Hereditas 139: 212–216 (2003)

Genetic parameters for agronomic characteristics. I. Early and intermediate breeding populations of true potato seed

RODOMIRO ORTIZ and ALI M. GOLMIRZAIE

Centro Internacional de la Papa, Lima, Perú

Ortiz, R. and Golmirzaie, A. M. 2003. Genetic parameters for agronomic characteristics. I. Early and intermediate breeding populations of true potato seed. — *Hereditas 139:* 212–216. Lund, Sweden. ISSN 0018-0661. Received April 28, 2003. Accepted November 4, 2003

The original variation in the source population as well as the selection method may influence the genetic variation in further cycles of genetic improvement. Therefore, the objectives of this research were to determine genetic parameters (variance components and heritability) in source and intermediate stages of a true potato seed (TPS) breeding population and to calculate the genetic and phenotypic correlations in this breeding material developed by the Centro Internacional de la Papa (CIP). The intermediate stage was derived from a source population adapted to the warm lowland tropics plus introduction of exotic germplasm from North America and Europe. Non-additive genetic variation was almost nil for plant survival, tuber yield and tuber shape uniformity in both stages of the breeding population and no quantitative genetic variation for uniformity of tuber color was observed in both source and intermediate breeding materials. Heritability was higher in the intermediate stage than in the source population for plant survival (0.86 vs 0.66), tuber yield (0.30 vs 0.14) and tuber shape (0.77 vs 0.51), but it was the reverse for tuber uniformity (0.11 vs 0.72). These results suggest that potato breeders at CIP were able to keep enough genetic variation for most important characteristics for potato production from true seed in their intermediate breeding materials by adding new sources of variation to the original breeding population. Additive genetic and phenotypic correlations were significant and positive between plant vigor after transplanting and tuber yield, and tuber shape and tuber uniformity, which suggest that high yielding offspring result from early vigorous growth, and that tuber uniformity could depend on tuber shape uniformity in this breeding material.

Rodomiro Ortiz, International Institute of Tropical Agriculture, c/o L.W. Lambourn & Co., Carolyn House, 26 Dingwall Road, Croydon, UK, CR9 3EE. E-mail r.ortiz@cgiar.org

A true potato seed (TPS) cultivar refers to a mixture of sexual seed-derived propagules ensuing from the same cross or open pollination from one clone or plants from the same cross (i.e. a synthetic) (ORTIZ 1997; SIMMONDS 1997). There are many advantages of TPS, which are mostly associated to health of planting materials (with a few important exceptions they are virus-free) and costs. TPS are also the source of new clones for cultivar development to potato breeders, which are accustomed to handle sexual seeds of potato in their genetic improvement programs for this crop.

To make further progress through selection, plant breeders undertake inheritance research. Narrow-sense heritability (h^2) or the ratio (additive genetic variance/phenotypic variance) is a scale-independent quantity that plays an important role in the theory of selection methods (BOS and CALIGARI 1995), because the response to selection (R) can be predicted if the breeder knows h^2 for the target trait(s). Genetic variances can be calculated from appropriate matings such as diallel crosses, hierarchical or nested design (North Carolina 1), or factorial or line-by-tester design (North Carolina 2), and parent-offspring regression (TAI and DE JONG 1991; TARN et al. 1992). Because of the breeding system of potato, North Carolina design 1 was recently recommended for calculating heritability in this crop (ORTIZ and GOLMIRZAIE 2002).

Plant breeding from the Centro Internacional de la Papa (CIP) developed experimental potato populations adapted to the lowland tropics and from some selected material, including sources from this population, for TPS. The original breeding population for the lowland tropics was assembled from various genetic sources, whose diversity was previously tested for tuber yield and its stability of performance across lowland tropic locations (MENDOZA 1982). The most important sources were clones from the groups Tuberosum, Neotuberosum (or Andigena selected under long-days), and 4x–2x hybrids (DTO) between Tuberosum and Phureja. Selection for adaptation, with earliness for tuber bulking under heat was the primary target trait, and high yield per se plus resistances to bacterial wilt, potato viruses Y and X as well as acceptable tuber quality. A few clones were selected from about thousands of genetic materials because they met above standard in the humid lowland tropics of Perú (0.06% selection intensity). Because of this very small frequency two approaches were taken 1) to continue testing foreign clones to select the best-adapted materials that may become

Table 1. *Analysis of variance of design I in an early true potato seed population pooled over sets and environments (San Ramon and La Molina, I).*

Source of variation	Degrees of freedom	Plant survival	Yield plant^{-1}	Tuber color	Tuber shape	Tuber uniformity
		#	kg	(1–9 scale: 1 = worst; 9 = best)		
Locations (L)	1	57.129**	7.339*	0.082	0.125*	2.247**
Replications (R)/L	4	0.292	0.046	0.024	0.016	0.094**
Sets (S)/R/L	18	1.049**	0.210**	0.373*	0.129*	0.069*
Males (M)/S	8	4.376**	0.143	0.250	0.152	0.181*
Female (F)/M/S	36	1.116**	0.127	0.312**	0.042	0.042
M/S × L	8	0.156	0.063	0.147	0.061	0.046
F/M/S × L	36	0.418**	0.129**	0.056	0.045*	0.034
Pooled error	176	0.133	0.040	0.038	0.030	0.028
Coefficient of variation (%)		8.14	7.49$^+$	7.27	6.49	6.84

* and ** indicate significant at 5% and 1% respectively.

$^+$ after logarithmic transformation.

parental sources in the breeding program, and 2) to select by bulk pollination of selected females materials from the breeding population. Early tuber initiation and fast tuber bulking rate under heat were the two main traits in this breeding program. Through a recurrent selection scheme the selection intensity increased to 10% in next cycles of selection (Mendoza 1985).

Years later, TPS breeding at CIP required new sources of genetic variation and an a heterogeneous breeding population was assembled using introductions from Europe and North America in crossed with selected CIP lowland breeding materials. The objective of this research were to investigate h^2 for several traits, which changed as per the breeding cycle stage, in CIP TPS breeding populations, as well as phenotypic and genetic correlations between characters that may be included in multitrait selection.

MATERIAL AND METHODS

Two experimental populations were included in this investigation at two contrasting Peruvian locations: La Molina (12°05′S, 240 m, coastal desert) and San Ramon (11°08′S, 800 m, humid mid-altitude on the eastern Andes slopes). For the original source, lowland tropic breeding population, 48 hybrid offspring were created using the design 1 mating scheme (Comstock and Robinson 1948), in which a sample of 12 male sources was crossed each to a random sample of four female clones. For the intermediate breeding population, 100 hybrid offspring were included following the design 1 using a random sample of 20 male clones that were individually crossed with a random sample of 5 female clones.

In all experiments, true potato seed (TPS) of each offspring were planted in flats at a greenhouse nursery, and 40 seedlings were transferred after eight weeks to single row plots in the field. The experimental layout was always a randomized block design with a maximum of three replications. Because a large number of offspring was sampled from the breeding population, those offspring sharing the same male were included in the same set. The characters recorded were tuber yield per plant in kg, plant survival in percentage, and using a 1 (worst) to 9-scale (best): plant vigor, shape and uniformity, vine earliness, plus uniformity of tuber color, shape and overall uniformity.

The analyses of variance for hierarchical (design I) and mating design combined across environments and sets followed Ortiz and Golmirzaie (2002). Because different sets of parents were used as males and females the analysis of variance for each design included a source of variation due to sets. However, the expectations of the mean squares of males, females, and their interaction are the same for the components of variance and covariance of the relatives. Genetic and phenotypic correlations were calculated between all traits.

RESULTS AND DISCUSSION

The source of variation location in the combined analysis of variance was significant for plant survival, tuber yield and uniformity because growing conditions were better in San Ramon than in La Molina in the fields where the early breeding cycle population were grown (Table 1). The source of variation, sets–nested within reps and locations that allowed a larger number of genotypes being sampled from the breeding population was significant for all traits. This experimental design approach showed that sets increase the precision of the experiment because this

Table 2. *Variance components, genetic variances and heritability (h^2) of agronomic and tuber characteristics in an early true potato seed population (San Ramon and La Molina, I).*

Item	Plant survival	Yield plant^{-1}	Tuber color	Tuber shape	Tuber uniformity
	#	kg	(1–9 scale: 1 = worst; 9 = best)		
Males (M)/S	0.1467	0.0034	0 (= −)	0.0039	0.0053
Female (F)/M/S	0.1164	0 (= −)	0.0426	0 (= −)	0.0013
M/S × L	0 (= −)	0 (= −)	0.0076	0.0013	0.0010
F/M/S × L	0.0949	0.0297	0.0061	0.0051	0.0020
σ^2_A	0.6070	0.0160	0	0.0184	0.0238
σ^2_D	0 (= −)	0	0.2556	0	0 (= −)
σ^2_{AL}	0	0	0.0315	0.0026	0.0034
σ^2_{DL}	0.5692	0.1780	0 (= −)	0.0230	0.0058
h^2	0.6642	0.1433	0	0.5079	0.7211

σ^2_A = additive variance; σ^2_D = non-additive variance; σ^2_{AL} = additive-by-location variance; σ^2_{DL} = non-additive-by-location variance.

Table 3. *Analysis of variance of design I combined over environments in an intermediate true potato seed population (San Ramon and La Molina, II).*

Source of variation	Degrees of freedom	Plant survival	Yield plant^{-1}	Plant vigor	Plant shape	Plant uniformity	Tuber color	Tuber shape	Tuber uniformity
		#	kg	(1–9 scale; 1 = worst; 9 = best)			(1–9 scale; 1 = worst; 9 = best)		
Locations (L)	1	19817.41**	23.661**	39.53**	10.67**	28.17**	24.00**	22.08**	45.38**
Replications (R)/L	4	7.27	0.023	1.59*	1.21	3.69**	1.16	0.35	0.24
R/Sets(S)/L	18	174.63**	0.254**	8.93**	4.36**	5.07**	12.64**	3.80**	0.33
R/S × L	16	50.63	0.030	1.92	1.31	1.82	1.26	1.07	0.34
Males (M)/S	16	532.41**	0.437	26.87**	6.39**	3.14	21.10	8.42**	1.20
Females (F)/M/S	80	59.69**	0.058	3.21**	1.05	1.13	13.69**	2.21**	0.83
M/S × L	16	75.08	0.301**	6.64*	1.73	4.97**	2.62	1.48	0.56
F/M/S × L	80	21.35**	0.042**	1.65**	0.77	1.05	1.14*	1.11	0.63
Pooled error	384	13.27	0.016	0.95	0.75	0.81	0.79	0.93	0.53
Coefficient of variation (%)		16.57	22.81	15.93	14.08	16.24	12.45	20.52	15.26

* and ** indicate significant at 5% and 1% respectively.

appears to be the preferred arrangement for local control of the experimental error (Hallauer and Miranda 1981).

Male sources were significantly different for plant survival and tuber uniformity, while females nested within males were significant for plant survival and tuber color uniformity (Table 1). Furthermore, the significant interaction between locations and females nested within males–against which the source of variation females nested within males was tested, was significant for plant survival, tuber yield and tuber shape uniformity. The male performance within sets was not influenced by the location for any trait as shown by the respective non-significant interaction. These results explain the large h^2 for plant survival and tuber shape in which the non-additive variance was zero because of the significant and large interaction between locations and non-additive variance (Table 2). The nil additive genetic variance for tuber color uniformity only reflects that this character should be a qualitative trait and with a few loci segregating for it as reported elsewhere with the aid of DNA markers (Eck et al. 1994). The low h^2 for tuber yield concurs with other reports after selection in potato breeding populations (Ortiz 1998; Tarn et al. 1992; Thompson et al. 1983).

There were significant differences between locations for all characters (Table 3) in the fields where the intermediate heterogeneous breeding populations were grown. However, it was the reverse than in the early breeding cycle population, the best performance was observed in La Molina, perhaps due to the genes added from the new parental sources (Europe and North America) being better adapted to the cooler environment in this locations that to the heat of San Ramon. The appropriate experimental arrangement of using sets and nesting reps was corroborated by the respective significant source of variation in this

Table 4. *Variance components, genetic variances and heritability (h^2) of agronomic and tuber characteristics in an intermediate true potato seed population (San Ramon and La Molina, II).*

Item	Plant survival	Yield plant^{-1}	Plant vigor	Plant shape	Plant uniformity	Tuber color	Tuber shape	Tuber uniformity
	#	kg	(1-9 scale; 1 = worst; 9 = best)			(1-9 scale; 1 = worst; 9 = best)		
Males (M)/S	13.9663	0.0040	0.6223	0.1460	0 (= –)	0.1977	0.1947	0.0147
Females (F)/M/S	6.3900	0.0027	0.2600	0.0467	0.0133	2.0917	0.1833	0.0333
M/S × L	3.5820	0.0173	0.3327	0.0640	0.2613	0.0987	0.02467	0 (= –)
F/M/S × L	2.6933	0.0087	0.2333	0.0067	0.0800	0.1167	0.0600	0.0333
σ^2_A	60.9162	0.0169	2.7309	0.6502	0 (= –)	0 (= –)	0.7862	0.0462
σ^2_{NA}	0 (= –)	0 (= –)	0 (= –)	0 (= –)	0.0800	11.3640	0 (= –)	0.1120
σ^2_{AL}	14.9204	0.0748	1.3969	0.2942	1.1662	0.3827	0.0751	0
σ^2_{NAL}	0 (= –)	0 (= –)	0 (= –)	0 (= –)	0 (= –)	0.1080	0 (= –)	0.2000
h^2	0.8630	0.2965	0.7683	0.6974	0	0	0.7722	0.1110

σ^2_A = additive variance; σ^2_D = non-additive variance; σ^2_{AL} = additive-by-location variance; σ^2_{DL} = non-additive-by-location variance.

experiment that removed statistics "noise" from the data.

Male clones were significantly different for plant survival, vigor, shape and tuber shape, whereas the females nested within males were significantly different for same traits but plant shape and also for tuber color uniformity (Table 3). The interactions with locations were significant for tuber yield and plant vigor for both males and females nested within males, and only for plant uniformity for males and for plant survival and tuber color uniformity for females nested within males. The h^2 was therefore high for plant survival, vigor and shape, plus tuber shape uniformity because the additive genetic variation accounted for most of the variation, since it was significantly larger (at least two-fold) than the interaction between this source and location for these traits and the non-additive genetic variation for them was nil. These results also indicate that influx of new genes from the exotic germplasm to this breeding germplasm increased the genetic variation and that steady gains can be therefore attained by further recurrent selection for these traits.

Though the non-additive genetic variation was zero for tuber yield, the h^2 was only intermediate for this character because of the significant additive × location interaction (at least 4-fold larger than additive genetic variation), which suggest the need of selecting male parents for each contrasting Peruvian lowland environment affected by temperature and rainfall pattern. Likewise, this significant interaction accounts for the nil h^2 for plant uniformity. Conversely the significant non-additive genetic variation accounted for the nil h^2 for tuber color uniformity, which confirms the results from observed in the early cycle breeding population about the qualitative nature of this character. Indeed, THOMPSON et al. (1983) reported nil h^2 for this trait in an advanced cycle of selection in Neotuberosum, a source population for CIP potato breeding program. The above results also clearly show the potential for improving plant survival, vigor and shape in CIP TPS breeding population, as well as that that additional cycles of hybridization with exotic sources and selection may affect positively the genetic variability for tuber yield in this breeding material.

The genetic (or among breeding values) and phenotypic correlations were significantly high and positive for plant vigor and tuber yield, and tuber shape uniformity and overall tuber uniformity (Table 4). The former correlations suggest that early selection for plant vigor in the nursery of after transplanting seedlings to the field will result in high tuber yield as already indicated by GOLMIRZAIE and ORTIZ (2002), because of the high proportion of heterozygous genotypes showing this outstanding plant vigor. This assertion was further corroborated by the significant and negative phenotypic correlation between plant uniformity with both plant vigor and tuber yield, i.e. the most heterogeneous hybrid offspring showed the most vigorous plants with the highest tuber yielding progeny. Similarly, the index-trait overall tuber uniformity appears to rely more on tuber color than on tuber shape, which may explain partially the low h^2 of this trait in the intermediate cycle breeding population (Table 5). Other significant phenotypic correlations were between following pairs of characters: plant vigor and vine earliness, vine earliness and plant uniformity, and tuber color uniformity with both plant uniformity and tuber shape uniformity.

Table 5. *Phenotypic (below diagonal) and breeding value (above diagonal) correlations between plant and tuber characteristics.*

Trait	Yield per plant	Plant vigor	Plant uniformity	Vine earliness	Tuber color	Tuber shape	Tuber uniformity
Yield per plant		0.755**	0.344	−0.302	0.029	0.362	0.160
Plant vigor	0.866**		0.554	−0.172	0.256	−0.124	0.452
Plant uniformity	−0.516**	0.614**		−0.316	0.266	−0.169	0.357
Vine earliness	0.090	0.374*	0.733**		0.196	0.090	−0.363
Tuber color	−0.101	−0.165	0.429*	0.234		0.491	0.512
Tuber shape	−0.182	−0.103	0.099	0.146	0.688**		0.605*
Tuber uniformity	−0.205	−0.533**	−0.171	−0.263	0.662**	0.577**	

* and ** indicate significant at 5% and 1% respectively.

Such correlations suggest that vigorous plants are late maturing, but late maturing plants are more uniform phenotypically and for the color of their tubers and tuber shapes. These results suggest therefore, that very plant vigorous TPS cultivars with high yields and phenotypically uniform offspring can be selected among these breeding materials.

REFERENCES

Bos, I. and Caligari, P. 1995. Selection methods in plant breeding. – Chapman and Hall, pp. 174–221.

Comstock, R. E. and Robinson, H. F. 1948. The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. – Biometrics 4: 254–266.

Eck, H. J., van, Jacobs, J. M. E., Stam, P. et al. 1994. The inheritance of anthocyanin pigmentation in potato (*Solanum tuberosum* L.) and mapping of tuber skin color using RFLPs. – Heredity 73: 410–421.

Golmirzaie, A. M. and Ortiz, R. 2002. Inbreeding and true seed in tetrasomic potato. III. Early selection for seedling vigor in open pollinated populations. – Theor. Appl. Genet. 104: 157–160.

Hallauer, A. R. and Miranda, J. B. 1981. Quantitative genetics in maize breeding. – Iowa State Univ. Press.

Mendoza, H. A. 1982. Development of lowland tropic populations. – In: Utilization of the genetic resources of the potato III. Centro Internacional de la Papa, Lima, Perú, pp. 40–53.

Mendoza, H. A. 1985. Selection of parental stocks for heat tolerance and earliness. – In: Page, O. T. (ed.), Present and future strategies for potato breeding and improvement. Centro Intenacional de la Papa, Lima, Perú, pp. 7–16.

Ortiz, R. 1997. Breeding for potato production using true seed. – Plant Breed. Abst. 67: 1355–1360.

Ortiz, R. 1998. Potato breeding via ploidy manipulations. – Plant Breed. Rev. 16: 15–86.

Ortiz, R. and Golmirzaie, A. M. 2002. Hierarchical and factorial mating designs for quantitative genetic analysis in tetrasomic potato. – Theor. Appl. Genet. 104: 675–679.

Simmonds, N. W. 1997. A review of potato propagation by means of seed, as distinct from clonal propagation by tubers. – Potato Res. 40: 191–214.

Tai, G. C. C. and De Jong, H. 1991. Evaluation of potato hybrids obtained from tetraploid-diploid crosses. – Plant Breeding 107: 183–189.

Tarn, T. R., Tai, G. C. C., De Jong, H. et al. 1992. Breeding potatoes for long-day temperate climates. – Plant Breed. Rev. 9: 217–332.

Thompson, P. G., Mendoza, H. A. and Plaisted, R. L. 1983. Estimation of genetic parameters for characters related to potato propagation by true seed (TPS) in an Andigena population. – Am. Potato J. 60: 393–401.