Analysis of genetic effects of major genes on yield traits of a pea (*Pisum sativum* L.) cross between the Santa Isabel x WSU 31 varieties

Análisis de efectos de genes mayores sobre rasgos de rendimiento en arveja (*Pisum sativum* L.) a partir del cruzamiento de las variedades Santa Isabel x WSU 31

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ABSTRACT

Generation means and heritability analyses were conducted to estimate dominance, additive, maternal and gene interaction effects controlling eleven agronomic characteristics related with production in the pea. Ten generations (P1, P2, F1, F2, RC1, RC2 and each reciprocal generation) from a cross between the Santa Isabel and WSU 31 varieties were sown in two different environments for the present study. Eleven characteristics were evaluated: the time between sowing and flowering (I), the time between sowing and pod formation in the first reproductive node (FPod) and the height of the first reproductive node (H1RN), which were used as earliness indicators; as components of yield, the number of pods per plant (PxP), number of seeds per plant (SxP), number of seeds per pods (SxPod) and 100-seed weight (W100) were evaluated; and as variables associated to the yield, the pod width (PW), pod length (PL), lateral branch number (LBN) and plant height (PH) were evaluated. The results did not show maternal gene effects for the evaluated traits; environmental effects were found in PxP, SxP, SxPod, SFl, FPod and PL; genotype x environment effects were found in PW and W100. All characteristics except SxP and PxP had additive gene effects. The results showed that W100, PW and PL were the characteristics with the highest values for selection.

Key words: heritability, heterosis, additivity, dominance, genotype x environment interaction.

RESUMEN

En este trabajo se realizó la estimación de los efectos genéticos dominantes, aditivos, maternos y de interacción genética en once caracteres agronómicos relacionados con la producción en arveja. En diez generaciones (P1, P2, F1, F2, RC1, RC2 y cada generación recíproca) originadas del cruzamiento entre las variedades Santa Isabel y WSU 31, sembradas en dos ambientes distintos. Se evaluaron once caracteres: tiempo de siembra a floración (I), tiempo entre la siembra a la formación de vainas en el primer nudo reproductivo (FPod) y la altura al primer nudo reproductivo (H1RN) como indicadores de precocidad; como componentes de rendimiento fueron evaluados el número de vainas por planta (PxP), número de semillas por planta (SxP), número de semillas por vaina (SxPod) y el peso de 100 semillas (W100); y como variables asociadas al rendimiento fueron evaluadas el ancho de la vaina (PW), longitud de la vaina (PL), número de ramas laterales (LBN) y la altura de la planta (PH). Los resultados no mostraron efectos ambiental para los caracteres estudiados; se encontró efecto materno en PxP, SxP, SxPod, SFl, FPod y PL; efecto de la interacción genotipo x ambiente detecto en PW y W100. Todos los caracteres presentaron efectos genéticos aditivos significativos con excepción del PxP y SxP. Los resultados mostraron que el peso de W100, PW y PL fueron los caracteres con valores más altos para selección.

Palabras clave: heredabilidad, heterosis, aditividad, dominancia, interacción genotipo x ambiente.

Introduction

Yield and production are affected by one or several major genes and also by multiple gene interactions, the separation of these effects is of great importance to understand the expression at the phenotypic level and to predict the segregation of a cross evaluated in the field (Changjian *et al*., 1994); this information is important to establish a crop strategy, in which a greater expression of the desired genes appears.

Genetic variation of phenologic, morphological and yield traits, such as flowering start, plant height and seed weight, can be the result of characteristic segregation coded by simple genes and also the interaction among multiple genes; the determination of genetic effects is of great importance to understand expression at the phenotypic level and to predict the segregation of characteristics when a cross between contrasting individuals is carried out (Changjian *et al*., 1994; Lou and Zhu, 2002), allowing the establishment of a cultivation strategy where a bigger expression of the desired genes is shown.

A way to evaluate the genetic components of a population is by starting with the study of its genetic and environmental

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variance; genetic variance can be divided into three components: additive variance, which is associated with the overall allele effects of the locus; dominance variance, due to the interaction of effects of the alleles in the locus and epistatic variance, due to the non-allelic interaction of two or more loci (Martínez, 1999; Hussein and Aastveit, 2000).

Different methods have been proposed that are based in populations generated from a cross between two pure parents (Lou and Zhu, 2002), for the identification of the effects of genetic components on quantitative traits using lineal models of mixed distribution generated from generation means, variances and likelihood based techniques (Mather and Jinks, 1971; Cockerham, 1980; Elston, 1984; Kearsey and Pooni, 1996). These types of models have been used in different crop species, evaluating different quantitative characteristics such as expression of dwarfism genes in rice (Changjian *et al*., 1994) and seed quality in cotton (Lou and Zhu, 2002). Starting with these models, it has been possible to differentiate additive and dominance effects in specific genes that affect seed quality and plant height, stability of the genotype among different environments, to determine patterns of additive heritage among maternal and embryo effects, and additive effects in oil content in cotton seeds to determine how susceptible it is to the influence of environment.

In the pea, the analysis of generation means has been used to study resistance to pea blight (*Mycosphaerella blight*) (Zhang *et al*., 2007) and it has been determined that additive and dominance effects are important in the genetic control of plant weight and the volume and weight of the root (Saleh and Gritton, 1994); the heritability, additive and dominance components that contribute to the inheritance of resistance to powdery mildew have also been studied (Kalia and Sharma, 1988).

Often, generation mean models ignore or do not isolate the maternal effects contribution, producing a bias in the intent to understand the genetics of a given quantitative trait (Kearsey and Pooni, 1996). Also, in studies carried out with generation means in different environments, often, each one of the environments is analyzed separately (Rodríguez-Herrera *et al*., 2000; Zalapa *et al*., 2006), which gives, in some cases, marked differences inside a non-segregate generation evaluated in different environments, which could generate an increase in the error variance of the generation means, producing non-valid estimators generated by this method (Mather and Jinks, 1971).

Genetic models that allow the determination and differentiation of major gene effects and those that analyze the interaction of these effects with an environmental component permit the selection, with more security, of the types of necessary crosses to increase the presence of important quantitative traits in a crop for the expression of desirable yield traits, which permits the determination of the environment effect on genotype expression.

In the pea, models have been formulated which facilitate predicting the behavior of yield characteristics and their interaction with the environment; however, these models have been carried out for use in areas with seasonal climate changes and they cannot be employed in the conditions of a tropical country, such as Colombia. It is also important to note that there is no knowledge about the specific cross between the pea variety Santa Isabel and the variety WSU 31 because all the studies have been done on dry peas.

In the present study, a model of generation means was formulated, including maternal effects, to analyze genetic effects on phenologic and yield traits in pea plants starting from the crossing of two contrasting pea varieties: the commercial climbing Santa Isabel pea variety and the shrub WSU 31 variety. The environmental effect and the genotype x environment interaction of cultivated generations in two different locations were analyzed. Relationships between different components of precocity and yield were also determined, and the individuals that presented a bigger yield inside each one of the segregating generations were selected.

Materials and methods

Plant materials

In this study, two pea varieties were used as parentals which presented morphologically contrasting characteristics in growth habits; the first parental was the Santa Isabel variety and the second one was the WSU 31 variety; Santa Isabel is a climbing pea and may present sizes up to a meter, its seed is flat and yellow at maturity, it presents medium or late precocity and does not present resistance to *Fusarium oxysporum* f.sp. *pisi*; while the WSU 31 variety, produced in the United States at the University of Wisconsin in 1980, is a shrub or half-climbing, with a height between 0.4 m and 0.8 m, its mature seed is green and wrinkled, it is a variety of early precocity and presents resistance to four breeds of *Fusarium oxysporum* f.sp. *pisi* (Haglund and Anderson, 1987).

Offspring generation

In order to produce the seeds of each one of the ten necessary generations to carry out the genetic model (P_1, P_2, F_1=(1x2), F_{1R}=(2x1), F2=(F_1xF_1), F_{2R}=(F_{1R}x F_{1R}), RC_1=(1xF_1) RC_{1R}=(F_1x1), RC_2=(2xF_1), RC_{2R}=(F_1x2)), three sowing cycles were performed under greenhouse conditions; in the first two cycles, the materials were crossed using the technique of artificial hybridization for emasculation in the pea (Ligarreto and Patiño, 2004).

In the first cycle, direct and reciprocal crosses were carried out between the Santa Isabel and WSU 31 varieties to obtain seed F_1; 30 plants of each variety were sowed in spaced rows of 1.5 m and with a distance of 0.2 m among plants, to guarantee the genetic constitution of each generation; the seeds morphological traits were examined because Santa Isabel produces yellow, flat seeds, WSU 31 produces green, rough seeds and the cross between them produces flat, yellow seeds easily identifiable from the parental seeds.

Sixty seeds, F_1, were sowed in the second cycle, 30 seeds of the direct crosses (F_1) and 30 seeds of the reciprocal ones (F_{1R}); and 30 seeds of each one of the parentals were also sowed, self-pollination was allowed in some flowers of F_1 plants to generate F_2; from the direct F_1 and reciprocal one (F_{2R}), direct and reciprocal backcrosses were carried out with the remaining flowers toward both parentals (RC_1, RC_{1R}, RC_2, RC_{2R}). Each material was sowed in independent rows spaced at 1.3 m, in 1 m long parcels and 0.5 m between parcels at a 0.2 m planting distance.

The third cycle was carried out on two different farms: the San Francisco farm in the municipality of Madrid, Cundinamarca; Laguna Large sidewalk and the San Jorge farm in the municipality of Mosquera, Cundinamarca; in each environment three replicates of ten generations produced in two previous cycles were sowed, arranged in a completely randomized design.

Collecting data

Eleven characteristics from each generation were evaluated, grouped in indicators of precocity and yield components. The time between sowing and flowering (SFl) was used as an indicator of precocity that was calculated as the days lapsed from sowing until the appearance of the first floral button, the days at fructification or time between sowing and pod formation in the first reproductive nod (FPod), measured as when flower petals fell off, leaving the pod exposed; and the height of the first reproductive nod (H1RN) taken from the base of the plant, these data were measured in each sampled plant.

The number of pods per plant (PxP), number of seeds per plant (SxP), number of seeds per pod (SxPod) and the 100-seed weight (W100) were measured as yield components. To determine the 100 dry seed weight, 10 replicates of 100 seeds were randomly taken for each studied generation; PxP, SxP and SxPod were taken in each sampled plant.

As variables associated to the yield, pod width (PW), pod length (PL), lateral branch number (LBN), and plant height (PH) were evaluated (Medina *et al*., 1989). To carry out the pod width and length measurement, the measure of the longitude and the width of 10 pods were averaged for sampled plants, the width was measured with the pod central region and the longitude from the union with the peduncle until the pod apex (Espinosa and Ligarreto, 2005). Width and length were measured in dry pods.

Genetic model used

One of the restrictions of the generation means analysis is that the generations used in the model must be originated from the crossing of two contrasting genotypes, for that reason, it was verified that the variables evaluated in this study were contrasting in the two parentals before beginning the analyses; for this purpose, paired comparisons were done for each variable evaluated among the parentals by using the Mann-Whitney non-parametric test, separately in each environment.

To evaluate major gene genetic effects, maternal effects, genetic interaction effects and the interaction with the environment, a lineal model was used employing the six basic generations P_1, P_2, F_1, F_2, backcrosses and the reciprocal of these generations to evaluate maternal effects. For the lineal model development, the parameter definition and coefficients, the terminology used by Mather and Jinks (1971), were adopted.

The phenotypic mean (y_{hijk}) of the k generation from the combination of the maternal i and the parental j inside the environment h can be expressed by a lineal model as follows:

$$y_{hijk} = \mu + G_{ij} + L_h + GL_{hij} + e_{hijk} \quad (1)$$

where μ is the general average, G_{ij} is the genotypic value or genetic main effect, L_h is the environmental effect from the h environment that is random in most of the genetic experiments and presents normal distribution $L_h \approx N(0, \sigma^2_E)$, GL_{hij} is the total effect of the interaction between genotype and environment and $e_{hijkl} \approx N(0, \sigma^2_e)$ is the residual effect.

The genotypic value can be fractioned as:

$$G_{ijk} = \alpha[a] + \delta[d] + \alpha_m[a]_m + \delta_m[d]_m + \gamma[c]$$

Where the additive parameter [a] denotes the net balance of genetic effects over all the genes that are being observed after the internal cancellations due to dispersion, the [d] parameter represents the dominance effects net balance and indicates the dominance direction in most of the genes pondered by the magnitude of their effects, the parameters $[a]_m$ and $[d]_m$ represent the additive and dominance effects of the maternal genes in P_1 and P_2 on the phenotype offspring; the cytoplasmic effects are managed adding an additional parameter [*c*] (Kearsey and Pooni, 1996). The additive, dominance and cytoplasmic effects of parameter coefficients are α, δ and γ, respectively (Tab. 1). The model can be extended to incorporate interactions of additive [aa], dominance [dd] and additive for dominance [ad] effects if the simple model of additive-dominance does not achieve a good adjustment.

TABLE 1. Genetic and maternal effect coefficients from the generation mean lineal model[1].

	Offspring genotype			Maternal genotype		
Generation	**m**	**α**	**δ**	**α_m**	**δ_m**	**γ**
P_1	1	1	0	1	0	1
P_2	1	-1	0	-1	0	-1
F_1	1	0	1	1	0	1
F_{1R}	1	0	1	-1	0	-1
F_2	1	0	0.5	0	1	1
F_{2R}	1	0	0.5	0	1	-1
RC_1	1	0.5	0.5	1	0	1
RC_{1R}	1	0.5	0.5	1	0	1
RC_2	1	-0.5	0.5	-1	0	-1
RC_{2R}	1	-0.5	0.5	-1	0	-1

[1] Source: Kearsey and Pooni, 1996.

In order to describe the differences completely with regard to the two evaluated environments, it is possible to carry out the analysis including a column in the design matrix that defines the differences among the two environments (Mather and Jinks, 1971). To evaluate the genotype x environment interaction, new columns are generated, as many as the interactions require, as can be observed in Tab. 2.

Then, the environmental genotype x environment interaction effects can be expressed in the lineal model as:

$$L_h = l\, GL_{hij} = \alpha\,[a]\, l + \delta\,\,[d]\, l \qquad (2)$$

Each one of the additive, dominance, maternal and cytoplasmic effects parameters estimators are obtained by regression approaches; to include and to estimate the parameters in the regression model, the test of joint scales proposed by Cavalli (1952) was used, using the available generation means and doing the multiple regression analysis with the generalized weighted least square procedure (Kearsey and Pooni, 1996); in this regression method, each generation mean calculated for each studied agronomic trait is used as a dependent variable, and the genetic parameter coefficients are taken as independent variables; the analyses were determined with the GLM procedure of the statistics package SAS® 9.0 version (SAS, 2004).

The obtained estimators are those that minimize the deviations between the observed and predicted values of the model. It is assumed that each one of the values of the generation means are known with the same precision, which implies that the variances of the generation means are all equal, which is not probable in practice because generations like F_2 and backcrosses can present higher variances among the individuals due to genetic segregation; this heterogeneity in the variances can make the prediction of estimators unequal and, therefore, make the models invalid (Beaver and Mosjidis, 1988). For this reason, the means of each generation are considered regarding the inverse of their variance multiplied by the number of individuals in each generation (Mather and Jinks, 1971; Beaver and Mosjidis, 1988; Foolad and Jones, 1992).

The results of this procedure include estimators for each genetic parameter and the environmental effect, their standard errors, t-values and the generation means predicted for the tested model. The residual sum of squares in this analysis is equivalent to the one pondered chi-square (χ^2) and, therefore, can be used to prove if the model is fitted using a F test and the R^2 coefficient of determination (Foolad

TABLE 2. Genotype x environment interaction coefficients for the three first generations in two environments.

		Offspring genotype		Environment	Genotype x Environment	
Family	***m***	**α**	**δ**	***l***	**α *l***	**δ *l***
P_1	1	1	0	1	1	0
P_2	1	-1	0	1	-1	0
F_1	1	0	1	1	0	1
P_1	1	1	0	-1	-1	0
P_2	1	-1	0	-1	1	0
F_1	1	0	1	-1	0	-1

and Jones, 1992). In the final model, only the parameters that were statistically significant were included.

Initially, it was determined if there existed significant maternal effects adjusting the data to a simple model with the additive, dominance and cytoplasmic maternal effects including the environmental effect and the interactions of this with the maternal effects.

Because there were no significant maternal effects observed for any of the evaluated variables (see results below), the data of the generations F_1, RC_1, RC_2 and F_2 were combined with their reciprocal ones. Then, the data were adjusted to a additive-dominance simple model including the environmental effect in the same way as described by Cockerham (1980). When the simple model was shown to be inadequate, the additive x additive, additive x dominance, dominance x dominance interaction effects and the effects of genotype x environment were included, adjusting each parameter in successive form, eliminating in the model the terms that progressively presented significant effects and maintaining the parameters that maximized the model adjustment; it was evaluated if the models were adequate, using the coefficient of determination value (R^2) (Kearsey and Pooni, 1996).

Heritability and heterosis estimation

Narrow sense heritability (h^2) was estimated separately for each environment and for all the environments as a whole following the method proposed by Warner (Warner, 1952):

$$\hat{h}^2 = \frac{2S^2_{F2} - \left(S^2_{RC1} + S^2_{RC2}\right)}{S^2_{F2}} \times 100 \quad (3)$$

where S^2_{P1}, S^2_{P2}, S^2_{F1}, S^2_{RC1}, S^2_{RC2} and S^2_{F2} are the variances of P1, P2, F1, RC1, RC2 and F2, respectively.

Heterosis was estimated as the deviation percentage from the F_1 mean value with regard to the parental mean value.

$$H = \frac{\overline{F1} - \frac{\overline{P1} + \overline{P2}}{2}}{\frac{\overline{P1} + \overline{P2}}{2}} \times 100 \quad (4)$$

Heterobeltiosis was estimated with regard to the best parental as:

$$HB = \frac{\overline{F1} - \overline{best\ parental}}{\overline{best\ parental}} \times 100 \quad (5)$$

The heterosis estimations were calculated in each environment and the joining data from the two environments.

Results and discussion

Highly significant differences were founded between the parentals in all studied variables except for the pod per plant and number of seeds per plant; for these two variables, the parentals did not present significant differences in the municipality of Mosquera, while in the municipality of Madrid, the WSU 31 variety presented a highly significant value (Tab. 3). This suggests that the resulting values in the municipality of Mosquera can be due to an environmental effect more than a genotypic effect.

With regard to the other variables, parental WSU 31 (P_2) was significantly more precocious, presenting a shorter duration of the vegetative stage evidenced in a shorter time for the formation of the floral button (SFl) and the formation of pods (FPod). It also presented a higher number of SxPod and a bigger PL. The parental Santa Isabel presented higher values in the variable LBN, W100, H1RN and PH (Tab. 3).

TABLE 3. Parallel between Santa Isabel and WSU 31 parentals with regard to the studied variables.

Environment		SF1 (d)	FPod (d)	H1RN (cm)	PH (cm)
Madrid	P1	68.79±2.98 a	78.27±2.73 a	75.71±7.12 a	188.60±11.63 a
	P2	66.10±2.96 b	74.88±2.34 b	50.31±7.60 b	149.59±15.99 b
Mosquera	P1	63.30±2.08 c	71.04±1.59 c	79.81±9.18 c	196.42±25.88 c
	P2	59.95±2.68 d	67.31±2.33 d	42.23±5.26 d	126.15±22.04 d

Environment		PxP	SxP	SxPod	PL (mm)	PW (mm)	LBN	W100 (g)
Madrid	P1	133.45±29.12 a	608.64±142.15 a	4.57±0.51 a	70.01±2.54 a	12.43±0.48 a	14.45±5.96 a	37.88±0.80 a
	P2	156.54±44.39 b	830.03±241.35 b	5.32±0.44 b	76.55±1.96 b	13.53±0.39 b	11.14±5.28 b	22.80±1.74 b
Mosquera	P1	85.73±26.20 c	333.19±92.35 c	3.93±0.40 c	68.71±5.32 c	13.62±1.16 c	13.92±4.55 c	38.45±0.69 c
	P2	76.23±20.72 c	325.62±92.45 c	4.29±0.50 d	71.91±3.75 d	12.30±0.81 d	8.88±3.66 d	22.52±0.65 d

SF1: time between sowing and flowering; FPod: time between sowing and the first pod formation; H1RN: height of first reproductive node; PH: plant height; PxP: pods per plant; SxP: number of seeds per plant; SxPod: number of seeds per pod; PL: pod length; PW: pod width; LBN: lateral branch number; W100: 100-seed weight.

Means in the same column followed by the same letter are not significantly different according to Mann-Whitney test ($P \leq 0.05$).

The analysis by means of lineal models of maternal effects presence did not show any genetic effect of maternal additive $[a]_m$, maternal dominant $[d]_m$ or cytoplasmic [c] which was significant for the precocity and the yield components studied (Tab. 4), therefore, for posterior data analysis, the joined data of generations F_1, RC_1, RC_2 and F_2, with the reciprocal ones, was used.

TABLE 4. P-Values from additive [*a*], dominance [*d*], maternal additive $[a]_m$ and dominance $[d]_m$, and cytoplasmic [*c*].

Parameters	W100	PxP	SxPod	H1RN	PH
[a]	<0.0001	0.8686	0.0312	<0.0001	0.0005
[d]	0.1381	0.0050	0.3906	<0.0001	<0.0001
$[a]_m$	0.4878	0.6385	0.5272	0.9465	0.7486
$[d]_m$	0.4713	0.1419	0.8728	0.1104	0.0177
[C]	0.5149	0.7385	0.8901	0.4681	0.7027
Env.	0.0111	<0.0001	<0.0001	0.1569	0.0818

Parameters	LBN	SF1	FPod	PL	PW
[a]	0.0063	0.0001	<0.0001	<0.0001	0.0959
[d]	0.1265	0.3781	0.8307	<0.0001	0.0006
$[a]_m$	0.6466	0.3481	0.4788	0.6850	0.7398
$[d]_m$	0.4810	0.8549	0.8355	0.6911	0.5098
[C]	0.8666	0.7838	0.6193	0.6912	0.7409
Env.	0.8287	<0.0001	<0.0001	<0.0001	0.0002

Env.: environment; W100: 100-seed weight; PxP: pods per plant; SxPod: seeds per pod; H1RN: height of first reproductive node; PH: plant height; LBN: lateral branch number; SF1: time between sowing and flowering; FPod: time between sowing and the first pod formation; PL: pod length; PW: pod width.

Number of pods per plant and number of seeds per plant

A significant dominant [d] genetic effect was found, and this effect is stronger than the environmental effect for these two variables. However, it is necessary to note that the model of generation means carried out for these two variables did not present a very good adjustment (Tab. 5); for the number of pods per plant, a R^2 of 0.78 was obtained; meanwhile for the number of seeds per plant it was 0.86. These results can be due to the fact that in the village of Mosquera, significant differences were not found among the parentals for these variables and the generation mean models only adapted if the restriction of using contrasting parentals was fulfilled.

The narrow sense heritability was superior to 65% for the number of pods and seeds per plant when it was evaluated, including the two environment data (Tab. 6). These results contrast with previously reported data, where it was observed that these variables presented a higher narrow sense heritability (Singh, 1985; Espinosa and Ligarreto, 2005).

Regarding the heterosis values, a higher value of heterosis was observed in the village of Mosquera than in the village of Madrid, according to the half parental heterosis; the results of the number of seeds per plant in the village of Madrid are concordant with those reported by Espinosa and Ligarreto (2005), where a heterotic effect of 16.44% was observed.

With the values of heterosis, the differences among environments are evidenced again, while in Madrid the best parental heterosis was 3.42%, in Mosquera it reached a value of 39.01% (Tab. 7), which again confirms that the environment significantly affects the expression of these characteristics.

Seeds per pod

According to the generation means analysis this variable was adapted to an additive-dominance model (R^2=0.90) with an additive effect higher than the environmental effect (Tab. 5). However, observing the heritability values, they are low due mainly to a lower value of the additive variance regarding the environmental one (Tab. 6). The differences

TABLE 5. Estimated parameters for additive, dominance and environmental effects from the joint scaling test of the agronomic traits evaluated for the six basic generations from crossing the Santa Isabel x WSU 31 varieties.

Parameters	PxP	SxP	SxPod	H1RN	PH	LBN
m	107.88±6.42 **	495.60±30.30 **	4.54±0.08 **	61.17±1.22 **	165.55±3.11 **	11.34±0.49 **
[a]	4.70±6.17 NS	-18.72±28.66 NS	-0.41±0.08 **	15.32±1.22 **	23.44±2.88 **	2.61±0.48 **
[d]	35.14±13.60 **	192.76±61.40 **	0.14±0.13 NS	32.04±2.78 **	50.81±6.97 **	2.76±0.88 **
Env.	19.71±4.67 **	134.95±21.86 **	0.33±0.05 **	1.41±0.95 NS	2.67±2.65 NS	-0.28±0.32 NS
R^2	0.781	0.864	0.905	0.980	0.937	0.864

Parameters	SFI	Fpod	PL	PW	W100
m	64.41±0.22 **	72.73±0.16 **	71.84±0.37 **	12.76±0.19 **	30.51±0.59 **
[a]	1.58±0.22 **	1.81±0.17 **	-2.76±0.35 **	-0.21±0.19 NS	7.56±0.57 **
[d]	-0.56±0.37 NS	-0.18±0.26 NS	4.22±0.63 **	0.93±0.28 **	1.36±0.92 NS
Env.	3.12±0.14 **	3.74±0.10 **	1.71±0.26 **	0.50±0.11 **	0.66±0.45 NS
R^2	0.986	0.994	0.944	0.777	0.961

Adjustment for an additive-dominance and environment model for each one of the agronomic traits evaluated. m=overall effect; [*a*] = additive effect; [*d*] = dominance effect; Env. = environment effect. * significant differences ($P \leq 0.05$); ** significant differences ($P \leq 0.01$); NS: non-significant parameter.

TABLE 6. Genetic and environmental variance and narrow sense (h^2, %) heritability for evaluated traits.

Parameters	Environment	PxP	SxP	SxPod	H1RN	PH	LBN	SF1	Fpod	PL	PW	W100
h^2	Madrid	72.504	72.533	10.495	67.621	54.518	23.538	50.844	40.191	83.477	90.425	89.608
	Mosquera	78.018	65.337	29.650	69.974	25.009	66.635	47.305	23.889	41.333	67.671	86.439
Parameters	**Environment**	**PxP**	**SxP**	**SxPod**	**H1RN**	**PH**	**LBN**	**SF1**	**Fpod**	**PL**	**PW**	**W100**
EV	Madrid	1094.27	29314.22	0.08	39.05	92.01	18.33	6.98	5.36	3.79	0.20	1.34
	Mosquera	854.02	17401.03	0.10	30.75	326.92	5.14	4.43	2.85	7.47	0.35	0.88
GV	Madrid	1546.17	39208.76	0.15	270.49	1544.52	1.44	7.41	5.32	23.79	0.99	26.95
	Mosquera	1833.68	39627.03	0.32	190.42	998.45	30.34	7.16	4.14	19.42	0.65	16.47
AV	Madrid	1914.42	49701.44	0.02	209.32	892.21	4.65	7.32	4.29	30.42	1.27	25.35
	Mosquera	2096.90	37260.67	0.12	154.76	331.46	23.64	5.48	1.67	11.11	0.68	15.00
DV	Madrid	-368.26	-10492.68	0.12	61.18	652.31	-3.21	0.09	1.03	-6.64	-0.28	1.60
	Mosquera	-263.22	2366.36	0.19	35.66	666.99	6.70	1.68	2.47	8.31	-0.03	1.47

PxP: number of pods per plant, SxP: number of seeds per plant, SxPod: number of seeds per pod, H1RN: height of the first reproductive node, PH: plant height, LBN: lateral branch number, SFI: time between sowing and flowering, FPod: time between sowing and pod of the first reproductive node, PL: Plant length, PW: plant width, W100: 100-seed weight. EV: environmental variance, GV: genetic variance, AV: additive variance and DV: dominance variance.

in these two analyses may be due to the following reasons: in the generation means analysis, the averages of each generation are evaluated, just like the differences between the two environments; while in the calculation of heritability that was carried out by separate environments, one keeps in mind a higher variation due to intrinsic conditions of each environment and microenvironment variations, these environmental variations influence to a large degree the values of variances of each generation and they can generate a decrease in the value regarding the additive variance. It was determined that SxPod does not present a high heterotic effect (Tab. 7), in concordance with that reported for this characteristic (Sarawat *et al*., 1994).

TABLE 7. Heterosis (H) and heterobeltiosis (HB) of evaluated traits in two locations.

Parameters	Madrid		Mosquera	
	H	HB	H	HB
PxP	11.906	3.426	45.095	39.010
SxP	15.501	-0.025	54.888	53.329
SxPod	2.862	-4.953	3.462	-1.811
H1RN	50.950	24.793	48.628	12.955
PH	30.045	16.204	25.587	3.289
LBN	2.677	-14.931	34.149	9.534
SFI	-0.025	2.087	-1.355	1.475
FPod	0.127	2.424	-0.465	2.324
PL	6.371	1.799	4.834	2.632
PW	9.265	5.460	1.569	-3.592
W100	8.559	-13.044	-2.356	-22.583

PxP: number of pods per plant; SxP: number of seeds per plant; SxPod: number of seeds per pod; H1RN: height of the first reproductive node; PH: plant height; LBN: lateral branch number; SFI: time between sowing and flowering; FPod: time between sowing and pod of the first reproductive node; PL: Plant length; PW: plant width; W100: 100-seed weight.

Height of the first reproductive node and height of the plant

According to the generation means model, environmental effects did not show up on H1RN and PH, moreover, a significant genotypic effect was seen in both dominant and additive variables (Tab. 5). However, dominance variance was higher than additive variance, due to this, the two characteristics presented a low narrow sense heritability (Tab. 6); Singh (1985) reported that although plant height is influenced by an additive effect, the dominance effect presents a higher influence. It is possible to think in a transgressive segregation or in overdominance effect in this two variables, keeping in mind that the overall values of F1 were higher than those of the parents in two evaluated environments, that is corroborated with the positive data of heterosis and heterobeltiosis (Tab. 7).

Plant height is closely related with the internode longitude which is managed by 15 different genes *Le*, *La, Cry*, *Lm*, *Na*, *Lh, Lk* y *Ls*, *Lw*, *Lv*, *Lka* y *Lkb*, *Lkc*, *Lkd* and *Sln*; mutations in eleven of these loci produce short internodes (Kusnadi *et al*., 1992).

Number of lateral branches

After analysis with the generation means model of this characteristic, the results did not show environmental or interaction effects; however regarding heritability, the results were contrasting between the two evaluated environments, while in Madrid the narrow sense heritability was 23.53%, in Mosquera this it was almost three times higher (Tab. 6). These results agree with results of previous studies, where it was found that the number of branches was highly influenced by the environmental conditions (Alcalde *et al*., 1999; Alcalde *et al*., 2000; Bourion *et al*., 2002).

Time between sowing and flowering and time between sowing and formation of the first pod

In the present study, it was found that SFl and FPod were subject to a significant additive genetic effect and also a

high environmental effect (Tab. 5). This result is confirmed by means of the values in additive variances that were 7.32 and 5.48 for SFl in Madrid and Mosquera, respectively, and 4.29 and 1.67 for FPod; with a near zero value for dominant variances (Tab. 6); the presence of a high additive effect leads to the expectation that these characteristics have potential for improvement. The beginning of the flowering and fructification have been considered traits determined by a polygenic action due to the fact that flowering frequently shows continuous variations under field conditions and they respond to temperature changes (Alcalde *et al*., 1999); it has been found that flowering delay can be due to the action of major genes such as *Sn* which produces a low number of vegetative nodes, producing a quantitative response to the photoperiod for flowering initiation or floral development and senescence with interaction with other major genes such as *E* and *Hr* (Weller *et al*., 1997; Alcalde *et al*., 1999; Bourion *et al*., 2002), which may explain the high environmental effects observed on these traits. In the pea, the study of these variables has shown that they are due to the action of interactions among genes or to the action of major genes (Bourion *et al*., 2002); also variation and stability can be largely affected by the environment. Moreover, the negative values with regard to heterosis suggest that the time of flowering and fructification presents partial or incomplete dominance (Tab. 7).

Pod length and width

It was found that these two variables are subject to significant environmental effects; PW did not show an important additive effect while the PL had both additive and dominant genetic effects (Tab. 5). These two variables presented higher narrow sense heritabilities in the village of Madrid (Tab. 6) which makes them good candidates for a breeding program, starting with the cross between the Santa Isabel and WSU 31 varieties. Furthermore, these two variables did not present very high heterosis values.

Weight of 100 seeds

In the additive-dominance model of generation means for the 100-seed weight, there were no significant effects of the environment or genetic dominance. Other studies have shown that this characteristic presents a higher effect from the additive genetic action than the non-additive action (Singh, 1985; Espinosa and Ligarreto, 2005), similar to that reported in this study. In general, W100 was the characteristic that presented the highest heritability, with a maximum narrow sense heritability of 89.60% (Tab. 6), which makes this characteristic important for breeding programs because it is only slightly influenced by the environment and is highly inheritable. The comparisons of F_1 with the parental mean and the best parental showed that there is not a heterotic effect; this variable presented the lowest heterobeltiosis with a decrease in F_1 of 13.04% in Madrid and 22.58% in Mosquera, suggesting that this characteristic presents partial or incomplete dominance (Tab. 7).

Conclusions

The models employed in this study have as an advantage the fact that environmental effects are included, to infer which genetic effect is really significant for all the evaluated environments for the cross between the Santa Isabel and WSU 31 pea varieties. In the eleven characters studied for this cross, significant maternal or cytoplasmic effects do not exist. The variables that had higher values for selection were 100-seed weight, pod length and pod width; the other yield variables presented lower heritabilities. One may consider that all the variables, except for the number of seeds per plant and the number of pods per plant, have potential for improvement taking into account that to outline a breeding program, it is necessary that the characteristics to be improved be subject to a significant additive effect. If a continued breeding program with the Santa Isabel x WSU 31 cross is desired, stronger pressures of selection should be applied to the 100-seed weight and the length and width of the pods.

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