (sib-full families) were obtained from crossing thirteen blackberry genotypes. According to the mixed model 2, the heritability estimations ranged from 0.14 to 0.93. The highest heritability ( $h^2 > 0.9$ ) was found in days to the first pick and harvest interval, while the lowest one ( $h^2 < 0.2$ ) in berry weight. The genotypes 'Chickasaw',

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'S3', 'Choctaw', 'Tupy', and 'S5' exhibited simultaneously positive breeding values for yield, and berry weight, whereas 'Natchez', 'S1', and 'S6' for earliness and harvest interval. For soluble solids content, 'S6', 'S3', and 'Kiowa' had the best breeding values. Based on our results, the germplasm used in the study has additive effects with high commercial value that could be used in the blackberry programs.

*Key words:* Blackberry breeding, Earliness, Heritability, *Rubus spp*; Yield

## INTRODUCTION

Blackberries' consumption has increased due to their healthy properties that contain the berries (SOUZA *et al.*, 2014). This situation has generated an increase of nearly 44% in the world's cultivated area (STRIK *et al.*, 2008). In 2020, the world production of blackberries was 927,344 t, obtained in a harvested area of 129,871 hectares. Mexico is considered the largest blackberry producer, followed by Vietnam (FAOSTAT, 2020). In 7 years, blackberry production in Mexico drastically increased from 26, 985 t in 2007 to 270, 399 t in 2017, and represents about \$ 255. 4 million dollars. Mexican blackberry production is mainly accounted for by the states of Michoacán, Jalisco, and Colima (SAGARPA, 2019), specifically, the municipalities of Los Reyes and Periban produce 70% of the Mexican blackberry production.

In Mexico, blackberry production is based on a few varieties, 'Tupy' being the main cultivar grown by the farmers (CLARK and FINN, 2014), followed by some private varieties (INFORURAL, 2018). The development of new blackberry varieties is focused mainly on high yield, adaptability to new production regions, erect growing habit, thornlessness, and high fruit quality (CLARK and FINN, 2008). Specifically, a high fruit quality means good sweetness, firmness, brightness, color, and shelf life.

At present, Mexican blackberry production mainly is based on floricane-fruiting varieties. In floricane-fruiting varieties, the occurrence of low temperatures below 7.2°C is necessary to stimulate the differentiation of buds (CLARK *et al.*, 2005). In Mexico, blackberry production is based on a forced production system as farmers manipulate the flowering in floricane-fruiting blackberries without a dormancy period. Therefore, the development of new blackberry cultivars adapted to this specialized production system has become a priority in the different blackberry programs established in some production areas in Mexico.

In berries, there is evidence that fruit quality and yield exhibit a moderate or low heritability, which suggests that both traits have a quantitative complexity. In blueberry, CELLON *et al.* (2018) found moderate heritability levels ( $h^2 < 0.6$ ) for yield, fruit weight, fruit diameter, fruit firmness, and scar diameter. MATHEY *et al.* (2017) in 36 crosses of strawberries measured the heritability of a large set of characteristics related to the quality of internal and external product, plant, and flowering. They reported that most of the traits had heritability estimates ranging from low to moderate, evidencing a high quantitative-genetic complexity in such traits. Similar results, but in blackberry, were reported by DANEK and ORZEL, (2004), who found heritability estimates of 0.36 and 0.32 for growth vigor and frost resistance, respectively. Although there is limited information about the heritability of most of the traits with economic importance in blackberry, CLARK and FINN (2011) suggest that fruit size and shape are quantitatively inherited. For traits such as primocane fruiting and thornless, the inheritance is not

complex as both traits are controlled by a single recessive in populations of tetraploid blackberries (CASTRO *et al.*, 2013).

Quantitative genetics theory states that individual selection based on breeding values may be very successful in characteristics with low or moderate heritability (BERNARDO, 2020). In this sense, CELLON *et al.* (2018) demonstrated that the estimation of breeding values using a REML/BLUP approach maximized the genetic gains and improved the selection process in blueberry. In addition, previous studies established that incorporating pedigree information increases the prediction accuracy of breeding values (CROSSA *et al.*, 2010; BURGUEÑO *et al.*, 2012). In blackberry, the knowledge about breeding potential, based on additive values, of blackberry cultivars grown in Mexico remains limited. Thus, knowing the additive values of the blackberry cultivars with low chilling as well as quantitative-genetic complexity of traits will provide relevant information to breeders about the best breeding strategy for incorporating superior traits in their blackberry breeding program. The present study aimed to study the breeding potential of 13 blackberry genotypes and estimate the genetic parameters of important traits in blackberry breeding.

## MATERIALS AND METHODS

### *Plant material*

The plant material consisted of fourteen crosses (full-sib families) obtained from crossing 13 parents. The parental material included 6 varieties ('Brazos', 'Chickasaw', 'Choctaw', 'Kiowa', 'Natchez' and 'Tupy') and 7 open-pollinated selections labeled as 'S1', 'S2', 'S3', 'S4', 'S5', 'S6' and 'S7' (Table 1). The seven open-pollinated selections were identified into F<sub>2</sub> populations from commercial varieties. The fourteen crosses were made manually, and the combination of parents was based on the complementation of traits exhibited by each parent.

Table 1. Qualitative traits in blackberry parents under warning environmental conditions present in Michoacan State, Mexico.

Parent	Fruit size	Plant habit	Sweetness	Firmness	Fruiting-type	Spines
'Brazos' <sup>a</sup>	intermedium	semi-erect	intermedium-high	low	Florican	Presence
'Chickasaw' <sup>a</sup>	large	semi-erect	intermedium	low	Florican	Presence
'Choctaw' <sup>a</sup>	intermedium	semi-erect	intermedium-high	intermedium	Florican	Presence
'Kiowa' <sup>a</sup>	intermedium	semi-erect	intermedium-high	intermedium	Florican	Presence
'Natchez' <sup>a</sup>	large	semi-erect	intermedium	intermedium	Florican	Absence
'Tupy' <sup>a</sup>	intermedium	semi-erect	intermedium	intermedium	Florican	Presence
'S1'	intermedium	semi-erect	intermedium-high	intermedium	Florican	Presence
'S2'	large	semi-erect	intermedium-high	high	Primocane	Presence
'S3'	extra large	semi-erect	high	high	Florican	Presence
'S4'	intermedium	semi-erect	intermedium	intermedium	Florican	Presence
'S5'	small	semi-erect	high	low	Florican	Presence
'S6'	intermedium	semi-erect	high	intermedium	Florican	Presence
'S7'	intermedium	semi-erect	intermedium	intermedium	Florican	Presence

<sup>a</sup>The information given in the varieties released is the opinion given by the Mexican farmers in Michoacán State.

After crossing, a total of 100 seeds per parental combination were extracted from mature fruits, scarified with sulfuric acid for 3 hours, and stratified to 4°C for 2 months. The sowing was carried in 2 L pots filled with peat moss and vermiculite in December 2016. In the stage of seedling, on average, a total of 60 seedlings were obtained per cross, however, forty seedlings per cross were only transplanted to the field. The fourteen crosses and the variety 'Tupy' (Check) were transplanted to open field during the season of 2017 at Tangancicuaro, Michoacan State, Mexico. The trial was performed under a randomized complete blocks design with four replicates. Each plot consisted of 10 plants spaced 1 m apart in the row and 2.5 m between rows.

#### *Agronomic management*

During the vegetative growth, the plants were grown using fertilization with a high percentage of nitrogen and phosphorus. After 6 months, the tip of the stem and shortening laterals were pruned, and immediately a chemical defoliant based on phosphonitrate (150 g/L of water), urea (12.5 g/L of water), copper sulfate (3 g/L of water), thidiazuron (50 g/2000 L of water) and one commercial adherent (1 mL/ L of water) was sprayed one time. After one week, the bud break was promoted by weekly spraying of thidiazuron (20 g/ 2000 L of water), N-(2-Chloro-4-pyridyl)-N'-phenylurea (CPPU) (3 g/ 2000 L of water) and gibberellic acid (50 g/ 2000 L of water) for 3 weeks.

#### *Data collection*

The data collection began about 90 days after defoliation. From here on, fruit harvest was performed every 4 days. A total of six phenotypic traits were collected in each family during the harvest period. The number of berries per plant was obtained as the total of fruits produced per plant during the harvest period. Similarly, yield per plant was measured as the total weight of berries produced per plant during the harvest period. Berry weight was evaluated from a set of 5 berries with commercial grade ten times into the harvest period. Using the same berries set used for berry weight, soluble solids content was measured using a refractometer Atago 3810 Pal-1. Days to the first pick were evaluated as the number of days elapsed from the transplant until the first harvest. Harvest interval was measured as the number of days elapsed from the harvest beginning to the last pick.

#### *Statistical Analysis*

Estimation of breeding values was performed employing three different univariate mixed models. All models were fitted according to the description of MRODE (2014). In general, models 1 and 2 employed the following equation:

$$y = X\beta + Zu + e$$

where  $y$  is the vector of phenotypic values,  $\beta$  is the vector of fixed effects,  $u$  is the vector of random effects,  $X$  and  $Z$  are the incidence matrices of the elements in  $\beta$  and  $u$ , respectively, and  $e$  is the vector of residuals.

Since there was no significant difference between blocks, then the intercept ( $\mu$ ) was considered the only estimator in the fixed effects in all models. Concerning the random effects, the individuals of each family and parents were considered as random effects in model 1, giving a total of 308 estimators or BLUPs, whereas only parents were fitted as part of the random effects in the 12, giving only 13 parental estimators.

For model 3, the statistical model was modified by adding one term which considered parental grouping. We grouped the parents into three groups: parents from North America ('Choctaw', 'Kiowa', 'Chickasaw', 'Brazos' and 'Natchez'), parents from South America ('Tupy'), and parents from unknown origin ('S1', 'S2', 'S3', 'S4', 'S5', 'S6', and 'S7'). In this model, the intercept was considered a fixed effect, whereas the individuals of each cross, parents, and group as random effects.

In all models,  $u$  was normally distributed with  $\mu=0$  and variance-covariance

$$G = \sigma_A^2 A.$$

Matrix A was obtained using pedigreeemm Package (VAZQUEZ *et al.*, 2010).

The breeding value for each parent was obtained from the parental estimators or best linear unbiased predictors (BLUP). The BLUPs for all models were calculated using the following equation:

$$\hat{u} = GZ^T V^{-1}(y - X\hat{\beta})$$

All models were fitted in the R language (R CORE TEAM, 2018) and Henderson's equations were solved employing the BGLR package (PEREZ and DE LOS CAMPOS, 2014). The best fitting model was chosen by the statistics AIC, BIC (CHAKRABARTI and GHOSH, 2011), and residual variance. Narrow-sense heritability was calculated according to BERNARDO (2020) and Tukey's test was performed using the agricolae package (DE MENDIBURU and SIMON, 2015).

## RESULTS

### *Performance of statistical models*

Based on the AIC and BIC values, models 2 and 1 had the lowest values of AIC and BIC, suggesting that both models performed similarly in most of the traits (Table 2). However, model 2 over performed models 1 and 3 for days to the first pick and harvest interval.

The relationship between the predicted breeding values (BV) and observed values of each model was analyzed based on Pearson's coefficient (Figure 1). It was observed that the correlation ranged from 0.41 to 1.0. Model 2 had the highest correlation values in berry weight, number of berries per plant, yield per plant, and soluble solids content. Similarly, models 1 and 2 exhibited a perfect fitting when both models were performed in days to the first pick and harvest interval. Interestingly, model 3 exhibited poor performance in the prediction of breeding values for soluble solids content because the additive-variance value was zero. This situation led to a null estimation of breeding values for all individuals.

Table 2. Genetic variance components of the six quantitative traits scored on the blackberry population evaluated at Tangancicuaro, Michoacan State, Mexico

Parameter	Berry weight	Number of berries per plant	Yield per plant	Soluble solids content	Days to the first pick	Harvest interval
Model 1						
$\sigma^2_A$	0.51	20814.00	305516.00	1.11	1349.00	1352.00
$\sigma^2_e$	2.87	21178.00	161667.00	1.20	0.00	0.00
$\sigma^2_P$	3.37	41992.00	467183.00	2.31	1349.00	1352.00
$\mu$	5.65	167.44	452.53	11.63	276.26	91.44
$h^2$	0.15	0.50	0.65	0.48	1.00	1.00
AIC	290.29	246.13	274.68	242.86	34.31	35.53
BIC	293.98	249.81	278.37	246.54	36.74	37.96
Model 2						
$\sigma^2_A$	0.51	20869.00	303422.00	1.11	4988.20	6095.00
$\sigma^2_e$	3.12	31583.00	314484.00	1.75	499.20	466.00
$\sigma^2_P$	3.63	52452.00	617906.00	2.86	5487.40	6561.00
$\mu$	5.65	167.44	452.53	11.63	276.26	91.44
$h^2$	0.14	0.40	0.49	0.39	0.91	0.93
AIC	290.29	246.13	274.68	242.86	24.41	20.28
BIC	293.98	249.81	278.37	246.54	26.84	22.71
Model 3						
$\sigma^2_A$	0.56	14382.00	137264.00	0.00	2244.00	292.30
$\sigma^2_{groups}$	0.00	33384.00	325101.00	12.97	17699.00	3096.80
$\sigma^2_e$	0.49	25863.00	256667.00	8.05	10613.00	1662.90
$\sigma^2_P$	1.06	73629.00	719032.00	21.03	30556.00	5052.00
$\mu$	5.65	167.44	452.53	11.63	276.26	91.44
$h^2$	0.53	0.20	0.19	0.00	0.07	0.06
AIC	313.38	275.26	301.57	315.00	97.43	100.57
BIC	317.13	279.01	305.32	318.75	100.07	103.21

$\sigma^2_A$  = additive variance;  $\sigma^2_{groups}$  = variance due to the grouping;  $\sigma^2_e$  = residual variance;  $\sigma^2_P$  = phenotypic variance;  $h^2$  = narrow-sense heritability;  $\mu$  = population mean.

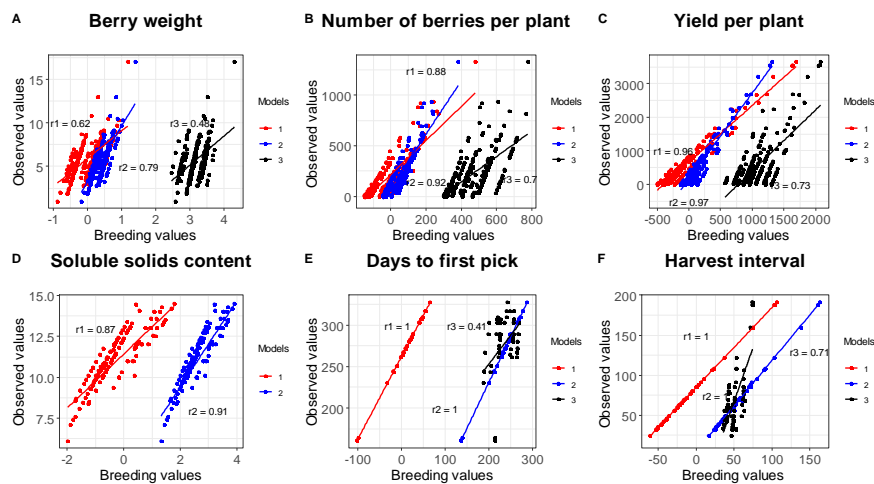


Fig. 1. Relationship between the observed phenotypic value and estimated breeding value by each model

*Agronomic performance of crosses*

The agronomic performance of each family is shown in Table 3. According to Tukey's test, there were non-significant differences ( $P < 0.05$ ) between 'Tupy' and most of the blackberry crosses for berry weight. In contrast, the crosses S2×Chickasaw, S4×S7, S2×Natchez, S2×Choctaw, and S2×Tupy were statistically higher in the number of berries per plant than 'Tupy'.

Concerning the yield per plant, the phenotypic values varied from 1761 to 120.4 g. The crosses S2×Chickasaw, Choctaw×S3, S3×Kiowa, S3×S6, and S2×S5, statistically yielded more than 'Tupy'; however, the best cross was S2×Chickasaw with a yield of 1761 g, and the worst was S2×Brazos with 120.4 g. For soluble solids content, there were non-significant differences between the best crosses and 'Tupy'. The highest value was observed in S3×S6 with 13.06 °Bx, and the lowest in S2×Natchez with 10.04 °Bx. For days to the first pick, S2×Natchez was the earliest cross in the study with 190.6 days. The harvest interval varied from 154.1 to 31.75 days. S2×Natchez had the widest harvest interval with 154.1 days, which was statically different from 'Tupy' (61 days).

Table 3. Agronomic performance of each cross during the season 2017 at Tangancicuaro, Michoacan State, Mexico

Cross	Berry weight		Number of berries per plant		Yield per plant		Soluble solids content		Days to the first pick		Harvest interval	
Choctaw x S3	6.75	a	189.10	bcd	1104.00	a	12.33	ab	247.00	cd	69.00	Bc
Kiowa x S6	4.55	b	53.93	d	152.20	b	12.70	a	244.00	cd	108.00	ab
S1 x Kiowa	5.41	ab	91.76	d	340.80	b	11.96	ab	247.00	c	105.00	ab
S2 x Brazos	5.75	ab	102.00	cd	120.40	b	10.90	bc	300.80	abc	44.67	bc
S2 x Chickasaw	6.90	a	572.00	a	1761.00	a	10.38	c	303.00	abc	49.00	bc
S2 x Choctaw	5.69	ab	284.10	abc	409.70	b	11.07	bc	298.20	abc	51.24	bc
S2 x Kiowa	6.21	ab	121.00	cd	292.00	b	11.40	abc	317.00	ab	32.50	bc
S2 x Natchez	5.42	ab	294.50	abc	333.20	b	10.04	c	190.60	d	154.10	a
S2 x S5	6.88	a	137.00	cd	555.20	ab	11.40	abc	318.00	a	31.75	c
S2 x Tupy	6.02	ab	257.30	abc	492.90	b	10.78	c	285.80	abc	62.82	bc
S3 x Kiowa	5.80	ab	137.00	cd	671.20	ab	12.16	ab	296.00	abc	56.00	bc
S3 x S6	6.61	ab	100.30	cd	571.00	ab	13.06	a	268.00	bc	100.50	ab
S4 x S7	5.02	ab	311.30	ab	353.10	b	10.68	c	275.80	bc	74.31	bc
Tupy	7.19	a	40.20	d	251.60	b	11.60	abc	265.30	bc	61.00	bc
Honestly Significant Difference	2.58		310.68		993.79		2.39		58.22		61.48	

*Genetic parameters*

Model 1 accounted higher additive-variance magnitudes than the rest of the models (Table 2) for most of the traits. However, models 1 and 3 exhibited the highest additive variances in berry weight and yield per plant, respectively. The importance of additive effects estimated by model 2 was analyzed by the magnitude of additive variance (Figure 2). In this case, the additive

variance was higher than the residual variance in days to first pick and harvest interval, whereas it was lower in berry weight. In the number of berries per plant, yield per plant, and soluble solids content, variance additive had moderate values which contributed to up to 50% of the phenotypic variance of those traits.

The differences in the heritability estimates between models 1 and 2 were lower than those observed between models 2 and 3 (Table 2). Based on the results observed in models 1 and 2, a high heritability ( $h^2 > 0.9$ ) was found in days to first pick and harvest interval; moderate values ( $h^2 = 0.39-0.65$ ) in berries per plant, yield per plant, and soluble solids content; and a low value ( $h^2 < 0.2$ ) in berry weight. In contrast, model 3 classified the number of berries per plant, yield per plant, soluble solids content, days to the first pick, and harvest interval as traits with low heritability, and berry weight as a trait with intermedium heritability.

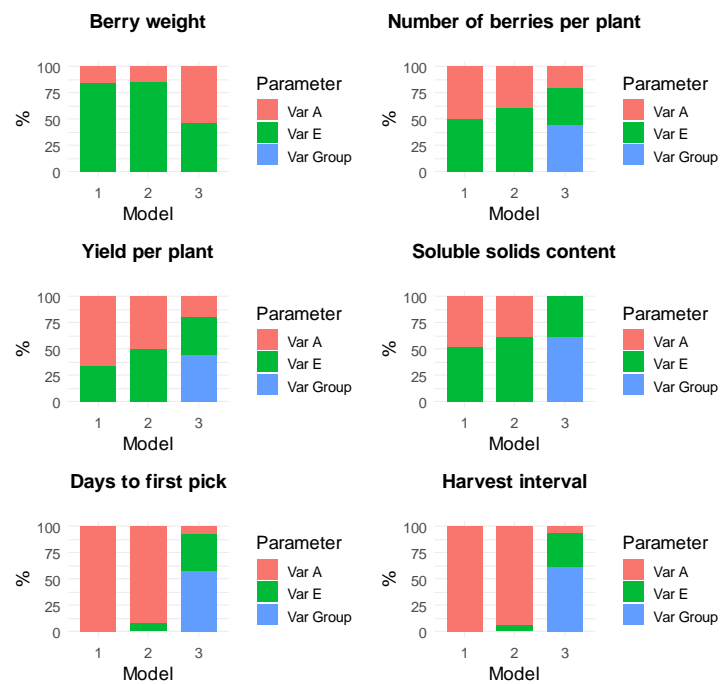


Fig. 2. Percentage explained for each variance component concerning the total variance estimated in each model. Var A= additive variance, Var E= Environmental variance, Var G= variance due to groups

### Breeding values

The breeding values of each parent by trait are shown in Table 4. Significantly positive effects in the breeding values for berry weight were detected in the genotypes ‘Choctaw’, ‘S3’, ‘Chickasaw’, ‘S5’, and ‘Tupy’. For the number of berries per plant, the genotypes ‘S2’, ‘S4’,



‘Chickasaw’, and ‘S7’ had the highest positive breeding values. In yield per plant, ‘Chickasaw’ and ‘S3’ exhibited high values, which significantly increased the yield of their progeny. In addition, significantly positive effects for yield were observed in the genotypes ‘Choctaw’, ‘Tupy’, and ‘S5’.

For soluble solids content, there were seven genotypes with positive values increasing the soluble solids content. However, ‘S6’, ‘S3’, and ‘Kiowa’ were ranked among the best genotypes. Concerning harvest interval, most of the genotypes showed negative effects, but ‘Natchez’, ‘S6’, and ‘S1’ had positive effects contributing to a wide harvest interval.

For days to first pick, the best genotypes were those with negative effects as the earliness genotypes are preferred by the farmers. In this sense, ‘Natchez’ was ranked as the earliest genotype, followed by ‘S1’ and ‘S6’.

Table 4. Breeding values of each blackberry parent for six quantitative traits.

Parental	Berry weight	Number of berries per plant	Yield per plant	Soluble solids content	Days to the first pick	Harvest interval
‘Brazos’	-0.01	-116.15 **	-277.70 **	0.02	22.67 **	-30.66 **
‘Chickasaw’	0.23 *	171.02 **	860.90 **	-0.26 **	16.59 **	-15.57 **
‘Choctaw’	0.22 *	33.96 **	129.83 **	0.46 **	18.65 **	-26.13 **
‘Kiowa’	-0.66 **	-118.75 **	-360.99 **	0.59 **	16.77 **	-14.30 **
‘Natchez’	-0.22 *	47.58 **	-131.15 **	-0.99 **	-146.75 **	135.38 **
‘Tupy’	0.26 *	4.28	99.14 *	-0.14	1.20	-5.79
‘S1’	0.07	-90.65 **	-63.08 **	0.32 **	-27.74 **	31.27 **
‘S2’	0.15	109.77 **	-243.12 **	-1.25 **	44.00 **	-35.75 **
‘S3’	0.93 **	-27.38 **	628.78 **	0.89 **	5.77	-10.90 *
‘S4’	-0.43 **	94.83 **	-177.37 **	-0.69 **	11.67 **	-8.88 *
‘S5’	0.29 **	-77.51 **	95.33 *	0.34 **	41.69 **	-42.98 **
‘S6’	-0.38 **	-125.82 **	-383.20 **	1.42 **	-16.21 **	33.18 **
‘S7’	-0.43 **	94.83 **	-177.37 **	-0.69 **	11.67 **	-8.88 *

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

## DISCUSSION

The breeding value of each parent is a piece of important information during the design of hybridization mating. (VAN GINKEL and ORTIZ, 2018). There are several approaches to measure the breeding values; however, estimation of breeding values based on the BLUP approach allows the estimation of those values using pedigree information (BERNARDO, 2020). Here, we evaluated three univariate mixed models used frequently in plant breeding. According to the AIC and BIC criteria, we found that model 2 presented the best fitting in all traits, and it was the most efficient in estimating additive values. Therefore, the estimation of breeding values through model 2 could serve as an auxiliary tool during the selection of the best individuals in the early evaluation stages.

It was observed that the correlation between observed (OV) and breeding values (BV) varied from 0.41 to 1.0. According to results of the model 2, most of the traits exhibited a strong correlation ( $r > 0.9$ ) between OV and BV, suggesting that the selection of high phenotypic values drags high breeding values for the next recurrent selection cycle. In berry weight, although the relationship between OV and BV was moderate, model 2 was able to detect most of the individuals with high breeding values. In blackberry breeding, the development of varieties takes

on average 6 years: evaluation of new crosses (2 years), evaluation of selections (2 years), and semi-commercial evaluation (2 years). According to COBB *et al.* (2019), compared to the rest of the parameters of the genetic gain equation, cycle time is the most important and cheapest parameter for increasing genetic gain. Based on our results, evaluation of new crosses for one year could be enough to select the best plants due to the high correlation between phenotypic and breeding values. This situation will lead to reducing costs and timesaving, as well as an increase in the genetic gain per year.

Another factor affecting the association between VO and BV is heritability. We observed that high heritability estimates led to a strong relationship between VO and BV. We found high heritability estimates for days to first pick and harvest interval, whereas moderate values for the number of berries per plant, yield per plant, and soluble solids content (0.39-0.49). Such results were like those reported by HERNANDEZ-BAUTISTA *et al.* (2018) in raspberry, who found similar moderate heritability values in yield per plant and soluble solids content.

In previous studies, GONZÁLEZ (2016) and HERNANDEZ-BAUTISTA *et al.* (2017) observed in red raspberry an intermedium narrow-sense heritability ( $h^2 = 0.52$  and  $h^2 = 0.48$ ) for berry weight. These values were different and higher than our estimation in blackberry for berry weight ( $h^2 = 0.14$ ), evidencing that the genetic complexity of berry weight varied among *Rubus* species. Another factor causing this difference could be the vegetative material employed by the previous authors as we mostly worked with genotypes with a floricanne-fruiting habit, whereas the previous study used genotypes with a primocane-flowering habit.

In blackberry breeding, breeders usually select simultaneously plants with large fruits (> 6.5 g), and high yields that are preferred by the market and farmers, respectively. According to the breeding values obtained in the present study, the genotypes 'Chickasaw', 'S3', 'Choctaw', 'Tupy', and 'S5' had significantly positive breeding values for yield, and berry weight. Therefore, these five varieties and selections could be an important gene source for obtaining progeny with good phenotypic values in both traits. Interestingly, most of the crosses on average were superior to the yield observed on the check 'Tupy'. However, the most outstanding crosses were S2×Chickasaw (1761 g/plant) and Choctaw×S3 (1104 g/plant). These results were expected as 'Chickasaw' and 'Choctaw' are considered productive varieties in some regions of the USA (CLARK and MOORE, 1999) as well as in warm regions of Mexico. Therefore, 'Chickasaw', 'S3', and 'Choctaw', could be considered good parental candidates to develop new cultivars adapted to a forced production system widely used in the blackberry growth of Mexico.

In Mexico, the exportation market demands high-quality fruit; optimal maturity, high firmness, null presence of fungal, soluble solids content > 8 °Brix, and no tan or white drupelets in fruit. In our study, all crosses showed upper values of 8 °Brix evidencing that the parents could be used to obtain progeny with an excellent soluble solids content for the exportation market. Specifically, genotypes as 'S6', 'S3', 'Kiowa', 'Choctaw', 'S5', 'S1', and 'Brazos' had positive breeding values for soluble solids content, which suggests that using these genotypes could be particularly attractive into blackberry breeding programs. Our results in soluble solids content were higher than those obtained by CLARK *et al.* (2005), who found values from 9.3 to 9.7 °Brix in cultivars such as Prime-Jan, Ouachita, Arapaho, and Choctaw. Such differences are caused by differences in the intensity of solar radiation and temperature ranges present at each site of evaluation (ALI *et al.*, 2011).

One variety with high earliness and wide harvest interval lets farmers offer their harvests when the demand is high. In Mexico, early blackberry production (period from October to November) is based mainly on primocane varieties and ‘Tupy’, whereas late blackberry production is mostly on floricanes varieties. In this sense, we identified genotypes as ‘Natchez’, ‘S1’, and ‘S6’ that exhibited interesting breeding values as well as good agronomic performance in their crosses for earliness and harvest interval. Such breeding values in these three genotypes were observed due to obtaining some floricanes and primocane-flowering progenies. In these crosses, the primocane progeny started their flowering stage ~1.5 months before the rest of the crosses that had only floricanes progenies. This situation caused S1×Kiowa, Kiowa×S6, and S2×Natchez to exhibit good breeding values and agronomic performance. Recently, the generation of primocane fruiting-varieties has gained interest in the blackberry production systems. Blackberry primocane varieties allow agronomic management more friendly to the environment as well as production in warm environments or sites with low chilling conditions (CLARK *et al.*, 2007). In this sense, our results proved that the combination of ‘Natchez’, ‘S1’, and ‘S6’ are an important source for obtaining primocane progeny.

### CONCLUSION

Most of the traits exhibited an intermedium heritability. The highest heritability was found in days to the first pick and harvest interval ( $h^2 > 0.9$ ), while berry weight exhibited the lowest values ( $h^2 < 0.2$ ). ‘Chickasaw’, ‘S3’, ‘Choctaw’, ‘Tupy’, and ‘S5’ showed high potential to be used in the developing yield-increased varieties with large fruits adapted to a forced production system. On other the hand, ‘Natchez’, ‘S1’, and ‘S6’ are attractive gene sources favoring the development of primocane-fruiting varieties. Finally, ‘S6’, ‘S3’, and ‘Kiowa’ had the highest breeding values for the soluble solids content. All these results showed the high importance of these genotypes to be used in blackberry breeding under ward weather.

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## GENETIČKI PARAMETRI I PROCENJENA OPLEMENJIVAČKA VREDNOST RODITELJA KUPINE U TOPLOJ SREDINI

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### Izvod

Kod kupine se identifikacija najboljih biljaka obično zasniva na fenotipskoj vrednosti. Međutim, fenotipska vrednost kompleksnih osobina nije uvek pouzdan parametar koji omogućava maksimalan genetski dobitak po ciklusu selekcije. Ova studija je imala za cilj da istraži selekcionu potencijal za trinaest roditelja kupine na osnovu njihovih selekcionih vrednosti i proceni genetske parametre važnih osobina u oplemenjivanju kupine. Ukrštanjem trinaest genotipova kupine dobijeno je ukupno četrnaest ukrštanja (sib-full porodica). Prema mešovitom modelu 2, procene heritabilnosti su se kretale od 0,14 do 0,93. Najveća heritabilnost ( $h^2 > 0,9$ ) utvrđena je u danima do prvog intervala branja i žetve, dok je najmanja ( $h^2 < 0,2$ ) za težinu bobica. Genotipovi 'Chickasav', 'S3', 'Choctav', 'Tupi' i 'S5' su istovremeno pokazivali pozitivne oplemenjivačke vrednosti za prinos i težinu bobica, dok su 'Natchez', 'S1' i 'S6' za rano i interval žetve. Za sadržaj rastvorljivih čvrstih materija, 'S6', 'S3' i 'Kiova' su imali najbolje oplemenjivačke vrednosti. Na osnovu naših rezultata germplazma korišćena u studiji ima aditivne efekte visoke komercijalne vrednosti koji bi se mogli koristiti u programima kupine.

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