EVALUATION OF GENETIC VARIABILITY AND THE NATURE OF GENE ACTION IN PEA
II. DEVELOPMENTAL AND PHYSIOLOGICAL CHARACTERS

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ABSTRACT

Six pea (*Pisum sativum* L.) varieties, fifteen F_1 hybrids and their reciprocals were used in this study as a source of variations to detect the performance and evaluate the variability and genetic architecture of some developmental and physiological characters during the seasons of 1997/98 and 1998/99 .

All the studied characters are largely determined by genes with dominant effects and to some extent by genes with additive effects except stem length and DNA content which were found to be determined by both types of gene effects.

Dominance with asymetrical gene distribution is suggested to be present in the parental genotypes for number of leaves and number of branches per plant, stem and leaves dry weight and RNA content.

Dominant factors are responsible for determining the low expression of stem length while these dominant factors are found to be responsible for the high values of stem and leaves dry weight, DNA and RNA content. Meanwhile, ambidirectional dominance is suggested for both number of leaves and number of branches per plant.

Non-independence of gene distribution among parents is observed for stem length, number of leaves and number of branches per plant, stem and leaves dry weight. In addition, non-allelic interaction of the complementary type is suggested for all the studied characters except for stem length.

A close association of dominance with high values was observed in Mammoth and Arica for both stem and leaves dry weight and in Mammoth, Little Marvel and Hunter for RNA and DNA contents.

Key words; Additive, Developmental characters, Dominance, Genetic variability, *Pisum sativum*.

INTRODUCTION

Improvement of developmental and physiological characters in pea (*Pisum sativus* L.) are desirable to offer better oportunities for having higher yield. However, not only the mean performance, of these characters is of great importance to identify the best genotypes which could be bred to increase yield (Partap *et al.,* 1992; Kumaran *et al.,* 1995) but also the information on the inheritance and the nature of gene action in these characters are essential to plan and organize a systematic breeding programme and in turn to develop varieties of desired developmental characters. Many researchers dealt with such developmental and yield

characters to emphasis the role of the genetic architecture in improving pea cultivars (Singh *et al.,* 1996 and Ahmed *et al.,* 1998).

Moreover, the performance of any genotype was, also, found to be related to the RNA and DNA contents of plant organs (Kinyapina, 1984). However, high-yielding hybrids generally had higher content of DNA and RNA in roots and leaf cells than low-yielding hybrids (Gilyazetdinov, 1985; Troshina, 1994).

The aim of this work is to evaluate the performance of six local and foreign pea cultivars and the drived thirty F_1 hybrids and to determine the nature of gene action concerning some important developmental and physiological characters.

MATERIALS AND METHODS

a. Materials:

Six pea (*Pisum sativum* L.) varieties, namely, Arica as P_1, Hunter as P_2, Ambassador, wav 505 as P_3, Master as P_4, Mammoth as P_5 and Little Marvel as P_6 were used as parental genotypes in this work to study the gene effects in some developmental and physiological characters in pea at the Experimental Farm of El-Kassassein Horticulture Research Station.

b. Methods:

In October 1997 all seeds of parental genotypes were sown. All combinations of diallel and reciprocal crosses were made among the parents. In October 1998, F_1's, reciprocals and parental seeds were sown in a randomized block design with three replicates. Each replication comprised thirty six entries; six parents and thirty hybrids. The agricultural treatments were similar for all entries under study and as recommended for pea plants.

Collecting data for diallel analysis:

Measurements from parents and F_1 genotypes for the characters under consideration were taken on ten randomly chosen plants of each replicate. Seven developmental and physiological characters were measured, they were stem length (cm), number of leaves/plant, number of branches/plant, average dry weight for each of stem and leaves/plant, bulk DNA and RNA were isolated and determined in three samples of one gram for each which were taken from the fourth leaf of randomly chosen mature plants (40 days from sowing date) according to Nistan and Lang (1966).

c. Statistical procedures:

The statistical analysis was carried out using the methods suggested by Hayman (1954) and Mather and Jinks (1971). The analysis involved grouping the data for each character into arrays, each consisted of one parent and all the F_1 hybrids in which this parent is involved.

The graphical analysis was achieved by plotting the variance of each array (Vr) against the covariance of the array with the non-recurrent parents (Wr) and the regression line Wr, Vr. Standardized deviations of both the parental measurements (Yr) and the values of dominance order (Wr+Vr) were also plotted graphically for the seven characters.

RESULTS AND DISCUSSION

I. Performance of Parental and F1 Hybrid Genotypes:

For the performance of parental genotypes, data showed that although P_5 (Mammoth) was found to have the highest mean values in all the seven characters except for RNA content, none of its drived F_1 hybrids showed to be superior in any character except in stem length. In the meantime, P_2 showed to have the lowest values, among parental values, in five out of the seven characters (Table 1).

Table 1: Mean performance of parental pea genotypes and F_1 hybrids over reciprocals for quantitative characters.

Genotype* or Hybrid	Stem length (cm)	No. leaves	No. branches	Stem dry wt. (gm)	Leaves dry wt. (gm)	DNA Content (μ g/g)	RNA Content (μ g/g)
P_1	85.33	70.0	3.33	11.79	15.69	1.48	8.24
P_2	41.67	13.33	1.33	1.73	1.82	1.91	17.26
P_3	93.0	50.33	3.0	8.37	6.33	1.86	8.49
P_4	53.33	28.0	1.67	2.97	6.56	2.47	14.34
P_5	198.67	85.33	3.33	21.29	18.63	3.28	15.17
P_6	92.0	45.67	1.33	4.54	5.33	3.11	17.32
$F_1(P_1XP_2)$	43.83	12.33	0.50	1.02	2.04	2.06	14.67
$F_1(P_1XP_3)$	75.0	64.0	5.0	15.29	18.07	2.36	11.21
$F_1(P_1XP_4)$	72.33	50.33	4.0	7.26	9.27	3.13	12.04
$F_1(P_1XP_5)$	124.0	60.83	4.83	12.71	13.51	3.48	14.78
$F_1(P_1XP_6)$	60.17	31.50	1.83	2.96	5.61	3.51	33.24
$F_1(P_2XP_3)$	98.0	153.0	14.33	29.63	38.44	2.88	20.01
$F_1(P_2XP_4)$	47.50	37.33	2.17	2.44	5.98	2.43	17.70
$F_1(P_2XP_5)$	100.17	36.67	2.33	11.30	10.40	2.58	15.93
$F_1(P_2XP_6)$	63.83	42.67	3.17	8.49	8.41	2.80	17.74
$F_1(P_3XP_4)$	53.0	32.0	3.0	4.78	7.28	3.45	23.49
$F_1(P_3XP_5)$	127.67	82.83	6.83	20.89	18.99	3.56	25.09
$F_1(P_3XP_6)$	93.0	93.17	4.83	19.33	22.03	3.27	18.87
$F_1(P_4XP_5)$	98.33	38.33	3.0	17.25	19.04	3.48	25.08
$F_1(P_4XP_6)$	46.0	78.0	4.33	2.42	4.03	2.26	12.45
$F_1(P_5XP_6)$	131.0	71.5	5.67	19.76	21.30	3.31	11.71

* P_1 = Arica, P_2 = Hunter, P_3 = Ambassador, P_4 = Master,
P_5 = Mammoth and P_6 = Little Marvel.

However, the F_1 (P_2XP_3); Hunter x Ambassador was found to have the highest mean values for four out of the seven characters. In addition, it had a considerable mean performance for the rest characters; plant height and DNA and RNA contents. These results agreed with those obtained by Guirgis and Swidan (1999). These findings suggest that the hybrid Hunter X Ambassador could be used successfully as a base population in raising high-yielding lines, since it had high levels of DNA and RNA contents. These results are in concordance with those of Kinyapina (1984); and Troshina (1994), Gilyazetdinov (1985).

II- Analysis of Variance and Uniformity Test:

The variances of thirty-six pea genotypes representing parents, F_1's and their reciprocals were highly significant for all the seven characters. The uniformity of Wr-Vr, as revealed by the non-significant t^2 values for three out of the seven charcters studied indicates the validity of the hypothesis of diallel analysis. Meanwhile, the analysis of variance of Wr-Vr shows significant array effects for number of leaves per plant, number of branches per plant and dry weight of each of stem and leaves indicating, thereby, the failure of one or more of the assumptions for diallel analysis (Table2).

Table 2: Mean squares and the t^2 values of uniformity test of Wr-Vr for seven quantitative characters in pea.

Parameter	Stem length (cm)	No. leaves	No. branches	Stem dry wt. (gm)	Leaves dry wt. (gm)	DNA content	RNA content
Mean squares	6058.**	4256.**	33.61**	303.25**	344.9**	2.04**	139.1**
t^2 of Wr-Vr	3.76	10.7**	108.01**	5.99*	24.1**	0.54	0.73
(b-0)/S_b	60.5**	-1.07	-0.29	-0.72	-2.4	3.58*	0.62
(1-b)/S_b	-10.5	8.32**	21.13**	6.28*	13.6**	-0.15	2.5

*,** significant at 5% and 1% levels, respectively.

The regression line does not significantly differ from a slope of b= 0 or b=1 revealing the presence of epistasis in RNA content. Meanwhile, the presence of non-additive gene action was demonstrated for both number of leaves and branches per plant, dry weight of leaves and dry weight of stem since the regression coefficients significantly differ from a slope of b=1.

For stem length and DNA content, the regression line significantly differs from a slope of b=0, but not from slop b=1, which indicates that the gene action for these characters are additive without any genic interaction. Meanwhile, Ammed *et al.,* (1998) demonstrated the prevailence of non-allelic interaction in the genetics of plant height in their parental genotypes.

III. Components of Genetic Variance and Gene Action:

The estimates of all the six components of variation, Viz. D, F, H1, H2, h2 and E and their standard errors, presented in Table (3), indicated that the additive (D) component was highly significant for stem length and DNA content. The insignificant values of (D) for number of leaves per plant, number of branches per plant, stem dry weight, leaves dry weight and RNA content were considerable in magnitude, indicating that these characters are largely determined by genes with dominant effects and to some extent by genes with additive effects. Epistatic gene effects are known to contribute a sizeable part of variation in the characters showed higher estimates of dominance gene effects (Gambel, 1962).

The dominance component (H1) of genetic variance was positively significant for number of leaves, stem dry weight and leaves dry weight and highly significant for stem length, DNA content and RNA content (Table 3). However, considerable and larger dominance component than additive one was observed for number of branches. This clearly indicates that for stem

length and DNA content which had significant D and H1 values, are determined by both types of gene effects; with additive and dominant effects. The importance of additive and non-additive gene effects for most of these characters has been reported by a number of workers; Kumar and Agrawal, (1981); Dubey and Lai, (1983); Venkateswarlu and Singh, (1983); and Moitra *et al.,* (1988).

The estimates of average value of dominance in loci having unequal positive and negative allelic frequencies (H2) were highly significant for stem length and DNA content. This indicates the presence of dominance with asymetrical gene distribution, for these characters, in the parental genotypes. The presence of dominance with asymetrical gene distributions was also reported for stem length by Ahmed et al. (1998) and Ahmed and Ismail (1999). Moreover, H2 values were insignificant but positive and were considerable, in respect to other components for number of leaves, number of branches, stem dry weight, leaves dry weight and RNA content. This suggests that dominance with asymetrical gene distribution might be present also for these characters in the concerning parental genotypes (Table 3).

The h2 estimates express the dominance effect were highly significant and positive for stem length, number of branches, stem dry weight, leaves dry weight, DNA and RNA content. This indicates the existence of more positive genes controlling these characters. However, the estimates of covariance of additive and dominance effects over the arrays (F) were highly significant and positive for stem length. Meanwhile, they were insignificant for the other six characters, suggesting that there could be an inequality of the relative frequencies of positive and negative alleles in the parents and that dominant alleles are more frequent than recessive ones for these characters (Table 3).

Data in Table (4) showed that the average degree of dominance over all loci $(H1/D)^{1/2}$ was more than one indicating that overdominance is controlling the allelic interactions for all characters studied except for stem length which clearly showed that partial dominance is controlling the allelic interaction in all loci of dominance genes for this character. However, the parameter "$H_2/4H_1$" which measures the proportion of positive genes x proportion of negative genes over all arrays "ui vi" was found to be the highest (0.22) for number of branches and the lowest (0.091) for RNA content. This clearly suggests the presence of some sort of asymmetry at loci showing dominance for almost all the characters studied ($u \neq v$).

Table 4: Proportions of genetic components and narrow sense heritability estimates (ns) for seven quantitative characters of pea.

Parameter or Proportion	Stem length (cm)	No. leaves	No. branches	Stem dry wt. (gm)	Leaves dry wt. (gm)	DNA Con-tent	RNA Con-tent
$(H1/D)^{1/2}$	0.53	2.54	6.28	1.90	2.78	1.46	1.95
H2/4H1	0.214	0.20	0.219	0.19	0.19	0.21	0.09
$(4DH1)^{1/2}$+F $(4DH1)^{1/2}$-F	1.63	1.71	0.858	3.06	1.60	1.618	1.59
h2/H2	3.14	0.48	2.26	1.18	1.35	6.78	6.02
h^2 (ns)	0.99	0.99	0.98	0.998	0.997	0.98	0.995

The value "$(4DH1)^{1/2} + F/(4DH1)^{1/2} - F$)" which reflect the proportion of dominant and recessive genes, was less than one for number of branches (Table 4). This estimate was associated with negative value of F (Table 3) indicating that recessive genes were higher in frequency than dominant ones in the parents for this character. This proportion exceeded the value of one for the other characters with positive values of F, showing that more dominant genes are controlling these characters over the six parents used in this study.

Estimates of number of gene groups controlling the characters and exhibit dominance (h2/H2) showed that DNA and RNA contents are controlled by seven and six dominant gene groups, respectively. However, least number of dominant gene groups were found for either number of leaves and stem dry weight (Table 4). The narrow-sense heritability estimates (h^2) showed high values for all the characters studied. These results aggreed with those obtained by Kumaran *et al.,* (1995) and Singh *et al.,* (1996).

It can be seen that the coefficient of correlation"r" between the parental order of dominance (Wr+Vr) and the parental measurements (Yr) was significant and positive for stem length indicating that, the parents containing the most dominant genes, which has the lowest Wr+Vr values, are characterized with the lowest Yr values. Hereafter, it suggests that dominant factors are responsible for determining the low expression for this character. In the meantime, significant and negative correlation cofficients between Wr+Vr and Yr were observed for stem dry weight, leaves dry weight, DNA content and RNA content indicating that the parental genotype with the lowest value of parental order of dominance (Wr+Vr); P_5 (Mammoth) is containing the most dominant genes and so the highest score (Yr) of three of these characters and P_2 for RNA content. Since, the parental measurement Yr is closely correlated with the number of dominant homozygotes and the value (Wr+Vr) is correlated with the number of recessive homozygotes (Hayman, 1954). However, both number of leaves per plant and number of branches per plant had insignificant values of "r" suggesting that dominance in the parents is ambidirectional (Table 5).

Considerable "r^2" values could suggest the existence of regression of "Yr" on "Wr+Vr" for all characters except for both number of leaves and number of branches per plant. This shows that P_5 (Mammoth) is the completely recessive parent and P_2 (Hunter) is the completely dominant one for stem length while P_5 had the most dominant genes for both stem and leaves dry weight and DNA content. However, P_2 had the most recessive genes for these characters. Meanwhile, P_2 (Hunter) had the most dominant genes for RNA content and P_1 (Arica) had the most recessive genes for this character. As for the other characters, none of r^2 values could suggest the existence of regression of Yr on Wr+Vr, hence prediction of completely dominant and recessive parents was not possible.

Table 5: Parental order of dominance (Wr+Vr) and parental measurements (Yr) and their correlation coefficients in seven quantitative characters.

Characters	Arica (P1)	Hunter (P2)	Ambass-ador (P3)	Master (P4)	Mam-moth (P5)	Little Marvel (P6)	r(Wr+Vr),Yr [r²(Wr+Vr)2yr]
Stem length Wr+Vr	2099.2	1877.70	1649.03	1382.8	3348	2484.2	0.878*
Yr (cm)	85.33	41.67	93.0	53.33	198.67	92.0	0.771
No. leaves Wr+Vr	936.5	2844.0	1406.7	408.9	898.0	605.0	-0.484
Yr	70.0	13.33	50.33	28.0	85.33	45.67	0.234
No.branches Wr+Vr	4.44	27.9	16.6	1.32	3.56	3.62	-0.258
Yr	3.33	1.33	3.0	1.67	3.33	1.33	0.067
Stem dry wt. Wr+Vr	61.21	135.74	84.48	73.48	31.69	98.89	-0.85*
Yr (gm)	11.79	1.73	8.37	2.97	21.29	4.54	0.72
Leaves dry wt Wr+Vr	63.03	179.64	118.02	58.42	19.73	86.84	-0.814*
Yr (gm)	15.69	1.82	6.33	6.56	18.63	5.33	0.663
DNA Wr+Vr	1.273	0.304	0.84	0.248	0.139	0.163	-0.821*
Yr (μ g/g)	1.48	1.91	1.86	2.47	3.28	3.11	0.674
RNA Wr+Vr	103.80	3.26	66.5	29.8	22.7	39.8	-0.872*
Yr (μ g/g)	8.24	17.26	8.49	14.34	15.17	17.22	0.76

*, significant at 5% level of probability.

IV. The Graphical Analysis and Relationship of Standardized Parental Measurements and the Order of Dominance:

It is worthy to mention that, overestimation of the degree of dominance was observed for stem length, number of leaves/plant, number of branches, stem dry weight and leaves dry weight; 0.53, 2.54, 1.9 and 2.78 (Table 4) while the regression line cuts the ordinate at a point higher than that estimated for stem length and above the origin for the other three characters (Fig. 1). This clearly indicates the presence of non-independence of gene distribution among parents for these characters. This explaination of over-estimation of the dominance level is based on a similar reasoning mentioned by Hill (1964).

Non-allelic interaction of the complementary type is suggested as almost all the array points lie below the dotted line of unit slops in all the studied characters except for stem length. Moreover, the array points are scattered, revealing the genetic diversity among the parents. With regard to RNA and DNA, the regression line cuts the ordinate below the point of origin indicating that overdominance is controling the allelic interaction for both characters (Fig. 1).

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Significant positive correlation coefficients between Wr+Vr and Yr values indicates that high stem length in P_5 is found to be closely associated with recessiveness. In addition, low values of this character is associated with dominance in P_2, P_4, P_1 and P_3, in ascending order for stem length. (Fig. 2).

For number of branches and number of leaves per plant, the insignificant negative correlation coefficient; -0.258 and –0.484; respectively indicated that there is only a tendency for high values of P_1 and P_5 to be associated with dominance and low ones in P2 and P3 with recessiveness (Fig. 2). In this concern, Hayman (1954) stated that the parental measurement Yr is closely correlated with the number of dominant homozygotes and the value (Wr+Vr) is correlated with the number of recessive homozyotes.

The standardized deviations of the parental order of dominance Wr+Vr and the parental measurements Yr for stem dry weight, leaves dry weight of leaves, RNA and DNA contents had negative and significant correlation coefficients (Table 5).

These relationships indicate a close association of dominance with high values in P_5 and P_1 for both stem and leaves dry weight and in P_5, P_6 and P_2 for RNA and DNA contents and conversely recessive genes with low values in P_2 for both dry weight of stem and leaves and in P_1 and P_3 for RNA and DNA contents (Fig. 2).

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تقييم الاختلافات الوراثية وطبيعة الفعل الجينى فى البسلة
2 ـ الصفات الفسيولوجية والنمو

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استخدم فى هذه الدراسة ستة أصناف من البسلة وخمسة عشرة هجينا من هجن الجيل الأول وهجنها العكسية كمصدر للاختلافات للتعرف على الأداء وتقييم الاختلافات والبناء الوراثى فى بعض الصفات الفسيولوجية والنمو أثناء الموسمين 1998/97، 1999/98.

وجد أن كل الصفات موضع الدراسة تكون محكومة الى حد كبير بالجينات ذات التأثيرات السائدة وإلى حد ما بالجينات ذات التأثير المضيف فيما عدا صفتى طول الساق ومحتوى الـ DNA والتى وجد أن كلاهما يتحدد بكل من نوعى التأثيرات الجينية (السائدة والمضيفة).

وتوضح الدراسة وجود سيادة مع توزيعات جينية غير متساوية فى التراكيب الوراثية الأبوية فيما يخص صفات عدد الأوراق فى النبات وعدد الفروع فى النبات والوزن الجاف للساق والوزن الجاف للأوراق ومحتوى الـ RNA.

كما أظهرت النتائج أن الجينات السائدة تكون مسئولة عن تحديد التعبير المنخفض لصفة طول الساق بينما وجد أن تلك الجينات السائدة تكون مسئولة عن القيم العالية لصفات الوزن الجاف لكل من الساق والأوراق والمحتوى لكل من الـ RNA والـ DNA، وفى نفس الوقت توضح الدراسة أن السيادة المختلفة الاتجاه تظهر فى تعبير الجينات التى تحكم كل من صفتى عدد الأوراق وعدد الفروع فى النبات.

لوحظ عدم استقلال التوزيعات الجينية على الآباء فيما يخص صفات عدد الفروع فى النبات والوزن الجاف لكل من الساق والأوراق، بالإضافة الى أن الدراسة تبين وجود تفاعل غير أليلى من النوع المكمل فى كل الصفات موضع الدراسة ماعدا صفة طول الساق.

كما لوحظ وجود تلازم بين السيادة وبين القيم العالية فى صفتى الوزن الجاف للساق والأوراق فى الصنف Mammoth والصنف Arica وكذلك فى صفتى محتوى الـ RNA والـ DNA فى الأصناف Mammoth و Hunter والصنف المحلى Little Marvel .

Table 3: Components of genetic variation for seven quantitative characters in pea.

Component	Stem length (cm)	No. leaves	No. branches	Stem dry wt. (gm)	Leaves dry wt. (gm)	DNA Content	RNA content
D	3076.6±84.2**	695.2±888.3	0.901±8.2	53.2±33.8	43.0±64.9	0.526±0.10**	16.7±20.6
F	774.9±205.7**	922.8±2169.8	-0.86±20.1	14.1±82.7	55.2±158.5	0.362±0.24	24.5±50.3
H1	883.4±213.7**	4486±2254*	35.6±20.9	191.9±85.9*	331.4±164.7*	1.12±0.25**	175.2±52.3**
H2	730.3±190.9**	3584.6±2014.2	31.5±18.7	149.3±76.7	257.8±147.1	0.942±0.22**	63.7±46.7
h2	2293.9±128.5**	1729±1355.7	70.4±12.9**	176.4±51.6**	347.5±99.0	6.38±0.15**	383.4±31.4**
E	9.1±31.9	2.2±336.0	0.08±3.1	0.07±12.8	0.10±24.6	0.003±0.037	0.25±7.8

*,** Significant at 5% and 1% levels of probability, respectively.