

Asian Journal of Crop Science

ISSN 1994-7879





Variation and Genetic Studies on Selected Sweet Corn Inbred Lines

P. Kashiani, G. Saleh, N.A.P. Abdullah and S.N. Abdullah Department of Crop Science, Faculty of Agriculture, Universiti Putra Malaysia, 43400 Serdang, Selangor, Malaysia

Abstract: Nine advanced tropical sweet corn (Zea mays L. saccharata) inbred lines were evaluated to determine their performance, to estimate broad-sense heritability of the traits measured and to determine phenotypic correlations among the traits. The inbred lines showed a wide range of performance for husked fresh ear yield and its components. Based on performance and earliness, inbred lines Bakti-1-S₇, TSS Melaka-S₅, Thailand-S₆, MM x Indonesia-S₄ and Manis Madu-S₇ were found to be superior and could be short-listed for further testing for general and specific combining ability analysis towards development of hybrid varieties. Broad-sense heritability (h²_B) estimates obtained from the variance components method were found to be high for number of days to silking (80.5%), plant height (79.9%), number of days to tasseling (66.9%) and ear height (63.7%), moderate for husked ear yield (56.7%), total soluble solid concentration (54.2%), number of kernel rows per ear (53.9%), ear diameter (46.7%), dehusked ear yield (43.1%), number of kernels per row (42.6%) and number of ear per hectare (34.5%), while lowest estimates for dehusked ear length (12.9%) and husked ear length (0.3%). Traits found to be highly correlated with husked ear yield were dehusked ear yield (0.97), number of kernel rows per ear (0.71), plant height (0.69), husked ear length (0.67), ear height (0.66), dehusked ear length (0.63), ear diameter (0.55), number of kernels per row (0.50) and number of ears per hectare (0.49). For selection purposes, it is therefore suggested that emphasis should be given on traits like number of kernel rows per ear, plant and ear height and ear length for yield improvement among the inbred lines.

Key words: Zea mays L. saccharata, inbred line, heritability, correlation

INTRODUCTION

In Malaysia there is an increasing trend in sweet corn production mainly due to its high economic return (Saleh *et al.*, 2001). However, the local varieties, which are currently planted throughout the country, are late in maturity, tall and less sweet. One of the most important approaches to improve the performance of the populations is by development of inbred lines which can produce high-yielding hybrid varieties. Inbred line development is the main prerequisite for production of hybrid varieties. This process is achieved through successive generations of inbreeding followed by repeated testing and selection. Inbreeding is the process of mating between genetically related individuals. The fundamental genetic change that inbreeding produces a loss of heterozygosity, was well understood early in the development of the field of genetics (Hill *et al.*, 2006; Marquez-Sanchez, 1998; Wright, 1921).

Selfing, the most extreme form of inbreeding, reduces heterozygosity by 50% each generation. The decrease in heterozygosity typically results in phenotypic changes that we call inbreeding depression, the genetic basis of which has been debated for almost a century. As a consequence of selfing, recessive genes, which were earlier masked in the heterozygous forms, become homozygous. These genes, if conferring to undesirable phenotypes, will result in the deterioration of the succeeding generations. In cross-pollinated crops which do not have self-incompatibility problems, like sweet corn, inbred lines for hybrid varieties are developed through selfing. Extensive studies on inbreeding depression in sweet corn (Zea mays L. saccharata) have indicated that selfing is important in inbred line development because it leads to rapid gene homozygosity, whereby desirable dominant genes can be accumulated while the undesirable ones are eliminated (Gallais, 2009; Saleh et al., 1993). Selected plants are usually self-pollinated for several generations until homozygosity is reached. Hallauer and Miranda (1988) reported that many undesirable recessive genes are eliminated from families as a result of the inbreeding process, then selection is applied within and between lines for the best individual plants (Acquaah, 2007). Hallauer (1990) added that corn inbred lines developed from improved source populations would have greater vigour and grain yield as compared to those developed from unimproved sources. Stoskopf et al. (1993) also cited that inbred lines are developed after five to seven generations of selfing, during which selection for characters of interest is also conducted. Heritability is a measure of the degree to which the variance in distribution of a phenotype is due to genetic causes (Ullrich, 2007; Sleper and Poehlman, 2006). Ali et al. (2003) found that broad-sense heritability estimated from their sweet corn population were moderate to high for the traits measured. The highest estimate was for ear height (99.8%), while the lowest was revealed by ear diameter (61.9%). Saleh et al. (2002a) reported that broad-sense heritability estimates for grain yield in maize were generally moderate. Correlation is the co-relationship between two variables and a correlation coefficient is the measure of the degree of association between two variables (Gepts, 2002; Wallace et al., 1993; Mayo, 1987). Correlations may occur in positive or negative values from zero to ± 1.0 . The closer the coefficient is to either -1 or 1, the stronger is the correlation between variables (Miles and Shevlin, 2001). Hence, correlation is an important parameter to be estimated as it helps to determine relationship among traits before selection is conducted (Kashiam et al., 2008). According to Saleh et al. (2002b), number of ears per hectare, plant height, ear weight, ear length and number of kernel rows per ear were found to be most correlated with ear yield. However, days to tasselling, days to silking, ear diameter and total soluble solids content were not correlated with ear yield. The objectives of this study were to determine the performance of nine inbred lines as potential hybrid parents, to estimate broad-sense heritability of the traits measured on the nine inbred lines and to determine phenotypic correlations among those traits.

MATERIALS AND METHODS

Location of Study

The study was conducted from March to May 2009, at filed 10, Faculty of Agriculture, Universiti Putra Malaysia, Serdang, Selangor, located at 3° 40' North; 101° 42' East and 31 m above sea level.

Plant Materials

This study was an advanced stage of a long-term tropical sweet corn inbred line development programme conducted at Universiti Putra Malaysia where a series of near-homozygous inbred lines were formed from various tropical origin source populations.

The inbred lines were namely Bakti-1-S₇, Mans Madu-S₇, TSS Tin-S₇, Mas Madu-S₆, Thailand-S₆, Indonesia-S₆, TSS Melaka-S₅, Mans Madu x Indonesia-S₄ and SBY-S₂.

Experimental Design and Plot Arrangement

The evaluation was carried out in a Randomized Complete Block Design (RCBD) with three replications. Each replicate consisted of nine plots, each represented by an inbred line. The planting density used was 0.75×0.25 m. Each plot consisted of seven 12 m long plant rows, where only the three middle rows measuring 4 m in length were used as the harvest area. All experimental plots were subjected to uniform agronomic practices.

Cultivation Practices

Before planting, the soil was ploughed twice to a depth of 15 to 30 cm, followed by rotorvation. The soil type in the evaluation plot was sandy loam (56% sand, 23% silt and 21% clay). The soil pH was raised up to 6.5 by applying ground magnesium limestone one month before planting. Planting was done manually, at the rate of two seeds per point and later thinned to just one plant per point at 10 days after planting. Fertilizer at the rate of 160 kg ha⁻¹ N, 100 kg ha⁻¹ P₂O₅ and 100 kg ha⁻¹ K₂O was given in split applications, where the balanced compound fertilizer (15:15:15) was used at seven days after planting, followed by Urea (46% N) at 20 and 35 days after planting. Weeds were controlled manually using a pre-emergence herbicide, Lasso (2-chloro-2'-6'-diethyl-N-methoxymethyl) and a post-emergence contact herbicide, Gramoxone (1,1, dimethyl-dimethyl-4, 4'-bipyridinium). A sprinkler irrigation system was used to supply water to the plants when necessary.

Data Collection

Data were collected from both pre- and post-harvest characters including days to tasselling, days to silking, plant height (cm), ear height (cm), number of ears per hectare, fresh ear yield (kg ha⁻¹), ear length (cm), ear diameter (mm), number of kernels per row, number of kernel rows per ear and Total Soluble Solids (TSS) concentration (%). Fresh ears were harvested from each plot separately, at 21 days after plant tasselling. Three middle rows of each plot measuring four meters long, giving an area of 9 m², were used as the harvest area for yield and number of ears per hectare estimations. Among the plants in the harvest area, 12 plants were used as samples for the measurements of individual plant and ear data.

Data Analysis

Data collected were analyzed using SAS computer package. The Analysis of Variance (ANOVA) was used to determine the significance of variation among inbred lines. Subsequently, the Duncan New Multiple Range Test (DNMRT) was applied for comparison of mean performance of the inbred lines.

Broad-sense heritability (h²_B) for the traits was estimated using the variance components method suggested by Becker (1984), as follows:

$$\begin{split} h^2_{\ B} &= \frac{\sigma^2_{\ G}}{\sigma^2_{\ P}} \\ \sigma^2_{\ G} &= \frac{(r\sigma^2_{\ I} + \sigma^2_{\ e}) - \sigma^2_{\ e}}{r} \\ &= \frac{MS_I - MS_e}{r} \\ \sigma^2_{\ P} &= \sigma^2_{\ G} + \sigma^2_{\ e} \\ &= \frac{MS_I - MS_e}{r} + MS_e \end{split}$$

Where:

 h_{B}^{2} : Broad-sense heritability σ_{G}^{2} : Genotypic variance σ_{P}^{2} : Phenotypic variance σ_{1}^{2} : Variance for inbred lines σ_{e}^{2} : Environmental variance

MS_t: Mean squares due to inbred line

 MS_e : Error mean squares r: No. of replications

Simple correlations among the characters measured were also analyzed using the formula based on Gomez and Gomez (1984), as follows:

$$r_{xy} = \frac{\sum [(X_i - \overline{X})(Y_i - \overline{Y})]}{\sqrt{[\sum (X_i - \overline{X})^2 \times \sum (Y_i - \overline{Y})^2]}}$$

Where:

 r_{xy} : Correlation between the traits X and Y

 $\begin{array}{ll} X_i & : \ X \ value \\ Y_i & : \ Y \ value \end{array}$

 \overline{X} : Mean value of character X \overline{Y} : Mean value of character Y

RESULTS AND DISCUSSION

Results of the analysis of variance showed significant effects among the inbred lines evaluated for all characters studied except husked and dehusked ear lengths. Mean values for the performance of the inbred lines are shown in Table 1. This indicates that the inbred lines evaluated varied substantially in many aspects and these differences could be exploited for specific purpose in breeding programmes. From separation of mean values indicated by DNMRT (Table 1), highest fresh husked ear yields were revealed by inbred lines Bakti-1-S₇, TSS Melaka-S₅, Thailand-S₆ and Manis Madu-S₇, with yields of 8043, 7532, 6053 and 5298 kg ha⁻¹, respectively. The superiority of inbred lines Bakti-1-S₇, TSS Melaka-S₅, Thailand-S₆ and Manis Madu-S₇ was also revealed by the high number of productive ears per hectare they produced, amounting to 35556, 41481, 44444 and 35556, respectively. There is therefore, a strong indication of the potential of these inbred lines for their utilisation towards production of new hybrid varieties. Bakti-1-S₇ was found to be significantly taller than other inbred lines with (175.1 cm) and also tasseled and silked significantly sooner than the others. Indonesia- S_6 was the only inbred line which tasseled about the same time as Bakti-1- S_7 . The lowest Total Soluble Solids (TSS) concentration was obtained from MM x Ind-S₄, while no significant difference among other inbred lines were observed. Kashiani et al. (2008) reported that the inbred lines extracted from the source populations including Bakti-1, TSS Melaka, Thailand and Manis Madu performed better than the rest in term of fresh ear yield, number of productive ears per hectare and days to silking and tasseling.

Genotypic and phenotypic variances and broad-sense heritability (h²_B) estimates for yield and yield components measured among the nine inbred lines evaluated are shown in Table 2. Days to silking was found to be the most heritable trait in the inbred lines, with heritability of 80.5%, followed by plant height (79.9%), number of days to tasselling (66.9%)

Table 1: Mean values for traits measured on nine sweet corn inbred lines evaluated

	Mean									
T 1 11'	Husked ear	Dehusked ear	No. of	Plant	Ear	Days to	Days to			
Inbred line	yield (kg ha ⁻¹)	yield (kg ha ⁻¹)	ears ha ⁻¹	height (cm)	height (cm)	tasseling	silking			
Bakti-1-S7	8043a	5899a	35556abc	175.1a	72.3a	52.5c	52.5d			
Manis Madu-S7	5298abcd	3761abc	35556abc	126.4b	59.3ab	57.3ab	60.0ab			
TSS Tin-S7	2651 d	1670c	25185c	88.6c	45.8bcd	57.0ab	58.3bc			
Mas Madu-S ₆	3012cd	1837c	32593abc	123.5b	49.3bcd	57.3ab	62.3a			
Thailand-S ₆	6053ab	3789abc	44444a	135.9b	54.8bc	59.0a	60.7ab			
Indonesia-S ₆	4555bcd	3634abc	28148bc	97.5c	42.5cd	55.0bc	56.3c			
TSS Melaka-S ₅	7532a	4534ab	41481ab	145.4b	70.9a	59.3a	60.3ab			
MM x Ind-S ₄	5638abc	4156abc	32593abc	143.0b	57.1abc	58.0a	60.3ab			
SBY-S ₂	3883bcd	2523bc	22222c	88.1c	38.5d	59.7a	62.0a			
	Moon									

Mean

Inbred line	Husked ear length (cm)	Dehusked ear length (cm)	Ear diameter (mm)	No. of kemels/row	No. of kernel rows/ear	TSS (%)		
Bakti-1-S ₇	16.9a	13.50a	34.3ab	24.4ab	13.4a	15.7a		
Daku-1-87	10.9a	13.30a	34.3au	24.4au	13.4a	13./a		
Manis Madu-S7	15.9a	12.00a	31.3abc	30.0abc	12.4a	15.8a		
TSS Tin-S ₇	13.9a	10.70a	17.8c	11.0c	9.3b	16.9a		
Mas Madu-S ₆	13.9a	10.60a	22.2bc	9.80c	9.5b	16.7a		
Thailand-S ₆	15.4a	11.40a	30.1abc	15.8bc	11.3ab	15.3a		
Indonesia-S ₆	12.1a	9.60a	40.4a	16.9bc	12.9a	16.9a		
TSS Melaka-S ₅	14.3a	16.50a	37.9a	12.6bc	12.6a	15.4a		
MM x Ind-S ₄	14.5a	54.60a	21.0bc	29.4a	12.1a	13.3b		
SBY-S ₂	12.4a	9.90a	17.2c	10.2c	11.2ab	15.3a		

 $Means \ followed \ by \ the \ same \ letter(s) \ in \ the \ same \ column \ are \ not \ significantly \ different \ at \ p \leq 0.05 \ based \ on \ DNMRT$

Table 2: Genotypic variances (σ^2_G) , phenotypic variances (σ^2_P) and broad-sense heritability estimates (h^2_B) for traits measured on nine sweet corn inbred lines

Traits	σ^2_{G}	σ^{2}_{P}	h ² _B (%)
Husked ear yield	2779638.70	4898228.3	56.7
Dehusked ear yield	1256925.40	2917614.1	43.1
No. of ears ha-1	31915867.30	92546835.3	34.5
Plant height	785.60	983.3	79.9
Ear height	117.70	184.7	63.7
Days to tasselling	4.50	6.5	66.9
Days to silking	8.90	11.0	80.5
Husked ear length	0.70	5.8	12.9
Dehusked ear length	0.05	13.6	0.3
Ear diameter	55.10	117.9	46.7
No. of kernels/row	32.60	76.5	42.6
No. of kernel rows/ear	1.60	3.1	53.9
TSS	0.90	1.8	54.2

and ear height (63.7%). This indicates that selection for these traits in these inbred lines would be most effective for the expression of these traits in the succeeding generations. Similar results on broad-sense heritability were reported by Kashiani *et al.* (2008) and Saleh (2003) showing high estimates for days to silking, plant height and ear height. Saleh *et al.* (2002c) also reported high broad-sense heritability estimates for plant height and number of days to tasselling on selected sweet corn synthetic populations. Moderate broad-sense heritability estimates were obtained from husked ear yield (56.7%), total soluble solids concentration (54.2%), number of kernel rows per ear (53.9%), ear diameter (46.7%), dehusked ear yield (43.1%), number of kernels per row (42.6%) and number of ear per hectare (34.5%), while lowest estimates were revealed by husked ear length (12.9%) and dehusked ear length (0.3%). Fresh ear yield, ear diameter and number of kernels per row were reported to possess moderate heritability estimates (54.7, 37.0 and 36.0%, respectively) in a study on sweet corn breeding population conducted by Nigussie and Saleh (2007).

Table 3: Simple correlation coefficients among traits measured on nine sweet corn inbred lines

Traits	1	2	3	4	5	6	7	8	9	10	11	12
Dehusked ear yield	0.96**	1										
No. of ears ha-1	0.48*	0.39*										
Plant height	0.69**	0.64**	0.42*									
Ear height	0.66**	0.59**	$0.35^{\rm ns}$	0.85**								
Days to tasselling	$-0.12^{\rm ns}$	$-0.23^{\rm ns}$	$0.22^{\rm ns}$	-0.39*	$-0.31^{\rm ns}$							
Days to silking	-0.32^{ns}	-0.41*	0.04^{ns}	-0.42**	-0.41*	0.87**						
Husked ear length	0.67**	0.68**	0.37^{ns}	0.53**	0.47*	-0.16^{ns}	-0.16^{ns}					
Dehusked ear length	0.63**	0.54**	$0.22^{\rm ns}$	$0.35^{\rm ns}$	$0.34^{\rm ns}$	0.08^{ns}	0.03^{ns}	0.48*				
Ear diameter	0.55**	0.58**	0.38*	0.30^{ns}	0.29^{ns}	$-0.15^{\rm ns}$	-0.28^{ns}	$0.22^{\rm ns}$	0.31^{ns}			
No. of kernels/row	0.50**	0.56**	$0.22 ^{\mathrm{ns}}$	0.38^{ns}	$0.27^{\rm ns}$	-0.29^{ns}	-0.35ns	0.46*	$0.21^{\rm ns}$	-0.03^{ns}		
No. of kernel rows/ea	r 0.71**	0.74**	0.18^{ns}	$0.35^{\rm ns}$	$0.37^{\rm ns}$	$-0.22^{\rm ns}$	-0.39*	0.29^{ns}	$0.34^{\rm ns}$	0.55**	0.53**	
TSS	-0.36^{ns}	-0.34^{ns}	-0.14^{ns}	-0.40*	-0.25^{ns}	-0.16^{ns}	-0.07^{ns}	$-0.22^{\rm ns}$	-0.14^{ns}	0.20^{ns}	-0.58**	-0.11^{ns}

**, *Significant at p = 0.01, p = 0.05, respectively, ns: Non-significant, TSS: Total soluble solids 1: Husked ear yield, 2: Dehusked ear yield, 3: No. of ears ha⁻¹, 4: Plant height, 5: Ear height, 6: Days to tasselling, 7: Days to silking, 8: Husked ear length, 9: Dehusked ear length, 10: Ear diameter, 11: No. of kernels/row, 12: No. of kernel rows/ear

Results on simple correlation among characters are presented in Table 3. Husked ear yield was found to be highly positively correlated ($p \le 0.01$) with dehusked ear yield, plant height, ear height, husked ear length, dehusked ear length, ear diameter, number of kernels per row and number of kernel rows per ear (with correlation coefficients of 0.96, 0.69, 0.66, 0.67, 0.63, 0.55, 0.50 and 0.71, respectively), while positively correlated ($p \le 0.05$) with number of ears per hectare (r = 0.48). This indicates that high measurements of these traits had direct positive contribution to husked ear yield. Therefore, for selection purposes to improve the inbred lines, it is suggested that emphasis should be given on these traits. Plant height was highly significantly correlated with husked and dehusked ear yields, indicating that taller plants were better yielding compared to the shorter ones. This might be attributed to the high dry matter accumulation function carried out by the high number of leaves possessed by tall plants. A similar finding has been reported by Kashiani *et al.* (2008), Sujiprihati *et al.* (2003) and Saleh *et al.* (2002b).

In conclusion, significant differences in performance indicated that lines varied among the inbred lines for the measured traits substantially in many aspects and these differences could be exploited for specific purposes in breeding programmes. This also gave an indication of positional of the inbred lines to be used as promising parents for potential hybrids in Malaysia. Genotyping of inbred lines can be performed as an extra tool to select superior inbred lines for further diallel analysis to reveal general and specific combing abilities.

ACKNOWLEDGMENT

The authors gratefully acknowledge the Ministry of Science, Technology and Innovation (MOSTI) for the financial support on the research under e-Science Fund (Project No. 05-01-04-SF0700).

REFERENCES

Acquaah, G., 2007. Principles of Plant Genetics and Breeding. Blackwell Publishing, Malden, USA., pp: 109-120.

Ali, E.S., G.B. Saleh, Z.B. Wahab and A.A. Rahim, 2003. Performance, heritability and correlation studies on varieties and population cross of sweet corn. Asian J. Plant Sci., 2: 756-760.

- Becker, W.A., 1984. Manual of Quantitative Genetics. 2nd Edn., Longman, London.
- Gallais, A., 2009. Full-Sib reciprocal recurrent selection with the use of doubled haploids. Crop Sci., 49: 150-152.
- Gepts, P., 2002. A comparison between crop domestication, classical plant breeding and genetic engineering. Crop Sci., 42: 1780-1790.
- Gomez, K.A. and A.A. Gomez, 1984. Statistical Procedures for Agricultural Research. 2nd Edn., John Wiley and Sons, UK., New York, pp. 1-680.
- Hallauer, A.R. and J.B. Miranda, 1988. Quantitative Genetics in Maize Breeding. 2nd Edn., Iowa State University Press, Ames.
- Hallauer, A.R., 1990. Methods used in developing maize inbreds. Maydica, 35: 1-16.
- Hill, W.G., N.H. Barton and M. Turelli, 2006. Prediction of effects of genetic drift on variance components under a general model of Epistasis. Theoretical Populat. Biol., 70: 56-62.
- Kashiani, P., G. Saleh, S.N. Abdullah and N.A.P. Abdullah, 2008. Performance, heritability and correlation studies on nine advanced sweet corn inbred lines. Proceedings of the 10th Symposium of Malaysian Society of Applied Biology, Nov. 6-8, Malaysia, 48-48.
- Marquez-Sanchez, F., 1998. Expected inbreeding with recurrent selection in maize: I. Mass selection and modified ear-to-row selection. Crop Sci., 38: 1432-1436.
- Mayo, O., 1987. The Theory of Plant Breeding. 2nd Edn., Oxford University Press, New York, USA., ISBN: 0198541716,.
- Miles, J. and M. Shevlin, 2001. Applying Regression and Correlation. 1st Edn., Introductory Text Built Around Model-Building Sage Publications Ltd., USA., ISBN: 9780761962304.
- Nigussie, M. and G. Saleh, 2007. Genetic variability and heritability within sweet corn (*Zea mays* L. *saccharata*) breeding population. Malays. Appl. Biol., 36: 15-20.
- Saleh, G., M.R. Yusop and T.C. Yap, 1993. Inbreeding depression and heterosis in sweet corn varieties Manis Madu and Bakti-1. Pertanika J. Trop. Agric. Sci., 16: 209-214.
- Saleh, G., K. Panaitan, A.R. Anuar and A.K. Mihdzar, 2001. Heterosis, combining ability and heritability studies on grain maize hybrids. UPM Research Report 2001. Faculty of Agriculture, pp. 19-21.
- Saleh, G., D. Abdullah and A.R. Anuar, 2002a. Effects of location on performance of selected tropical maize hybrids development in Malaysia. Pertanika J. Trop. Agric. Sci., 25: 75-86.
- Saleh, G.B., D. Abdullah and A.R. Anuar, 2002b. Performance, heterosis and heritability in selected tropical maize single, double and three-way cross hybrids. J. Agric. Sci., 138: 21-28.
- Saleh, G.B., S.A.S. Alawi and K. Panjaitan, 2002c. Performance, correlation and heritability studies on selected sweet corn synthetic populations. Pak. J. Biol. Sci., 5: 251-254.
- Saleh, G., 2003. Grain maize and sweet corn production guidelines. University Putra Malaysia, Serdang.
- Sleper, D.A. and J.M. Poehlman, 2006. Breeding Field Crops. 5th Edn., Wiley-Blackwell Publ., USA., ISBN: 978-0-8138-2428-4, pp: 424.
- Stoskopf, N.S., D.T. Tomes and B.R. Christie, 1993. Plant Breeding Theory and Practice. Westview Press Inc., San Francisco,.
- Sujiprihati, S., G. Saleh and E.S. Ali, 2003. Heritability, performance and correlation studies on single cross hybrid of tropical maize. Asian J. Plant Sci., 2: 51-57.
- Ullrich, S.E., 2007. Breeding Field Crops. Crops Sci., 47: 900-904.
- Wallace, D.H., J.P. Baudoin, J. Beaver, D.P. Coyne and D.E. Halseth *et al.*, 1993. Improving efficiency of breeding for higher crop yield. Theor. Applied Genet., 86: 27-40.
- Wright, S., 1921. Systems of mating. II. The effects of inbreeding on the genetic composition of a population. Genetics, 6: 124-143.