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GENETIC AND ENVIRONMENTAL VARIABILITY IN SEGREGATING PIGEON PEA POPULATIONS

By Raul Abrams

INTRODUCTION

It is apparent in a general way that progress in breeding is conditioned by the nature, magnitude and interrelations of genetic and nongenetic variations in the various significant plant characters.

The ability to identify a desirable plant with high yield potentiality in a segregating population is one of the most difficult problems that a plant breeder faces. Most of the commercial agronomic attributes are quantitatively inherited, and consequently highly influenced by environmental conditions. It is very difficult to judge whether the observed variability is heritable or due to environment. This suggests the importance of partitioning the overall variability into its heritable and non-heritable components, so that this information might be useful in the breeding programme. Knowledge of heritability may be useful in increasing the efficiency of breeding methods, since it is a measure of the success in separating genotypes by selection.

The association of plant characters with yield should also be of great value for the selection of desirable strains.

The present investigation is, therefore, undertaken to determine the heritability of quantitative characters such as flowering date, plant height, and seed weight in different populations of pigeon peas, and to find out the degree of association if any, between these attributes.

MATERIALS AND METHODS

Three varieties and an irradiation-derived line of pigeon peas were used as parents in five crosses as follows: P.I. 5690 (Plant introduction from Trinidad) X Kaki, P.I. 5690 X Saragateado, P.I. 5690 X 526, Kaki X 526 and Saragateado X 526. The parents were chosen on the basis of previous data to contrast for earliness, yield, plant height, and weight per 100 seeds. Each variety used was considered to be homozygous.

The F_2 , F_3 , and parents of each cross were planted in the field at the Isabela Substation during 1966-67 in a randomized block design with three replicates, except for cross 526 X Saragateado that consisted of two replicates. Planting distance was 8 feet between rows and 4 feet in the row. The F_2 and F_3 populations consisted of 200 seeds per replicate with the same spacing and row length as the non-segregating generations.

The following data were recorded for each plant in the F_2 , F_3 and parental progenies.

Flowering date: recorded as number of days from planting to first flowers on plants.

Plant height: measured to the nearest tenth of a foot when harvesting time.

Seed weight: recorded in grams per 100 dry seeds.

The sums of squares were calculated for each replication separately. The resulting F_2 and F_3 pooled variance contained two parts, namely, the genotypic fraction due to additive gene action including dominance and epistasis, and the fraction due to environment. The environmental variances and covariances were calculated from parental values. The F_2 and F_3 genotypic variance were determined by subtracting the environmental variances from the total F_2 and F_3 variances, respectively. The same method was used in calculating the covariances. Estimates of heritability were obtained by the following formula, estimating environmental variance by the parental variance:

$$H = \frac{\frac{F_2 - P}{-2}}{-2}$$

Where $\frac{F_2}{2}$ is the F_2 variance and $\frac{P}{2}$ the joint mean square of the parental lines. Both $\frac{F_2}{2}$ and $\frac{P}{2}$ were calculated after removing the block effect. The same formula was used for estimating $\frac{F_3}{2}$. The estimate of genetic correlation was calculated for each pair of the characters measured by the following formula:

$$\text{Genotypic } r_{xy} = \frac{\text{COV}_{xy_g}}{\frac{x_g}{2} \frac{y_g}{2}}$$

where

COV_{xy_g} = genotypic portion of the covariance between the characters X and Y.

$\frac{x_g}{2}$ and $\frac{y_g}{2}$ = genotypic portion of the variance in the expression of the characters X and Y.

Frequency distributions were prepared for plant height, flowering date, and seed weight for both F_2 and F_3 , generations together with parental means for all crosses.

RESULTS

The mean and range for date of flowering, plant height, seed weight, and number of seeds per pod of parental, F_2 , and F_3 generations of five pigeon pea crosses are presented in Table 1. For all characters studied the range of variability was greater in F_2 and F_3 generations with increasing contrast in parents characteristics. The number of seeds per pod in segregating generations had a lower range of variability than the other characters studied. This seems to indicate that no appreciable progress could be made for this attribute. The means of the five crosses give additional evidence for this conclusion.

The coefficients of variation (Table 2) for flowering, height, seed weight, and number of seeds per pod were low, with the exception of number of seeds per pod for cross Saragatcado X 526. There is no known reference of previous research work with this crop which could be used to compare degree of precision on the attributes studied. These low coefficients of variation indicate a good degree of precision for the experiment of the attributes under consideration.

Heritability estimates for the F_2 and F_3 generations for all characters of the five pigeon pea crosses are presented in Table 3. Heritability values for date of flowering were high and comparative for all crosses.

Estimated heritabilities for plant height in F_2 and F_3 generations were similar in magnitude to those attained for date of flowering except for crosses Kaki X 526 and Saragatcado X line 526.

Seed weight, except for crosses Saragatcado X 526 and P.I. 5690 X 526 in the F_2 generations, also showed a high heritability percentage and of similar magnitude as flowering and plant height.

Number of seeds per pod showed the lowest heritability values for all traits of the five crosses. This low heritability for number of seeds per pod can be explained on the basis of a very narrow amount of genetic variation as indicated by the parental means and ranges in Table 1.

Heritability values for seed yield and number of pods per plant were estimated for only one of the five crosses; Kaki X P.I. 5690. The heritability estimates for the other four crosses were too erratic due to the fact that late parent varieties produced low seed yield and were heavily infested with pod borers, therefore, they were excluded from the analyses. Estimates of heritability for F_2 and F_3 generation were 45.1 and 52.1 per cent for seed yield and 45.3 and 52.9 for number of pods per plant.

The genetic coefficients of variation are presented in Table 4. In general, the highest coefficients of genetic variation were observed in crosses where the parents contrasted in the attributes under consideration. An exception can be observed in number of seeds per pod in cross Saragatcado X 526 where the genetic coefficient of variation was relatively large. This situation can be explained on the basis of a relatively small plant population, and small population mean which biased the genetic coefficient of variation.

In order to study intercharacter associations, correlation coefficients were computed for the four attributes studied. Phenotypic and genotypic correlations

are presented in Tables 5 and 6. In general, the genotypic correlations for any pair of traits seem to be of comparable magnitude. Likewise, the values observed for any two characters are rather similar for the five crosses.

Plant height, in general, is highly positively correlated with late flowering and tends to be negatively correlated with seed weight and number of seeds per pod. As mentioned previously, late flowering plants are subject to severe pod borers and other insects attack than early flowering types, because insect population is larger later in the season. Late types also are more exposed to environmental stresses like higher temperatures and drought conditions which are adverse to yield and its components.

Genotypic and phenotypic correlations between all six pairs of traits which include yield and yield components are presented in Tables 7 to 10. These data were included even though the author is aware of the fact that the number of parental plants is small. Interesting data resulted from two crosses where parents showed extreme contrast in most traits. Seed yield is highly positively correlated with number of pods per plant, as expected, in both crosses. Of particular interest is the negative correlation in both crosses between seed yield and late flowering date. Since pigeon pea is a seasonal crop and very sensitive to photoperiod, apparently the amount of flower induction is smaller in late flowering types than in early ones. Correlations between other traits followed the same trend as the ones discussed earlier.

DISCUSSION

Pigeon peas form an important constituent of our diet in Puerto Rico, not only because of consumer's preference but also because of their high protein content. They are also of importance in our economy their farm value being estimated in approximately two million dollars with a good potential for increasing.

The main objective of the present study was to evaluate five pigeon pea crosses from parents contrasting in different quantitative characters and also to find out if these characters have any bearing on seed yield. There was much greater variation, in general for all crosses, in seed weight, plant height, and flowering date than in number of seeds per pod. The heritable and non-heritable components of variation were estimated with the help of some genetic parameters like heritability and genetic coefficients of variation.

High heritability values were obtained for some of the characters studied, i.e., flowering date, plant height, and seed weight. The relatively high heritability values for flowering date and plant height might justify the selection for these characters in F_2 and F_3 segregating generations. Apparently these traits are not largely affected by environmental factors and genetic advances under selection would be expected to be high.

In two particular crosses, namely Saragatcado X 526 and Kaki X 526, plant height heritability values obtained were 36.7 and 45.1 for F_2 generation and 38.6 and 41.8 for F_3 generation, respectively. The low values obtained for these two crosses seems to be due to the small genetic variation for this trait in the parents involved. Line 526 is a line derived from radiation-treated Kaki, with similar mean

plant height, therefore, we can assume that the gene system for plant height is the same or very similar for both entries. Saragateado is a late flowering tall variety with a mean plant height equal to Kaki and line 526. This reasoning could be explained based on the findings that the progenies from the crosses involving these parents have a mean plant height equal to the parents and also a small genetic variance as indicated in Tables 1 and 4.

Seed weight heritability was next highest to flowering date and plant height. Seed weight is one of the yield components, therefore, the number of genes responsible for the expression of this trait should be smaller than for total yield and should be less affected by environmental factors. In general, the complexly inherited characteristics have lower heritability than those simply inherited. The genetic coefficients of variation for seed weight were also relatively large for all crosses, thus, good genetic progress through selection could be made for this trait whenever a good screening technique is used during the early segregating generations.

Small genetic variation and heritability estimates were obtained for number of seeds per pod. Even though wide ranges were observed for this attribute, the extremes were represented by few plants and the means were practically the same for parental, F_2 and F_3 populations. Not too much progress by selection could be expected for this yield component from the parental material used in this study. All four parents used in this study had similar or same number of seeds per pod. Observations made by Abrams¹ in crosses between Florido, a 7-8 seeds per pod variety, with Kaki, 4-5 seeds tend to indicate that 1 or 2 more seeds per pod on the average could be incorporated in selected progenies from this particular cross.

Heritability estimates for seed yield and number of pods per plant made for cross P.I. 5690 X Kaki indicated that these characters were influenced by non-heritable effects. These results are in close agreement with the work done by Weber and Moorthy (26) and Mahmud and Kramer (18), in another legume crop, soybeans, for early generation segregating populations and substantiates the established belief among plant breeders that selection for yield should be based upon progeny tests rather than upon individual plant values.

In general the heritability values in F_3 generation were higher than in F_2 for all traits in the five crosses. This trend was expected since both generations were grown in the same year and same location, therefore reducing to a minimum the genotype X year and genotype X location interactions. Under these conditions the additive genetic variance would show greater expression in F_3 generation as expected.

It appeared probable that these pigeon pea varieties differed in some genes conditioning most characters studied. Thus plus and minus gene effects conditioning an attribute in different parents permitted a complementary type of gene action in F_2 and F_3 segregates, and it explains the indicated transgressive segregation observed in F_2 and F_3 generations for some attributes of the five crosses. The characteristic number of seeds per pod, does not show this complementary type of gene action in the F_2 and F_3 segregates as shown in Table 1. Apparently the four parents used in this study have a similar gene system for number of seeds per pod.

¹Personal Communication.

With the exception of number of pods per plant, the correlations between seed yield and other traits were not sufficiently large to provide reliable indications for yield. The phenotypic and genotypic correlations between seed yield and number of pods per plant was high, above 0.90. We might expect to improve seed yield by selecting for large number of pods. However, its low heritability, 45.3 and 52.1 per cent in F_2 and F_3 generations tends to indicate that not too much progress for seed yield improvement could be expected by selecting for large number of pods per plant. Perhaps the initial selection should be directed to seed weight which has a relatively high heritability, postponing selection for number of pods per plant. According to Frey (9) and Jones and Frey (15), (a) heritability of a trait approaches its maximum in successive generations following hybridization and (b) selection for number of seeds per plant could be based on counts from normal planting rates to avoid environmental effect associated with spaced plants.

All other genotypic and phenotypic correlations between pair of traits were of small magnitude to attain maximum values for a given pair of traits.

TABLE I

Mean and Range for Flowering Date, Plant Height, Seed Weight, and Number of Seeds per Pod of Parental, F_2 , and F_3 Generation of Five Pigeon Pea Crosses

Parent or Generation	FLOWERING DATE (days)		PLANT HEIGHT (feet)		SEED WEIGHT (grams)		AVERAGE SEEDS PER POD (numbers)	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
P.I. 5690 ...	123.7	105-130	4.1	3.4-4.7	13.9	11-17	3.6	2.6-4.2
Kaki ...	153.8	137-166	6.5	5.9-7.8	23.8	20-26	3.8	3.8-4.4
F_2 ...	139.1	103-159	5.8	3.8-7.8	19.2	11-28	3.7	2.3-5.1
F_3 ...	143.7	105-173	5.9	3.2-8.4	18.0	11-23	3.8	2.0-5.1
P.I. 5690 ...	123.7	105-130	4.1	3.4-4.7	13.9	11-17	3.6	2.6-4.2
Saragateado ...	204.2	186-215	7.0	5.6-8.5	17.6	24-21	3.8	3.6-4.2
F_2 ...	152.4	110-190	6.2	3.5-9.0	19.2	12-24	3.8	2.0-5.3
F_3 ...	154.1	110-190	5.9	3.3-7.9	18.0	10-24	3.6	2.1-5.7
Kaki ...	153.8	137-166	6.5	5.9-7.8	23.8	20-25	3.8	3.8-4.4
526 ...	192.9	167-215	7.0	5.7-8.4	16.3	12-20	3.5	3.1-4.8
F_2 ...	163.2	144-187	7.0	4.0-8.8	21.7	15-26	3.7	3.0-4.8
F_3 ...	156.4	138-187	7.0	4.5-9.3	20.4	12-25	3.9	2.7-5.4
P.I. 5690 ...	123.7	105-130	4.1	3.4-4.7	13.9	11-17	3.6	2.6-4.2
526 ...	192.9	167-215	7.0	5.7-8.4	16.3	12-20	3.5	3.1-4.8
F_2 ...	158.8	116-210	5.8	3.8-7.7	16.2	11-23	3.8	2.1-5.5
F_3 ...	161.1	110-210	6.0	3.8-8.1	15.4	10-23	3.7	2.2-4.9
Saragateado ...	204.2	186-215	7.0	5.6-8.5	17.6	14-21	3.8	3.6-4.2
526 ...	192.9	167-215	7.0	5.7-8.4	16.3	12-20	3.5	3.1-4.8
F_2 ...	192.6	151-224	6.5	5.2-8.4	18.3	12-22	3.8	2.2-4.4
F_3 ...	173.8	145-215	6.5	4.1-8.9	18.4	14-23	3.4	2.3-5.1

TABLE 2

Co-efficients of Variations (per cent) for Flowering Date, Plant Height, Seed Weight, and Number of Seeds per Pod of F₂ and F₃ Generations of Five Pigeon Pea Crosses

Generation	Flowering Date	Plant Height	Seed Weight	Number of Seeds per Pod
P.I. 5690 X Kaki:				
F ₂	8.8	15.8	11.9	11.6
F ₃	8.6	16.8	12.7	13.7
P.I. 5690 X Saragateado				
F ₂	10.5	14.5	12.1	14.9
F ₃	9.2	14.2	15.2	21.5
Kaki X 526				
F ₂	5.5	9.3	10.2	11.5
F ₃	6.1	9.0	14.2	12.1
P.I. 5690 X 526				
F ₂	9.5	13.7	10.6	12.6
F ₃	12.1	14.5	14.3	17.2
Saragateado X 526				
F ₂	7.6	8.9	12.1	25.6
F ₃	10.0	13.2	12.9	13.9

TABLE 3

Heritability Estimates (per cent) for Flowering Date, Plant Height, Seed Weight, and Number of Seeds per Pod in Each of Five Pigeon Pea Crosses

Characters	HERITABILITY IN PERCENT				
	P.I. 5690 X Kaki	P.I. 5690 X Saragateado	Kaki X 526	P.I. 5690 X 526	Saragateado X 526
Flowering Date					
F ₂	72.9	81.8	72.5	76.9	60.7
F ₃	73.5	76.8	74.7	86.1	72.2
Plant Height					
F ₂	70.8	75.3	45.1	65.6	36.7
F ₃	74.4	71.7	41.8	71.7	38.6
Seed Weight					
F ₂	75.6	64.4	55.4	35.9	36.3
F ₃	75.6	75.9	73.7	61.0	65.3
Number of Seeds per Pod					
F ₂	-37.4	33.3	-6.1	-20.8	55.2
F ₃	8.2	64.1	9.6	30.5	64.1

TABLE 4

Genetic Co-efficient of Variability (per cent) for Flowering Date, Plant Height, Seed weight, and Number of Seed per Pod in F₂ and F₃ Generations of Five Pigeonpea Crosses

	Flowering Date	Plant Height	Seed Weight	Number of Seeds per Pod
P.I. 5690 X Kaki ...				
F ₂	7.52	13.32	10.36	-7.11
F ₃	7.39	14.57	11.06	3.94
P.I. 5690 X Saragateado				
F ₂	9.50	12.64	9.72	8.66
F ₃	8.06	12.04	13.32	17.26
Kaki X 526				
F ₂	3.38	5.84	7.63	-2.86
F ₃	3.91	5.38	12.20	3.75
P.I. 5690 X 526				
F ₂	8.39	11.10	6.40	5.77
F ₃	11.29	12.30	11.22	9.55
Saragateado X 526				
F ₂	5.95	5.43	7.29	19.07
F ₃	8.54	8.22	8.73	19.19

TABLE 5

Genotypic and phenotypic correlations between all pairs of 4 traits measured in the F₂ generations for 5 pigeon pea crosses (genotypic correlations are on the left side of the diagonal, phenotypic on the right)

Trait	Cross*	Flowering	Height	Seed Weight	Seeds per Pod
Flowering	1	—	0.61	0.35	0.22
	2	—	0.60	-0.08	-0.25
	3	—	-0.05	-0.07	-0.31
	4	—	0.46	-0.09	-0.01
	5	—	-0.24	-0.36	-0.25
Height	1	0.67	—	0.26	0.36
	2	0.75	—	0.01	0.06
	3	0.30	—	0.06	0.24
	4	0.71	—	0.12	0.37
	5	-0.32	—	0.18	0.14
Seed Weight	1	0.55	0.36	—	0.21
	2	-0.03	-0.12	—	0.06
	3	0.01	0.22	—	-0.06
	4	0.07	0.36	—	0.06
	5	-0.31	-0.33	—	0.44
Seeds per Pod	1	0.68	0.47	0.22	—
	2	-0.27	-0.03	-0.11	—
	3	0.97	0.26	1.46	—
	4	0.60	0.54	0.03	—
	5	-0.35	0.10	0.29	—

*1, 2, 3, 4, 5 denote P.I. 5690 X Kaki, P.I. 5690 X Saragateado, Kaki X 526, 526 X P.I. 5690 and 526 X Saragateado, respectively.

TABLE 6

Genotypic and Phenotypic Correlations between all Pairs of 4 Traits Measured in the F₂ Generation for 5 Pigeon Pea Crosses (Genotypic Correlations are on the Left Side of the Diagonal, Phenotypic on the Right)

Trait	Cross*	Flowering	Height	Seed Weight	Seeds per Pod
Flowering ...	1	—	0.44	0.28	0.06
	2	—	0.38	-0.23	0.02
	3	—	-0.01	0.15	-0.30
	4	—	0.40	-0.20	-0.24
	5	—	0.17	-0.51	-0.70
Height ...	1	0.43	—	0.16	0.48
	2	0.49	—	-0.11	0.20
	3	0.38	—	0.11	0.39
	4	0.55	—	0.03	0.37
	5	-0.14	—	0.16	0.29
Seed Weight ...	1	0.39	0.22	—	0.09
	2	-0.23	-0.25	—	0.05
	3	0.37	0.28	—	0.06
	4	-0.18	0.09	—	0.19
	5	-0.60	-0.07	—	0.41
Seeds per Pod ...	1	0.69	1.56	0.07	—
	2	0.16	0.21	-0.02	—
	3	0.53	1.09	-0.32	—
	4	-0.17	0.53	0.34	—
	5	-0.72	0.34	0.29	—

*1, 2, 3, 4, 5, denotes P.I. 5690 X Kahi, P.I. 5690 X Saragateado, Kahi X 526, 526 X P.I. 5690 X Saragateado, respectively.

TABLE 7

Genotypic and Phenotypic Correlations of 6 Traits Measured in the F₂ Generation for P.I. 5690 X Saragateado Pigeon Pea Crops (Genotypic Correlations are on the Left Side of the Diagonal, Phenotypic on the Right)

Trait	Yield	Number of Pods	Flowering	Height	Seed Weight	No. of seeds per Pod
Yield ...	—	0.90	-0.14	0.25	0.11	0.39
Number of Pods ...	0.91	—	-0.11	0.20	-0.14	0.31
Flowering ...	-0.12	-0.08	—	0.60	-0.08	-0.25
Height ...	0.25	0.18	0.75	—	0.01	0.06
Seed Weight ...	0.09	-0.21	-0.03	-0.12	—	0.06
Number of Seeds per Pod	0.52	0.30	-0.27	-0.03	-0.11	—

TABLE 8

Genotypic and phenotypic correlations between all pairs of 6 traits measured in the F₃ generation for P.I. 5690 X Saragateado pigeon pea cross (genotypic correlations are on the left side of the diagonal, phenotypic on the right).

Trait	Yield	Number of Pods	Flowering	Height	Seed Weight	No. of seeds per Pod
Yield	—	0.91	-0.07	0.33	0.29	0.11
Number of Pods	0.93	—	-0.04	0.30	0.10	0.11
Flowering	-0.04	0.03	—	0.38	-0.23	0.02
Height	0.34	0.31	0.49	—	-0.11	0.20
Seed Weight	0.31	0.10	-0.23	-0.25	—	0.05
Number of Seeds per Pod	0.05	-0.01	0.16	0.21	-0.02	—

TABLE 9

Genotypic and phenotypic correlations of 6 traits measured in the F₂ generations for 526 X P.I. 5690 pigeon pea cross (genotypic correlations are on the left side of the diagonal, phenotypic on the right)

Trait	Yield	Number of Pods	Flowering	Height	Seed Weight	No. of seeds per Pod
Yield	—	0.89	-0.03	0.46	0.13	0.52
Number of Pods	0.89	—	0.05	0.42	-0.08	0.40
Flowering	-0.17	0.17	—	0.46	-0.09	-0.01
Height	0.47	0.39	0.71	—	0.12	0.37
Seed Weight	0.19	-0.10	0.06	0.36	—	0.06
Number of Seeds per Pod	0.57	0.35	0.60	0.54	0.03	—

TABLE 10

Genotypic and phenotypic correlations between all pairs of 6 traits measured in the F₃ generation for 526 X P.I. 5690 pigeon pea cross (genotypic correlations are on the left side of the diagonal, phenotypic on the right)

Trait	Yield	Number of Pods	Flowering	Height	Seed Weight	No. of seeds per Pod
Yield	—	0.90	-0.18	0.45	0.27	0.62
Number of Pods	0.90	—	-0.07	0.43	0.01	0.45
Flowering	-0.30	-0.02	—	0.40	-0.20	-0.24
Height	0.46	0.41	0.55	—	0.03	0.37
Seed Weight	0.34	0.04	-0.18	0.09	—	0.19
Number of Seeds per Pod	0.83	0.55	-0.17	0.53	0.34	—