

INHERITANCE OF SEED WEIGHT IN LARGE-SEED GRASS PEA *Lathyrus sativus* L.

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ABSTRACT

Mean seed weight (MSW) is a relevant trait in grass pea (*Lathyrus sativus* L.) commercialization because large grains are preferred in Western markets. Extending the knowledge on its mode of inheritance among large-seeded types would be useful in breeding programs, and therefore it was the objective of this work. A broad range of MSW is found in grass pea, starting at about 30 mg. Three lines (LS-97, LS-8, and LS-2026) within the large-seeded group but with significantly different MSW (179, 360 and 470 mg, respectively), were crossed in a complete diallel. Part of the F₁ seed was sown and the remainder was stored. F₁ plants from each cross were allowed to produce F₂ seed and some were backcrossed to their respective parents. Parents, F₁, F₂, and backcross populations were grown in the field in 2006. MSW was obtained from single plants in each population. No difference was observed between reciprocals of crosses LS-97 × LS-8 and LS-8 × LS-2026; therefore, data from reciprocals were combined, assuming nuclear inheritance. However, F₂ segregating population from cross LS-97 × LS-2026 and its reciprocal gave significantly different means, suggesting cytoplasmic inheritance. Consequently, F₂ and backcross data were handled separately to calculate heritability. Parent lines with high MSW, particularly LS-2026, had greater variances, raising the estimate of environmental variance. Broad sense heritability estimates for MSW were 0.50 and 0.32 for crosses LS-97 × LS-8 and LS-8 × LS-2026, respectively, and 0.23 and 0.24, for cross LS-97 × LS-2026 and its reciprocal, respectively. Narrow sense heritabilities were 0.42 and 0.28, and 0.15 and 0.22, respectively. In all crosses, the genetic effects were predominantly additive, predicting a good response to selection for increased MSW in early segregating generations. Thus, the prospects to improve MSW in large-seeded grass peas are auspicious.

Key words: grass pea, heritability, cool-season grain legumes.

INTRODUCTION

Grass pea (*Lathyrus sativus* L.) is a protein-rich (27-29%) grain legume crop used for human and animal consumption since ancient times (Campbell, 1997; Hanbury *et al.*, 2000). The environmental conditions of southern Chile often allow the achievement of relatively high yields and large grains, even when grass pea is cultivated on soils that are generally eroded due to poor management. The large grain type is attractive to southern European markets that seek large, unspotted grass pea grains traditionally used to prepare local dishes. According to Jackson and Yunus (1984), *L. sativus* with small seeds have a distribution to the East of the Mediterranean (Turkey, Transcaucasia,

Afghanistan), while larger-seeded forms have been selected in the Mediterranean. The mostly white-seeded, westerly-type grass peas grown in Chile typically weigh around 250-300 mg seed⁻¹, and though indeed large-seeded compared to types grown in Asia, are smaller than some ecotypes found in Europe. Populations in central Italy, for instance, may exceed 350 mg seed⁻¹ (Tavoletti *et al.*, 2005) and reach 10 mm in diameter (Hammer *et al.*, 1989). Thus, an increased seed size would make grass peas produced in Chile more attractive for markets that prefer large-seeded types. Seed weight is also important from the agronomic viewpoint because is positively associated with seed yield per plant (Tiwari and Campbell, 1996a).

Grass pea breeding is also concerned with the presence of β-ODAP (β-N-oxalyl-L-α,β-diaminopropionic acid) (Tiwari and Campbell, 1996b) and low content of the essential amino acid methionine in the seed, which are thought to increase vulnerability to neuroletharism, a neurodegenerative disease (Lambein *et al.*, 2007). In an effort to make grass pea safer for human consumption,

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low-ODAP lines (Campbell *et al.*, 1994) and cultivars (Siddique *et al.*, 2006) have been obtained. However, these materials are small-seeded; therefore, crosses aimed to incorporate the low-ODAP genes would produce progenies with relatively low seed weights requiring further work to recover the desired large-seeded type. The existence of low-ODAP, high-yielding, large-seeded materials would give grass pea the chance of becoming a more interesting protein crop. It is already a hardy crop that can be grown on a wide range of soils, from fine silts to heavy clays, including soils with low fertility and poor structure (Siddique *et al.*, 1996), it tolerates salinity, drought and water logging in the soil (Campbell, 1997; Malek *et al.*, 2000), shows resistance to various diseases and insects that affect other grain legumes (Palmer *et al.*, 1989; Vaz Patto *et al.*, 2006), and under favorable climatic conditions may yield over 3 t ha⁻¹ of seed (Krarup, 2002; Mera *et al.*, 2003b; Montenegro and Mera, 2009).

The objective of this work was to estimate the proportion of the phenotypic variation in seed weight within large-seeded grass peas that is controlled by additive gene action. Such index would lead to an educated guess of the response to selection in breeding programs involved in the simultaneous improvement of seed size and other quantitatively inherited traits. Seed weight heritability estimates have been reported (Tiwari and Campbell, 1996a; Kumar and Dubey, 2001) for small-seeded grass peas far below the weight range of the parent lines used in this study. Türk *et al.* (2007) included at least one large-seeded line in their study but estimated broad sense heritability only.

MATERIALS AND METHODS

Lines LS-97 and LS-8, from the *L. sativus* germplasm held by the Institute for Agricultural Research (INIA-Chile), were chosen for this study. These lines represent the smallest and largest materials within a collection of ecotypes from diverse Chilean areas where grass peas may be found. Mean seed weight (MSW) for LS-97 and LS-8 is about 179 and 360 mg, respectively. Line LS-2026, selected in Chile from a heterogeneous ecotype received from Italy was also included in the study because –with a MSW of 470 mg– it is probably one of the largest-seeded materials within this species. The three lines had similar phenology, with close matching of flowering initiation, flowering period, seed filling period and harvesting. Since a high proportion of *L. sativus* in the world is small-seeded and with a MSW of less than 100 mg, we regarded the lines in our study as “medium” (LS-97), “large” (LS-8), and “extra-large” (LS-2026). Yet, relative to the whole range of seed size within the species, these three lines are large-seeded materials. Our three parental lines originated

from single-plant selections and during winter (July) 2004 were grown in a glasshouse, where crosses were made in a complete diallel fashion.

The experiments were conducted at Carillanca Research Center, near Temuco (38°41' S, 72°25' W; 200 m.a.s.l.), La Araucanía Region, Southern Chile. Parent lines and six F₁ progenies from three crosses with reciprocals were sown in the field in September 2005, with row and plant spacing at 1.0 and 0.5 m, respectively. Part of the F₁ seed was reserved. Backcrosses were performed in November 2005, crossing each of the six F₁ progenies –including reciprocals– with both parents. Parent lines, F₁, F₂, and backcross (BC) populations were sown under field conditions in September 2006 and rainfed-grown with row and plant spacing at 1.0 m and 30 cm, respectively. The soil was a silty loam (Vilcun series, Medial family, Mesic of the Pachic Melanudands) with 13% organic matter and pH 6.0. According to soil test results and observed response of grass peas to fertilizers in previous trials, 80 kg P₂O₅ ha⁻¹ as superphosphate and 50 kg K₂O ha⁻¹ as potassium chloride were applied in the furrow. Grass pea plants had been observed to nodulate adequately in the same soil, thus inoculation with rhizobia was not practiced nor was N fertilization. Simazine was applied at pre-emergence at the rate of 1.0 kg ha⁻¹ (active ingredient) to suppress weed growth and complementary hand-weeding followed in November. Parent, F₁, F₂, and BC plants were harvested individually in February 2007. After threshing and cleaning, the seeds of all populations were allowed to air-dry in the same room in order to homogenize moisture to approximately 10%. MSW was determined by dividing total seed weight by the number of seeds produced by plant.

Statistical procedures were performed using JMP version 8 software (SAS Institute, 2009). Environmental variance was regarded as the mean of variances of both parent lines (L₁ and L₂) and F₁, including reciprocals. Genotypic variance was estimated by subtracting the environmental variance from the phenotypic variance (variance of F₂). Broad sense heritability (H²) was estimated as the ratio between genotypic (V_G) and phenotypic variances (V_P). Narrow sense heritability (h²) was estimated as the ratio between additive (V_A) and phenotypic variances. Additive variance was calculated following the Mather-Warner method (Nyquist, 1991) by subtracting the sum of backcrosses variances from twice the phenotypic variance. Therefore:

$$H^2 = V_{F2} - [(V_{L1} + V_{L2} + V_{F1})/3]/V_{F2} = V_G/V_P \quad [1]$$

$$h^2 = 2V_{F2} - (V_{BC1} + V_{BC2})/V_{F2} = V_A/V_P \quad [2]$$

An ANOVA (F ratio) was used to determine significant differences between the means of reciprocal crosses.

RESULTS AND DISCUSSION

Rainfall for the 2006-2007 growing season was 593 mm, 70% in August-October and 30% during November-February. These figures are within the normal range for the study area.

The number of plants evaluated, parents and generation means, standard errors, standard deviations, and coefficients of variation for the three crosses are shown in Table 1 (cross 1: LS-97 × LS-8), Table 2 (cross 2: LS-8 × LS-2026) and Table 3 (cross 3: LS-97 × LS-2026). ANOVA confirmed that the three parent lines used in the study had significantly ($P < 0.01$) different MSW means. The F_1 and F_2 progenies of the

three crosses had MSW values intermediate between the parent lines, as expected for a quantitatively inherited trait.

The F_2 of cross 1 (LS-97 × LS-8) fitted a normal distribution with slight skewness (0.13) and mass distribution toward the parent with smaller seed and the F_2 of cross 2 (LS-8 × LS-2026) had a notably symmetric normal distribution (Figure 1). In the case of cross 3, the normally distributed F_2 of LS-97 × LS-2026 was slightly skewed (0.09) with sidedness toward the parent with smaller seed; the F_2 of LS-2026 × LS-97 was also skewed (0.10) with sidedness toward LS-97 but did not fit a normal distribution ($P < 0.05$) according to a Shapiro-Wilk test (SAS Institute, 2009).

Table 1. Number of plants (N), mean, standard error (SE), standard deviation (SD) and coefficient of variation (CV) for mean seed weight of parent lines, F_1 , F_2 , and backcross populations corresponding to *Lathyrus sativus* cross LS-97 × LS-8 (medium-seeded × large-seeded) and reciprocal.

Population	Line/Cross	N	Mean	SE	SD	CV
			mg			%
L ₁	LS-97	113	165.9**	2.3	24.3	14.7
L ₂	LS-8	84	333.6**	3.5	31.7	9.5
F ₁	L ₁ ×L ₂	12	236.1	9.8	33.9	14.4
F ₁ reciprocal	L ₂ ×L ₁	23	224.8	5.9	28.2	12.6
F ₂	L ₁ ×L ₂	134	279.5	3.5	40.8	14.6
F ₂ reciprocal	L ₂ ×L ₁	122	272.8	3.7	41.3	15.1
BC ₁	(L ₁ ×L ₂)×L ₁	9	232.1	13.1	39.4	17.0
BC ₁	(L ₂ ×L ₁)×L ₁	16	234.9	9.7	38.9	16.5
BC ₂	(L ₁ ×L ₂)×L ₂	10	280.2	8.0	25.2	9.0
BC ₂	(L ₂ ×L ₁)×L ₂	17	323.8	7.1	29.3	9.0

**Parent lines means significantly different at $P < 0.01$ according to the F ratio of an ANOVA with two samples.

Table 2. Number of plants (N), mean, standard error (SE), standard deviation (SD) and coefficient of variation (CV) for mean seed weight of parent lines, F_1 , F_2 , and backcross populations corresponding to *Lathyrus sativus* cross LS-8 × LS-2026 (large-seeded × extra-large-seeded) and reciprocal.

Population	Line/Cross	N	Mean	SE	SD	CV
			mg			%
L ₁	LS-8	84	333.6**	3.5	31.7	9.5
L ₂	LS-2026	107	443.4**	5.3	54.9	12.4
F ₁	L ₁ ×L ₂	27	356.9	9.0	46.8	13.1
F ₁ reciprocal	L ₂ ×L ₁	17	375.6	11.5	47.4	12.6
F ₂	L ₁ ×L ₂	125	414.5	4.8	53.9	13.0
F ₂ reciprocal	L ₂ ×L ₁	89	405.6	6.1	57.4	14.1
BC ₁	(L ₁ ×L ₂)×L ₁	9	410.0	20.5	61.4	15.0
BC ₁	(L ₂ ×L ₁)×L ₁	16	417.1	11.4	45.6	10.9
BC ₂	(L ₁ ×L ₂)×L ₂	7	436.0	22.1	58.4	13.4
BC ₂	(L ₂ ×L ₁)×L ₂	12	465.0	13.6	47.2	10.2

**Parent lines means significantly different at $P < 0.01$ according to the F ratio of an ANOVA with two samples.

Table 3. Number of plants (N), mean, standard error (SE), standard deviation (SD) and coefficient of variation (CV) for mean seed weight of parent lines, F₁, F₂, and backcross populations corresponding to *Lathyrus sativus* cross LS-97 × LS-2026 (medium-seeded × extra-large-seeded) and reciprocal.

Population	Line/Cross	N	Mean	SE	SD	CV
			mg			%
L ₁	LS-97	113	165.9*	2.3	24.3	14.7
L ₂	LS-2026	107	443.4*	5.3	54.9	12.4
F ₁	L ₁ ×L ₂	16	262.6	7.9	31.7	12.1
F ₁ reciprocal	L ₂ ×L ₁	16	278.1	8.5	34.2	12.3
F ₂	L ₁ ×L ₂	144	280.0*	3.7	44.7	15.9
F ₂ reciprocal	L ₂ ×L ₁	164	320.8**	3.6	45.6	14.2
BC ₁	(L ₁ ×L ₂)×L ₁	15	249.8	11.0	42.6	17.0
BC ₁	(L ₂ ×L ₁)×L ₁	18	248.4	8.1	34.5	13.9
BC ₂	(L ₁ ×L ₂)×L ₂	13	358.0	12.0	43.4	12.1
BC ₂	(L ₂ ×L ₁)×L ₂	19	320.3	11.5	50.1	15.6

*Parent lines means significantly different at $P < 0.01$ according to the F ratio of an ANOVA with two samples.

**Reciprocal F₂ means significantly different at $P < 0.01$ according to the F ratio of an ANOVA with two samples.

The differences between the reciprocal F₁ hybrids from the three crosses were non-significant. Only in the cross between medium-seeded LS-97 and extra-large-seeded LS-2026 (Table 3), the reciprocal F₂ populations had significantly different MSW means, suggesting a cytoplasmic effect. Therefore, reciprocals were reunited for the variance components analysis in the case of crosses 1 and 2, and considered separately in the case of cross 3 (Table 4). Tiwari and Campbell (1996a) found non-significant differences between the reciprocal crosses of small-seeded lines and assumed only nuclear control in the inheritance of MSW.

The variances of the parent lines were directly associated with their seed weight. The variance of the large-seeded line was nearly double the variance of the medium-seeded line and the variance of the extra-large-seeded line was three times the variance of the large-seeded line (Table 4). The magnitude of the variances of parent lines is a relevant issue because, as a result of these differences, crosses with LS-2026 as a parent had a greater estimate of the environmental variance, with concomitant reduction in the estimate of the genotypic variance. Genotypic differences in seed weight are mainly correlated with differences in seed growth rate in soybean (*Glycine max* (L.) Merr.) (Egli *et al.*, 1981), pea (*Pisum sativum* L.) (Munier-Jolain and Ney, 1998), and narrow-leaved lupins (*Lupinus angustifolius* L.) (J. Palta, CSIRO, Australia, personal communication, 2009). Accordingly, grass peas with larger seeds would most probably have greater seed growth rates. Higher temperatures and drought late in the growing season are common in areas like southern Chile and may limit seed growth rate. Munier-Jolain *et al.* (1998) found that a reduction in

assimilate availability did not decrease seed growth rate in white lupin (*Lupinus albus* L.), pea, and soybean, but the duration of seed filling was reduced. Since individual seed weight is the product of seed growth rate by duration of seed filling, a reduced seed filling period caused by environmental conditions such as higher temperatures and terminal drought would leave the seeds in pods formed late during reproductive stage without sufficient time to be fill to their maximum capacity. In any case, underdeveloped seeds formed late in the season may be the origin of greater MSW variances in larger-seeded grass peas.

Cross 2 showed the largest phenotypic (F₂) variance. However, no transgressive segregants were observed since no F₂ individuals had MSW values smaller than the lower range of parent line LS-8 or larger than the upper range of parent line LS-2026. Transgressive segregants were not found in the F₂ of crosses 1 and 3 either. This point to the lack of complementary genes, whose action has been identified as the primary cause of transgression (Rieseberg *et al.*, 1999), and means that alleles with additive effects responsible for increased seed weight in the medium-seeded parent line would also be present in the large-seeded parent line. In turn, such alleles in the large-seeded line would also be present in the extra-large-seeded parent line.

Broad sense heritability was calculated at 0.50 and 0.32 for crosses 1 and 2, respectively, and for the reciprocals of cross 3, the estimates were 0.23 and 0.24 (Table 5). The results for crosses 2 and 3 are in agreement with the broad-sense heritability values of 0.31 and 0.26 obtained by Tiwari and Campbell (1996a) in two crosses involving a parent of MSW of 132 mg with parents

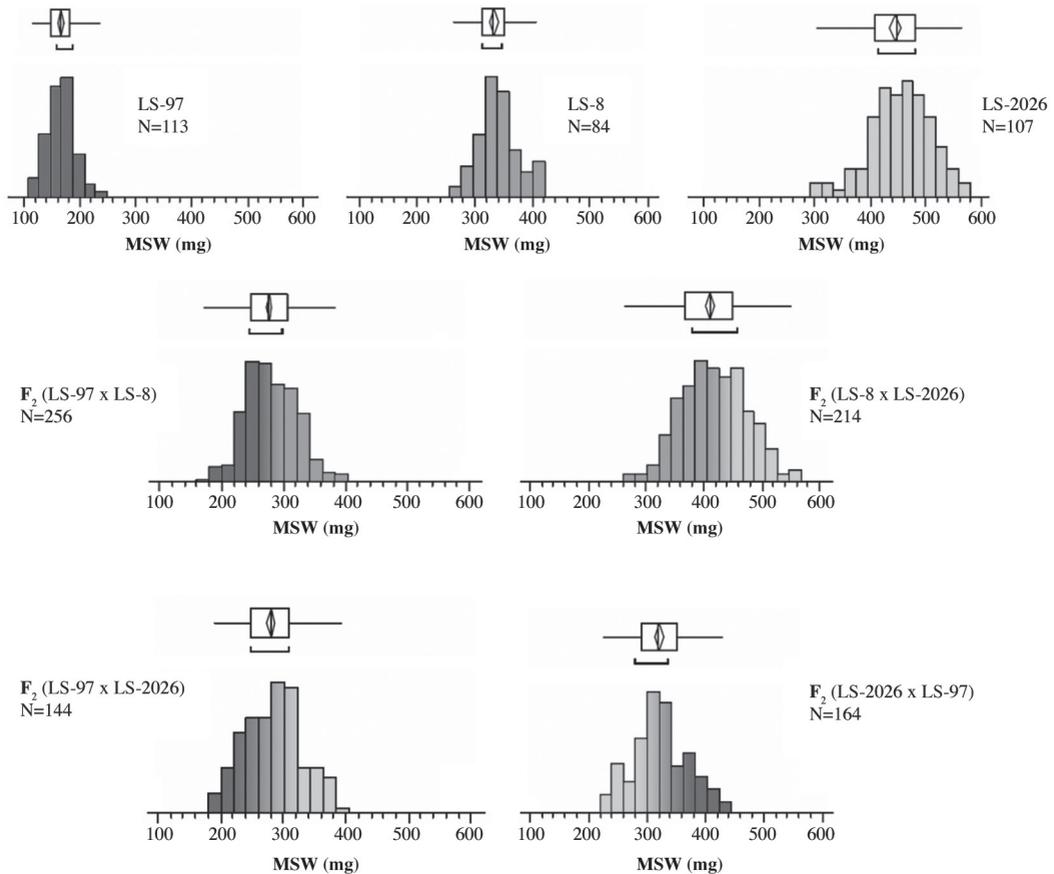


Figure 1. Distribution histograms of mean seed weight (MSW) for seven *Lathyrus sativus* populations: parents (upper row), F_2 of crosses LS-97 \times LS-8 and LS-8 \times LS-2026 including reciprocals (middle row), and F_2 of cross LS-97 \times LS-2026 and its reciprocal LS-2026 \times LS-97 (bottom row). Above each histogram, the ends of the box are the 25th and 75th quantiles. The line across the middle of the box is the median and the diamond indicates the mean and 95% confidence interval. The bracket along the edge of the box identifies the densest 50% of the observations.

of 90 and 87 mg, respectively, and with preliminary reports of 0.23 by Mera *et al.* (2003a) for a large-seeded population. All our estimates are lower than the broad-sense heritability value of 0.65 obtained by Kumar and Dubey (2001) with small-seeded grass peas averaging only 62 mg MSW, and far lower than the 0.75 broad-sense heritability value reported by Türk *et al.* (2007), who calculated variance components in trials with 15 grass pea genotypes averaging 126 mg MSW. An even higher heritability estimate of 0.96 has been reported (Milczak *et al.*, 2001) with no mention made to the method utilized.

In all crosses, most of the genotypic variance was due to additive effects (Table 4), which is consistent with findings of Dixit (1999). Dominance and other non-additive effects were relatively minor, except for cross LS-97 \times LS-2026. As a result, narrow-sense heritability estimates were close to broad-sense estimates (Table 5). Narrow-sense heritability estimates were 0.42 and 0.28 for crosses 1 and 2, respectively, which are usually considered

medium values. The estimates for the reciprocals of cross 3 were 0.15 and 0.22, which are considered relatively low values.

Parent lines LS-97, LS-8, and LS-2026 differed amply in number of seeds per plant, with means and standard deviations of 77.6 ± 44.6 , 40.5 ± 25.2 , and 28.7 ± 20.8 , respectively. Yet, they varied little in yield per plant, with means and standard deviations of 12.8 ± 7.5 , 13.3 ± 7.8 , and 12.5 ± 8.6 g, respectively. Mean seed weight and number of seeds per plant were inversely correlated with coefficients of -0.08 (SE = 0.095), -0.27 (SE = 0.093), and -0.20 (SE = 0.090) for LS-97, LS-8, and LS-2026, respectively. No significant correlation was detected between MSW and yield per plant in any parent line. Taking into account the F_2 populations from the three crosses (N = 778), MSW was inversely correlated ($r = -0.20$, SE = 0.034) with number of seeds per plant and positively correlated ($r = 0.25$, SE = 0.034) with yield per plant. Also Krarup (1983) observed a negative

Table 4. Variances and variance components for mean seed weight in three grass pea crosses. Cross 1: medium × large-seeded; Cross 2: large × extra-large-seeded; Cross 3: medium × extra-large-seeded.

Variance or component of variance	Estimator	Cross 1	Cross 2	Cross 3	
		LS-97 x LS-8	LS-8 x LS-2026	LS-97 x LS-2026	LS-2026 x LS-97
Parent line 1	V _{L1}	591	1007	591	3009
Parent line 2	V _{L2}	1007	3009	3009	591
F ₁	V _{F1}	918	2244	1007	1169
Phenotypic (V _P)	V _{F2}	1689	3071	1994	2081
Backcross 1	V _{BC1}	1462	2570	1813	1193
Backcross 2	V _{BC2}	1210	2709	1880	2508
Environmental (V _E)	(V _{L1} + V _{L2} + V _{F1})/3	839	2086	1536	1590
Genotypic (V _G)	V _P - V _E	850	983	458	491
Additive (V _A)	2V _{F2} - (V _{BC1} + V _{BC2})	706	861	295	461
Non-additive (V _{NA})	V _G - V _A	144	122	163	30

Table 5. Heritability estimates for mean seed weight in three grass pea crosses. Cross 1: medium × large-seeded; Cross 2: large × extra-large-seeded; Cross 3: medium × extra-large-seeded.

Heritability	Estimator	Cross 1	Cross 2	Cross 3	
		LS-97 x LS-8	LS-8 x LS-2026	LS-97 x LS-2026	LS-2026 x LS-97
Broad sense (H ²)	V _G /V _P	0.50	0.32	0.23	0.24
Narrow sense (h ²)	V _A /V _P	0.42	0.28	0.15	0.22

correlation ($r = -0.18$) between MSW and seeds per plant. In agreement with our results, Kumar and Dubey (2001) found a positive phenotypic correlation ($r = 0.28^*$) between seed weight and yield per plant. An even larger ($r = 0.45^{**}$) positive association between seed weight and yield per plant has been reported, suggesting that selection for greater MSW would facilitate selection for high seed yield (Tiwari and Campbell, 1996a).

CONCLUSIONS

Our results indicate that the environment exerts a strong effect on the mean seed weight of grass pea, and the effect is stronger as seed weight increases. The outsized variance of extra-large-seeded parents contributes powerfully in dropping the estimates of the genotypic variance and heritability. On the other hand, most of the genetic control appears to be based upon additive effects. This means that selection for increased seed weight in early segregating generations should be effective. The prospects to improve seed weight in large-seeded grass peas are good, although since the effect of the environment on these types is

stronger the process may become increasingly difficult as heavier seeds are sought. Any effort aimed to reduce the environmental influence should enhance the effectiveness of selection.

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RESUMEN

Herencia del peso de grano en *Lathyrus sativus* L. de semilla grande. Los granos de chícharo (*Lathyrus sativus* L.) de mayor tamaño son preferidos en mercados occidentales, por tanto, el peso medio de grano (PMG) es un carácter comercialmente relevante. Extender el conocimiento sobre su modo de herencia sería útil para

programas de mejoramiento y fue el objetivo de este trabajo. El chícharo presenta amplio rango para PMG, partiendo desde 30 mg. Tres líneas (LS-97, LS-8, LS-2026) consideradas de semilla grande, pero con PMG significativamente diferentes (179, 360 y 470 mg, respectivamente) se cruzaron en un dialelo completo. Parte de la semilla F_1 se sembró y otra se conservó. Flores en plantas F_1 de cada cruce se retrocruzaron con sus respectivos progenitores y el resto produjo semilla F_2 . En 2006 se sembraron progenitores, poblaciones F_1 y F_2 , y retrocruzamientos. Se midió PMG de plantas individuales de cada población, cultivadas en secano. Las medias de recíprocos de cruces LS-8 \times LS-2026 y LS-8 \times LS-97 no fueron significativamente diferentes, y en ambas los datos se reunieron, asumiéndose herencia del PMG controlada sólo por genes nucleares. Sin embargo, la población F_2 de la cruce LS-97 \times LS-2026 y su recíproco presentaron medias diferentes, sugiriendo presencia de herencia citoplasmática. Por ello, los datos de estos recíprocos se mantuvieron separados para calcular heredabilidad. Las heredabilidades en sentido amplio de PMG para las cruces LS-97 \times LS-8 y LS-8 \times LS-2026 fueron estimadas en 0,50 y 0,32 respectivamente, y en 0,23 y 0,24 para la cruce LS-97 \times LS-2026 y su recíproco, respectivamente. Las heredabilidades en sentido restringido fueron 0,42 y 0,28, y 0,15 y 0,22, respectivamente. La varianza de las líneas parentales de mayor PMG, particularmente LS-2026, fue mucho mayor, incrementando la estimación de la varianza ambiental en las cruces donde participaron. En todas las cruces los efectos genéticos predominantes fueron aditivos, prediciendo buena respuesta a la selección durante generaciones segregantes tempranas. Por tanto, los prospectos para aumentar PMG en chícharos de grano grande son auspiciosos.

Palabras clave: chícharo, almorta, heredabilidad, leguminosas de grano.

LITERATURE CITED

- Campbell, C.G. 1997. Grass pea. *Lathyrus sativus* L. Promoting the conservation and use of underutilized and neglected crops. Vol. 18. Institute of Plant Genetics and Crop Plant Research, Gatersleben, Germany/International Plant Genetic Resources Institute, Rome, Italy.
- Campbell, C.G., R.B. Mehra, S.K. Agrawal, Y.Z. Chen, A.M. Abd El Moneim, H.I.T. Khawaja, *et al.* 1994. Current status and future strategy in breeding grasspea (*Lathyrus sativus*). *Euphytica* 73:167-175.
- Dixit, G.P. 1999. Inheritance of plant height, branch number, pod length and seed weight in two crosses of grasspea. *FABIS Newsletter* 42:18-20.
- Egli, D.B., J. Fraser, J.E. Leggett, and C.G. Poneleit. 1981. Control of seed growth rate in soybeans. *Annals of Botany* 48:171-176.
- Hammer, K., G. Laghetti, and P. Perrino. 1989. Collection of plant genetic resources in South Italy, 1988. *Kulturplanze* 37:401-414.
- Hanbury, C.D., C.L. White, B.P. Mullan, and K.H.M. Siddique. 2000. A review of the potential of *Lathyrus sativus* L. and *L. cicera* L. grain for use as animal feed. *Animal Feed Science and Technology* 87:1-27.
- Jackson, M.T., and A.G. Yunus. 1984. Variation in the grass pea (*Lathyrus sativus* L.) and wild species. *Euphytica* 33:549-559.
- Krarp, A. 1983. Caracterización de una población heterogénea de chícharos (*Lathyrus sativus* L.) y análisis de causa y efecto entre rendimiento y sus componentes, bajo efectos de distintas épocas y densidades de siembra. *Agro Sur* 11:30-37.
- Krarp, A. 2002. Blanco Austral, cultivar de chícharo (*Lathyrus sativus* L.) obtenido por selección del rendimiento por planta y de sus componentes. *Agro Sur* 30:40-46.
- Kumar, S., and D. Dubey. 2001. Variability, heritability and correlation studies in grass pea (*Lathyrus sativus* L.). *Lathyrus Lathyrism Newsletter* 2:79-81.
- Lambein, F., Y.H. Kuo, K. Kusama-Eguchi, and F.I. Ikegami. 2007. 3-N-oxalyl-L-2,3-diaminopropanoic acid, a multifunctional plant metabolite of toxic reputation. *Arxivoc* 9:45-52.
- Malek, M.A., A. Afzal, M.M. Rahman, and A.B.M. Salahuddin. 2000. *Lathyrus sativus*: a crop for harsh environments. p. 369-373. In R. Knight (ed.) *Linking research and marketing opportunities for pulses in the 21st century*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Mera, M., A. Montenegro, N. Espinoza, N. Gaete, and L. Barrientos. 2003a. Heritability of seed weight in an inbred population of large-seeded *Lathyrus sativus*. *Lathyrus Lathyrism Newsletter* 3:24-25.
- Mera, M., J. Tay, A. France, A. Montenegro, N. Espinoza, N. Gaete, and L. Barrientos. 2003b. Luanco-INIA, a large-seeded cultivar of *Lathyrus sativus* released in Chile. *Lathyrus Lathyrism Newsletter* 3:26.
- Milczak, M., M. Pedzinski, H. Mnichowska, K. Szwed-Urbas, and W. Rybinski. 2001. Creative breeding of grass pea (*Lathyrus sativus* L.) in Poland. *Lathyrus Lathyrism Newsletter* 2:85-89.
- Montenegro, A., and M. Mera. 2009. Phosphate fertilization can increase yield of productive grass pea (*Lathyrus sativus* L.) crops on P-retentive soils. *Chilean Journal of Agricultural Research* 69:244-251.

- Munier-Jolain, N.G., N.M. Munier-Jolain, B. Ney, R. Roche, and C. Duthion. 1998. Seed growth rate in grain legumes. I. Effect of photoassimilate availability on seed growth rate. *Journal of Experimental Botany* 49:1963-1969.
- Munier-Jolain, N.G., and B. Ney. 1998. Seed growth rate in grain legumes. II. Seed growth rate depends on cotyledon cell number. *Journal of Experimental Botany* 49:1971-1976.
- Nyquist, W.E. 1991. Estimation of heritability and prediction of selection response in plant populations. *Critical Reviews in Plant Sciences* 10:235-322.
- Palmer, V.S., A.K. Kaul, and P.S. Spencer. 1989. International network for the improvement of *Lathyrus sativus* and the eradication of lathyrism (INILSEL): A TWMRF initiative. p. 219-223. In P.S. Spencer (ed.) *The grass pea: Threat and promise*. Third World Medical Research Foundation, New York, USA.
- Rieseberg, L.H., M.A. Archer, and R.K. Wayne. 1999. Transgressive segregation, adaptation and speciation. *Heredity* 83:363-372.
- SAS Institute. 2009. JMP User's Guide. SAS Institute, Cary, North Carolina, USA.
- Siddique, K.H.M., C.L. Hanbury, and A. Sarker. 2006. Registration of 'Ceora' grass pea. *Crop Science* 46:986.
- Siddique, K.H.M., S.P. Loss, S.P. Herwig, and J.M. Wilson. 1996. Growth, yield and neurotoxin (ODAP) concentration of three *Lathyrus* species in Mediterranean-type environments of Western Australia. *Australian Journal of Experimental Agriculture* 36:209-218.
- Tavoletti, S., L. Iommarini, P. Crinò, and E. Granati. 2005. Collection and evaluation of grasspea (*Lathyrus sativus* L.) germplasm of central Italy. *Plant Breeding* 124:388-391.
- Tiwari, K., and C. Campbell. 1996a. Inheritance of seed weight in grasspea (*Lathyrus sativus* L.). *FABIS Newsletter* 38/39:30-33.
- Tiwari, K.R., and C.G. Campbell. 1996b. Inheritance of neurotoxin (ODAP) content, flower and seed coat colour in grasspea (*Lathyrus sativus* L.). *Euphytica* 91:195-203.
- Türk, M., S. Albayrak, and N. Celik. 2007. Estimates of broad-sense heritability for seed yield and yield components of grass pea (*Lathyrus sativus* L.). *Turkish Journal of Agriculture and Forestry* 31:155-158.
- Vaz Patto, M., B. Skiba, E. Pang, S. Ochatt, F. Lambein, and D. Rubiales. 2006. *Lathyrus* improvement for resistance against biotic and abiotic stresses: From classical breeding to marker assisted selection. *Euphytica* 147:133-147.