Genetic Analysis of Tuber Dormancy and Related Traits in Potato (*Solanum tuberosum* L.)

M.H. Rashid and A.L. Carpena[1]

Tuber Crops Research Centre
Bangladesh Agricultural Research Institute
Joydebpur, Gazipur, Bangladesh

ABSTRACT. *Five potato varieties in three dormancy groups, long, medium and short, were crossed in all possible combinations to produce five self and ten each of F1, reciprocal, F2 (self) and F2 (random) populations following Gardner and Eberhart's variety diallel method to find out the genetic nature of tuber dormancy and its related traits. Analysis of variance showed that there was high variability for each of the traits considered. Genetic analysis showed that tuber dormancy was predominantly controlled by additive genes although significant amount of non additive effect was present. Significant GCA effects (but not SCA) indicated that the non additive portion might be due to the result of some interference such as epistasis and linkage. Presence of high proportion of residual effects provided the same evidence. Similar genetic effects were found for seedling emergence and sprout weight. Both additive and dominance effects were significant, but the former was predominant. Only non additive gene effect was predominant for tuber size and tuber yield. Significant SCA effects, and total and average heterotic effects also gave similar indications. Significant additive, but insignificant non additive effects, and significant GCA, but insignificant SCA effects proved that the trait tuber dry matter is controlled mainly by additive genes. Similarly, weight loss due to respiration of tubers and TTC colour index of tubers showed predominant additive gene effects, although there were some evidences of non additive effects. The existence of high proportion of variance for each of the traits was probably due to the 4X nature of the crop where higher order epistasis such as additive X additive, additive X dominance, dominance X dominance, etc. and linkage might have influenced the results.*

INTRODUCTION

Potato has become a potential food crop in the tropical and sub-tropical countries in recent years due to its high return in short time. Compared to other crops, potato can provide more food with better quality for the increasing human population. However, the genetic variability and available germplasm resources are extremely limited in these areas.

The existence of variability in a particular trait is an important prerequisite for its improvement. The proportion of heritable and non heritable variation should be estimated for use in any successful breeding program (Sharma, 1989). As tuber dormancy in potato is an important trait of varieties under tropical conditions because of the rapid depletion of

---

[1]   Department of Agronomy, University of the Philippines Los Baños (UPLB), Philippines.

short dormant tubers under high temperature, the knowledge on the type of gene action for the trait and its degrees of relationship with other traits is of immense importance in designing breeding programs for the development of long dormant potato varieties. Simmonds (1963) stated that tuber dormancy and seed dormancy are correlated. Thompson *et al.* (1980) found from diploid *Solanum stenotonum* and *S. phureja* potatoes that the genetic variance for tuber dormancy is high and largely additive in nature.

The following study was undertaken to determine the type of gene action for tuber dormancy and its genetic relationship with other traits of tetraploid potatoes under tropical conditions.

MATERIALS AND METHODS

Twenty parental clones were collected from CIP (International Potato Centre) station at MMSU (Mariano Marcos State University), Batac and BSU (Benguet State University), La Trinidad in 1995 and evaluated at Los Baños, Philippines under ambient condition to identify genotypes with different dormancy groups. Five selected parents in three dormancy groups (long, medium and short) were crossed in a full diallel method in 1995 and 1996 to produce 20 F_1s and 20 F_2s (F_1 self and F_1 random mated), and evaluated with their parents and selfed populations in 1996–97 in the field (at BSU) as well as in storage (at UPLB, Los Baños) using randomized complete block design with three replications. Gardner and Eberhart's (1966) analysis I was carried out to find the genetic parameters. The assumptions of arbitrary gene frequency for each locus, diploid inheritance and no epistasis were largely met by 4X parent materials due to their high proportion of bivalent formation during meiosis (Swaminathan and Hawkes, 1953; Hawkes, 1978; Peloquin *et al.*, 1989). *S. tuberosum* is considered to be an amphidiploid of *S. stenotonum* and *S. sparsiphilum* (Hawkes, 1956 and 1978).

Data were collected on rate of seedling emergence, tuber yield, tuber size, dry matter content, tuber dormancy, sprout weight and weight loss after 150 days of harvesting. Seedling emergence and dormancy breaking rates were measured by an index using the following formula:

$$I = \frac{\Sigma\,(No.\ of\ seedlings\ emerged\ /\ day \times No.\ of\ days\ sowing)}{Total\ number\ of\ seedlings\ emerged}$$

Maturity period was measured from the date of planting to 80% leaf senescence. Tuber size and yield measured at harvest from the whole plot. Dry matter content of tubers (%) was measured one week after harvest by drying a transverse section taken from the middle of each tuber at 105°C for 48 h (until a constant weight was reached).

Genetic analysis

The statistical genetic model presented by Gardner and Eberhart (1966) was used to obtain useful genetic information from a set of potato varieties, their diallel crosses and related populations.

The means of the varieties (V_i), varieties selfed (V_i^s), variety crosses (C_{ij}), variety cross selfed (C_{ij}^s) and variety cross random mated (C_{ij}^r) were estimated as follows:

$$V_i = \mu - a_i + d_i$$

$$V_i^s = \mu + a_i + \tfrac{1}{2}\, d_i$$

$$C_{ij} = \mu + \tfrac{1}{2}\,(a_i + a_j) + \tfrac{1}{2}\,(d_i + d_j) + h_{ij}$$

$$C_{ij}^s = \mu + \tfrac{1}{2}\,(a_i + a_j) + \tfrac{1}{4}\,(d_i + d_j) + \tfrac{1}{2}\, h_{ij}$$

$$C_{ij}^r = \mu + \tfrac{1}{2}\,(a_i + a_j) + \tfrac{1}{2}\,(d_i + d_j) + \tfrac{1}{2}\, h_{ij}$$

where,

μ	=	mean of the random inbred lines from all varieties,
a_i	=	additive effects or contribution of homozygous loci
d_i	=	dominance effects or contribution of heterozygous loci
h_{ij}	=	heterosis effects due to difference in gene frequencies in i and j varieties and to dominance

To provide additional information, the parameter h_{ij} was further partitioned as follows:

$$h_{ij} + \bar{h} + h_i + s_{ij}$$

where,

$\bar{h}$	=	average heterosis contributed by a particular set of varieties used in the crosses
h_i	=	average heterosis contributed by variety i in its crosses measured as a deviation from average heterosis ($\Sigma h_i = 0$)
s_{ij}	=	specific heterosis of the cross involving varieties i and j.

Restrictions used were $\Sigma_i s_{ij} = \Sigma_j s_{ij} = 0$

The genetic parameters were estimated by least squares method using the matrix equation:

$$B = [X'X]^{-1}\,[X'Y]$$

where, B is the genetic parameter, X is the coefficient matrix of the independent variable, and Y is the population mean. The expectations of the coefficients of genetic parameters were used to estimate B.

Since reciprocal effects were not significant, Griffing's (1956) Method 4, Model II analysis which gives similar genetic information to that of Gardner and Eberhart's (1966) analysis III (Baker, 1978; Gardner and Eberhart, 1966) was used to estimate additive variances and covariances from F_1 progenies which would be used to calculate genetic correlations between tuber dormancy and other traits.

Genetic correlation coefficients (r_A) among the traits were estimated using the following formula:

$$r_A = \sigma_{A(xy)} / \sigma_{A(x)} \cdot \sigma_{A(y)}$$

where, $\sigma_{A(xy)}$ = Additive covariance between two traits, $\sigma_{A(x)}$ and $\sigma_{A(y)}$ = additive standard deviations of the two traits x and y, respectively. Estimates of additive variances and covariances were obtained from the relationship: $\sigma^2_{gca} = \frac{1}{2}\sigma^2_A$, and $\sigma_{gca(xy)} = \frac{1}{2}\sigma_{A(xy)}$, respectively.

RESULTS AND DISCUSSION

Genetic analysis of variance (Table 1) showed that tuber dormancy is predominantly controlled by additive genes although significant amount of non additive effect was present. The proportion of non-additive effects (d_i) was very low compared to additive effects (a_i). The presence of a high proportion of additive genetic variance for tuber dormancy was also reported by Thompson et al. (1980) from diploid potatoes. Simmonds (1964) studied diploid and tetraploid potatoes and concluded that the trait is of polygenic control.

Genetic effects associated with seedling emergence seemed to be both additive and non-additive, but the non-additive effects were much lower than the additive effects. Specific heterosis (s_{ij}) was non-significant, but variety heterosis ($\bar{h}$) was significant. Results indicated that the additive effects are more important than non additive effects. For sprout weight, both additive and non-additive effects seemed to be important.

For tuber yield and tuber size, only dominance effects were significant. For tuber dry matter and weight loss, only additive effects were significant. Sharma (1986) found significant additive effects for dry matter content and significant non-additive effects for tuber yield. Tai (1976), Killick (1977) and Mendoza (1984) found predominant non-additive gene effects or nonsignificant additive variance for tuber yield in potato. Zhan (1993) found that both additive and non additive gene actions influenced the dry matter content of the tubers, but additive effects predominated the dominant ones.

Genetic correlation coefficients (r_A) (Table 2) showed that tuber dormancy was significantly correlated with days to seedling emergence (0.63*) and dry matter content (0.63*), and negatively correlated with sprout weight (-0.92**), tuber size (-0.93**), weight loss (-0.69*) and TTC colour index (-0.82**). Addison (1986) also stated that larger tubers have shorter dormancy. Simmonds (1963 and 1964) studied S. phureja (short or no dormancy) and S. stenotonun (long dormancy) for several cycles with selected and

Table 1. Analysis of variance of different traits of potato in a 5x5 variety diallel using analysis 1 of Gardner and Eberhart.

Source of Variation	D.F.	Mean squares							
		Tuber Dormancy Index	Seedling Emergence Index	Weight of Sprout (g/tuber)	Tuber Yield (g/plant)	Tuber Size (g)	Tuber Dry Matter (%)	Weight Loss (%)	TTC Colour Index
Population	49								
a_i	4	1776.56**	15.54**	0.162**	4464.5	36.97	0.883**	1.88**	90.85**
d_j	5	153.45**	7.07**	0.042**	61254.2**	574.38**	0.024	0.72	11.06*
h_{ij}	10	144.64**	19.62**	0.038**	110868**	2033.2**	0.036*	0.48	28.28**
$\bar{h}$	1	49.73	169.41**	0.160**	1029406**	18874.1**	0.052	2.22*	189.60**
h_i	4	73.17	5.46	0.040	6728.8	358.57	0.058	0.22	3.10
s_{ij}	5	220.80*	0.99	0.011	13651.0	4.74	0.015	0.34	16.15
Residual	30	64.96	10.74	0.015	34063.2	574.58	0.039	0.44	14.29

*, ** = Significant at 5% and 1% levels, respectively.

Table 2. Percent variation of genetic effects for different traits in a 5X5 variety diallel.

Source of Variation	D.F.	Mean squares							
		Tuber Dormancy Index	Seedling Emergence Index	Weight of Sprout (g/tuber)	Tuber Yield (g/plant)	Tuber Weight (g)	Tuber Dry Matter (%)	Weight Loss (%)	TTC Colour Index
Population	49								
a_i	4	63.06	10.09	38.51	0.73	0.36	68.04	25.94	32.15
d_j	5	6.81	5.74	12.50	12.48	7.08	2.31	12.40	4.89
h_{ij}	10	12.84	31.86	22.38	45.17	50.09	6.90	16.53	25.02
$\bar{h}$	1	0.44	27.51	9.52	41.94	46.50	1.00	7.65	16.78
h_i	4	2.60	3.54	9.52	1.10	3.53	4.43	3.00	1.10
s_{ij}	5	9.80	0.81	3.33	2.78	0.06	1.46	5.89	7.15
Residual	30	17.29	52.30	26.61	41.63	42.47	22.74	45.13	37.94
Percent accounted for by the model		82.71	47.70	73.39	58.37	57.53	77.26	54.87	62.06

unselected materials of both 2X and 4X levels, and concluded that seed dormancy is correlated with tuber dormancy, and suggested that progress could be made by selection for long or short dormancy.

As potato can be propagated vegetatively, the presence of non-additive effects along with additive effects does not matter much for selecting varieties for desirable tuber dormancy. Hybrid vigour in the F_1 can be fixed by clonal propagation. However, for heritable genetic improvement, sexual breeding must be practised. In order to improve the genetic base of the population, recurrent selection breeding may be practised utilising the existing additive effects. For utilization of both additive and non additive effects, reciprocal recurrent selection breeding followed by clonal selection may be the best one to use.

As both tuber yield and tuber size showed predominant nonadditive effects, biparental crosses to combine desirable traits, followed by clonal selection may be practised to utilize the nonadditive effects. The presence of high amount of dominance effects could also be utilised through hybrid breeding or reciprocal recurrent selection breeding. On the contrary, genetic information available from the study on the dry matter content of potato tubers could be utilised through recombination of genes using recurrent selection method.

Results of the correlation analysis revealed that selection for long dormancy could be accelerated or the lengthy process of testing dormancy could be shortened or avoided by selection on the basis of correlated traits like seed dormancy and tuber dry matter content. Tuber size may have negative impact on tuber dormancy as they are negatively correlated.

CONCLUSIONS

From this study it was revealed that the traits tuber dormancy as well as tuber dry matter content and weight loss are largely controlled by additive gene effects, while tuber size and tuber yield are controlled by dominant genes. On the other hand, days to seedling emergence and sprout weight are controlled by both additive and non additive genes. Hence, for the genetic improvement of the three group of traits, specific breeding programs should be undertaken such as recurrent selection, biparental cross and reciprocal recurrent selection methods respectively.

REFERENCES

Addison, W.G. (1986). Potato physiology and storage for seed. Farm Building Progress. 83: 21-26.

Baker, R.J. (1978). Issues in diallel analysis. Crop Sci. 18: 533-536.

Eberhart, S.A. (1964). Least square method for comparing progress among recurrent selection methods. Crop Sci. 4: 230-231.

Gardner, C.O. and Eberhart, S.A. (1966). Analysis and interpretation of the variety cross diallel and related populations. Biometrics. 22: 349-453.

Griffing, B. (1956). Concept of general and specific combining ability in relation to diallel crossing systems. Aust. J. Biol. Sci. 9: 463-493.

Harris, P.M. (1978). The potato crop: scientific basis for improvement. In: Harris, P.M. (Ed). Chapman and Hall, London. Pp. 730.

Hawkes, J.G. (1956). Biosystematics of the Potato. pp. 15-69. In: Harris, P.M. (Ed). The potato crop. Chapman and Hall, London. Proc. Linn. Soc., London. 166: 97-144.

Hawkes, J.G. (1978). Biosystematics of the potato. pp. 15-69. In: Harris, P.M. (Ed). The potato crop: scientific basis for improvement. Chapman and Hall, London.

Killick, R.J. (1977). Genetic analysis of several traits in potatoes by means of a diallel cross. Ann. Appl. Biol. 86: 279-289.

Mendoza, H.A. (1984). Selection of uniform progenies to use TPS in commercial potato production. pp. 5-16. In: Innovative methods for propagating potatoes. CIP, Peru.

Peloquin, S.J., Jansky, S.H. and Yerk, G.L. (1989). Potato cytogenetics and germplasm utilization. Am. Potato J. 66: 629-638.

Sharma, D. (1989). Concepts and methods. pp. 21-70. In: Chopra, V.L. (Ed). Plant breeding. Oxford and IBN Pub. Co. India.

Simmonds, N.W. (1963). Correlated seed and tuber dormancy in potato. Nature. 197: 720-721.

Simmonds, N.W. (1964). The genetics of seed and tuber dormancy in the cultivated potatoes. Heredity. 19: 489-504.

Swaminathan, M.S. and Howard, H.W. (1953). The cytology and genetics of the potato (Solanum tuberosum) and related species. Bibl. Genetica. 16: 1-192.

Tai, G.C.C. (1976). Estimation of general and specific combining abilities in potato. Can. J. Genet. Cytol. 18: 463-470.

Thompson, P.G., Haynes, F.L. and Moll, R.H. (1980). Estimation of genetic variance components and heritability for tuber dormancy in diploid potatoes. Am. Potato J. 57: 39-46.

Zhan, J. (1993). Genetic analysis of dy matter and reducing sugar content in potato (S. tuberosum). M.Sc. thesis (Plant Breeding); UPLB, Philippines. Pp. 80.