

Genetic Control of Root Weight, Root Volume and Root to Shoot Weight Ratio in Peas

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ABSTRAK

Pengawalan genetik atas berat akar, isipadu akar dan nisbah berat akar dengan pucuk telah dikaji bagi kacang pea (*Pisum sativum* L.) pada peringkat berbunga. Empat populasi yang digunakan telah dibentuk daripada kacukan di antara warisan-warisan dan kultivar-kultivar yang berbeza saiz sistem akarnya. Tumbuhan daripada generasi F_1 , F_2 , kacukan-balik dan induk telah dinilai dalam pasu yang diisi dengan campuran tanah: pasir, dalam rekabentuk berawak lengkap. Analisis min generasi telah digunakan untuk menentukan pewarisan ciri-ciri akar tersebut. Berat dan isipadu akar memberikan nilai keboleharisan luas yang sederhana hingga tinggi (0.41 – 0.81 bagi berat akar, dan 0.44 – 0.77 bagi isipadu akar). Kesan penambah dan kesan dominan penting dalam pewarisan berat dan isipadu akar dalam semua populasi, manakala kesan epistasis hanya penting dalam dua populasi. Kepentingan parameter-parameter genetik dalam pewarisan nisbah berat akar dengan pucuk tidak begitu jelas. Dengan wujudnya kesan penambah yang besar dan nilai keboleharisan yang tinggi bagi berat dan isipadu akar, pemilihan untuk warisan-warisan tulen unggul yang mempunyai sistem akar yang besar akan memberikan kesan.

ABSTRACT

The genetic control of root weight, root volume and root to shoot weight ratio was studied in peas (*Pisum sativum* L.) at flowering. The four populations used were developed from crosses between lines and cultivars differing in size of the root systems. Plants of the F_1 , F_2 , backcross and parental generations were evaluated in pots filled with soil: sand mixture, in a completely randomized design. A generation means analysis was used to determine the inheritance of the root characteristics. Root weight and volume exhibited moderate to high broad-sense heritability (0.41 – 0.81 for root weight, and 0.44 – 0.77 for root volume). Additive and dominance effects were important in the inheritance of root weight and volume in all populations, while epistatic effects were important only in two populations. The importance of the genetic parameters in the inheritance of root to shoot weight ratio was unclear. With the presence of large additive effects and high heritability, estimates for root weight and volume, selection for superior pure lines with large root systems should be effective.

INTRODUCTION

In spite of the vital roles it plays, the plant root system has not been studied as extensively as the above-ground parts. Desirable root characteristics

and development in crops have been associated with efficiency of water and nutrient uptake and tolerance to water stress and root disease conditions (Derera *et al.*, 1969; Ekanayake *et al.*,

1985; Epstein, 1972; Hurd, 1974; Steponkus *et al.*, 1980; Taylor and Klepper, 1978).

Very few studies have been conducted on the variability of the pea (*Pisum sativum* L.) root system, especially at the mature plant stage. Veitenheimer (1981) indicated the presence of variability for various root characteristics measured among diverse pea genotypes grown both in hydroponics and soil. It was also noted that differences in the root characteristics were very pronounced when values were compared at flowering. Ali-Khan and Snode (1977) reported a considerable amount of genetic variability existing for root characteristics of 10-day old pea seedlings. Broad-sense heritability estimates for root weight and number of lateral roots were relatively high, being 67.5% and 53.7%, respectively. High heritability estimates for root characteristics were also indicated in other crops including common beans (Fawole *et al.*, 1982), kidney beans (Lindgren, 1977), oats (Barbour and Murphy, 1984) and rice (Ekanayake *et al.*, 1985).

No study has been reported to identify kinds and amount of gene effects involved in the control of root characteristics in peas. In cotton, Eissa *et al.* (1983) found large amounts of additive, dominance and additive x additive epistatic effects for primary root traits of 16-day old seedlings. In rice, Ekanayake *et al.* (1985), with 50-day old hydroponically grown plants reported that additive and dominance effects had equally important contributions to the expression of all root traits measured.

The objectives of this study were (i) to determine kinds and amount of gene effects and to estimate heterosis, inbreeding depression and heritability for root weight, root volume and root to shoot weight ratio, and (ii) to determine relationships among root characteristics and between root and other plant characteristics, in peas measured at flowering.

MATERIALS AND METHODS

Experimental Materials and Procedures

Parents used in this study were two cultivars and six breeding lines chosen for their diverse root characteristics revealed in the study by Veitenheimer (1981). 'Sprite' and 'Dark Skin Perfection' (DSP) were the two cultivars used, having very small and small root systems, respectively.

'Minnesota 108' (Mn 108) and 'Minnesota 494-All' (Mn 494-All) were two root-rot resistant lines used, with relatively small and large root systems, respectively. Four other lines used were 'L 1073', 'L 1254' and 'L 1482' all with large root systems, and 'L 1532', with small root system.

Four populations were generated from crosses between the parental lines, namely Population 1 (Sprite x L 1482), Population 2 (DSP x L 1973), Population 3 (Mn 108 x L 1254) and Population 4 (Mn 494-All x L 1532). Initial parental crosses were made in the greenhouse in February and March of 1983. Seeds of the P₁, P₂, F₁, F₂, BC₁P₁ and BC₁P₂ generations were produced either in the field or in the greenhouse later in the same year. Only seeds produced in a common environment were used for evaluation of a population.

Due to space limitations in the greenhouse and the amount of labour involved in root washing, only two populations were evaluated at a time: Populations 1 and 2 in June to September, while Populations 3 and 4 in September to December of 1984. Generations in each population were represented by the following number of plants: 14 plants for each of the parents and the F₁'s, 30 plants for each of the backcrosses, and 58 plants for the F₂'s. To minimize reciprocal effect, an equal number of individuals from a cross and its reciprocal was used. The evaluation within each population was conducted in a completely randomized design, in which a plant was a replicate for the generation it represented.

Seeds were first germinated in petri dishes with silica sand medium, and then planted in individual clay pots filled with autoclaved 1:1 soil-sand mixture. Each pot contained 3800 cm³ of the medium, with an average bulk density of 1.25 g cm⁻³. Only one plant was grown in each pot. The pots were placed on capillary watering mats laid on benches in a temperature-controlled greenhouse. Water was supplied by wetting the mat at regular intervals through dew hoses and controlled by an automatic timer. Water status in the pot was monitored by tensiometers placed in pots on each bench.

Every plant was harvested individually when the first flower appeared. The roots were carefully washed in a screen-lined box placed in a sink filled up with water. Root volume was taken on fresh

roots of each plant by the water displacement method. Root and shoot weights of each plant were taken on oven dried samples. Leaf area, number of nodes on the main stem, number of branches and number of days to flowering were also recorded for each plant.

Genetical and Statistical Procedures

Analysis of variance was employed separately for each population to determine the significance of the generation effects on root weight and volume and root to shoot weight ratio. Mid-parental heterosis was determined by the difference between the F_1 mean and the mid-parental value, expressed as a percentage of the mid-parental value. Inbreeding depression was calculated as the difference between the F_1 mean and the F_2 mean expressed as a percentage of the F_1 mean.

Broad-sense heritability was estimated following the equation:

$$h_B^2 = (V_{F_2} - \sqrt[3]{V_{P_1} \times V_{P_2} \times V_{F_1}}) / V_{F_2}$$

while narrow-sense heritability was estimated following the equation:

$$h_N^2 = [2V_{F_2} - (V_{BC_1P_1} + V_{BC_1P_2})] / V_{F_2}$$

where h_B^2 and h_N^2 are the broad-sense and narrow-sense heritabilities, respectively, and V_{F_2} , V_{P_1} , V_{P_2} , V_{F_1} , $V_{BC_1P_1}$ and $V_{BC_1P_2}$ are variances associated with the F_2 , P_1 , P_2 , F_1 , BC_1P_1 and BC_1P_2 generations, respectively.

Where generation effects were significant, the generation means analysis procedure was used to estimate gene effects for each of the root characteristics, following the model and assumptions outlined by Mather and Jinks (1971). Mean values of each of the six generations were used for the analysis. The expected relationships among genetic parameters were tested by the joint-scaling test procedure as described by Rowe and Alexander (1980). A weighted least square procedure (Mather and Jinks, 1971) was used in the generation means analysis to compensate for the difference in precision involved in the estimation of mean values among the six generations. Each characteristic in each population was tested for

fit to the additive-dominance model by the Chi-square procedure. Where the model did not fit, the analysis was further carried out with comparisons to fit models that include digenic epistatic parameters in the expectations. Values for individual genetic parameters were considered significant if they exceeded twice their standard errors.

Simple correlation coefficients were calculated among root characteristics and between root and other plant characteristics using data from the F_2 generation.

RESULTS AND DISCUSSION

Generation mean squares in the analyses of variance were significant for all root characteristics, root weight, root volume and root to shoot weight ratio in all four populations, indicating that phenotypic variation exists among generations. Means and variances of these characteristics are shown in Table 1. The more favourable summer growing conditions at the time Populations 1 and 2 were evaluated led to larger mean values compared to the less favourable fall growing conditions at the time Populations 3 and 4 were evaluated.

Estimates of mid-parental heterosis were generally high for root weight and volume (ranged from 10.6 to 126.2 percent) in all four populations (Table 2), indicating a preponderance of dominance towards the larger parents was present for these traits. The two root traits showed almost similar estimates of heterosis. Population 4 exhibited the highest degree of heterosis, being 115.9 and 126.2 percent for root weight and volume, respectively. The results showed good agreement with high heterosis and inbreeding depression for yield and yield components in peas, as reported by Gritton (1975) and Krarup and Davis (1970). Heterosis for root to shoot weight ratio was not consistent; positive in Populations 1 and 4, but negative in Populations 2 and 3. Estimates of inbreeding depression for root weight and volume were high in Populations 3 and 4 (ranged from 28.8 to 30.1 percent), but low in Population 1 (6.1 and 7.9 percent for root weight and volume, respectively). Estimates of inbreeding depression for root to shoot weight ratio were generally low or negative. Negative estimates of inbreeding depression for all traits in Population 2 were due

TABLE 1
 Generation means and variances for root characteristics measured at flowering in four pea populations.

Generation	Root Weight		Root Volume		Root to shoot weight ratio	
	Mean	Variance	Mean	Variance	Mean	Variance
	g		cm ³			
Population 1						
L 1482 (P ₁)	1.68a ^a	0.130	32.2a	46.20	0.95a	0.040
Sprite (P ₂)	0.55c	0.016	10.4c	6.43	0.48d	0.015
F ₁	1.38ab	0.263	26.1ab	90.20	0.66bc	0.058
F ₂	1.29b	0.321	24.1b	93.74	0.65bc	0.047
BC ₁ P ₁	1.67a	0.186	29.3a	34.19	0.73b	0.030
BC ₁ P ₂	0.84c	0.165	16.9c	48.34	0.53cd	0.045
Population 2						
L 1073 (P ₁)	2.77ab	1.308	42.9a	166.13	0.55a	0.019
DSP (P ₂)	1.27d	0.086	23.2c	16.85	0.50abc	0.018
F ₁	2.23bc	0.121	37.6ab	17.82	0.42c	0.005
F ₂	2.79a	1.240	41.5a	161.48	0.48abc	0.016
BC ₁ P ₁	2.78ab	0.562	42.5a	86.13	0.51ab	0.011
BC ₁ P ₂	2.04c	0.411	33.2b	97.98	0.46bc	0.031
Population 3						
L 1254 (P ₁)	0.99b	0.058	16.3a	16.04	0.30a	0.001
Mn 108 (P ₂)	0.47e	0.015	7.1c	2.50	0.27ab	0.004
F ₁	1.13ab	0.114	17.6a	36.65	0.26ab	0.007
F ₂	0.80c	0.079	12.3b	20.49	0.25b	0.005
BC ₁ P ₁	1.15a	0.059	18.0a	20.42	0.26ab	0.004
BC ₁ P ₂	0.67d	0.028	10.5b	8.48	0.26ab	0.004
Population 4						
Mn 494-A11 (P ₁)	0.67d	0.038	11.0d	7.30	0.32a	0.003
L 1532 (P ₂)	0.60d	0.034	9.1d	7.91	0.15d	0.002
F ₁	1.38a	0.054	22.8a	20.16	0.30ab	0.003
F ₂	0.98c	0.088	15.9c	23.69	0.26b	0.003
BC ₁ P ₁	1.14b	0.069	18.8b	19.52	0.31a	0.006
BC ₁ P ₂	0.93c	0.091	14.7c	24.69	0.23c	0.004

^aMeans followed by the same letters in the same column and population are not significantly different at P = 0.05 level.

to values of F₂ means larger than those of the F₁'s (Table 2).

Broad-sense heritability estimates for root weight and volume were moderate to high (0.75, 0.81, 0.41 and 0.53 in Populations 1, 2, 3 and 4, respectively, for root weight; and 0.68, 0.77, 0.44 and 0.56 in Populations 1, 2, 3 and 4, respectively, for root volume), indicating the presence of relatively high genetic variance for these traits (Table 2). Broad-sense heritabilities for root to shoot weight ratio were low to moderate

(0.31, 0.25, 0.24 and 0.19 in Populations 1, 2, 3 and 4, respectively).

Narrow-sense heritability estimates were highly variable for all characteristics measured (Table 2). Estimates ranged from 0.18 to 0.91 for root weight, 0.13 to 1.00 (calculated value is 1.12) for root volume and zero (calculated value is -1.23) to 0.40 for root to shoot weight ratio. The wide range in values (including negative estimates and estimates exceeding 1.00) suggests that the estimates were very imprecise. Con-

TABLE 2

Estimates of mid-parental heterosis, inbreeding depression and heritability for root characteristics measured at flowering in four pea populations.

Population	Mid-parental heterosis	Inbreeding depression	h_B^2	h_N^2
	%	%		
Root weight				
Pop. 1 (Sprite x L 1482)	23.2	6.1	0.75	0.91
Pop. 2 (DSP x L 1073)	10.6	-24.8	0.81	1.22
Pop. 3 (Mn 108 x L 1254)	55.2	29.5	0.41	0.90
Pop. 4 (Mn 494-All x L 1532)	115.9	28.8	0.53	0.18
Root volume				
Pop. 1	22.8	7.7	0.68	1.12
Pop. 2	13.7	-10.4	0.77	0.86
Pop. 3	49.8	30.1	0.44	0.59
Pop. 4	126.2	30.1	0.56	0.13
Root to shoot weight ratio				
Pop. 1	7.7	1.5	0.31	0.40
Pop. 2	-20.0	-14.3	0.25	-0.63
Pop. 3	-6.8	3.8	0.24	0.33
Pop. 4	27.7	13.3	0.19	-1.23

h_B^2 = broad-sense heritability, h_N^2 = narrow-sense heritability.

sequently, we make no inference regarding the narrow-sense heritabilities.

From the generation means analysis, it was found that an additive dominance model was adequate in explaining the variation in generation means for root weight and volume in Populations 1 and 4, as indicated by the non-significant Chi-square values in the joint-scaling tests (Table 3). Both additive [d] and dominance [h] parameters were significant for these characteristics in both populations, as shown by their values larger than twice their standard errors. This indicates that significant additive and dominance gene effects, in the direction of the larger parents were present for root weight and volume in Populations 1 and 4. Magnitude of additivity was larger than that of dominance in Population 1, but was the opposite in Population 4.

The five-parameter model fits in explaining the genetic control of root weight and volume in

Populations 2 and 3 (Table 3). Additive effects [d] were significant for both characteristics in both populations. Dominance effects [h] were significant and in the direction of the larger parents for these two characteristics only in Population 3. Dominance was towards the smaller parent in Population 2 (negative values of [h]). These negative estimates of dominance were not expected and were contrary to the presence of heterosis for these characteristics in Population 2, as shown in Table 2. These estimates of dominance effects, was thus, felt unreliable. The negative estimates might have been caused by mean values of the F_2 generation higher than the F_1 's (Table 1). It might have also been possibly caused by the presence of linkage or generation x environment interaction. Linkage between the root characteristics and other traits in any of the two parents in a population could have led to the weakness of the generation means analysis (Jinks, 1979). Attempts

TABLE 3

Estimates of gene effects in three-parameter and five-parameter genetic models for root characteristics measured at flowering in four pea populations.

Population	[m] ^b	[d] ^b	[h] ^b	[i] ^b	[j] ^b	χ ² ^c	P ^c
Root weight							
Pop. 1 (Sprite x L 1482)	1.16 ± 0.05 ^a	0.62 ± 0.05	0.21 ± 0.10			5.25	0.10 - 0.25
Pop. 2 (DSP x L 1073)	3.28 ± 0.26	0.74 ± 0.12	-1.05 ± 0.32	-1.27 ± 0.31	-0.02 ± 0.51	0.17	0.90 - 0.95
Pop. 3 (Mn 108 x L 1254)	0.45 ± 0.12	0.27 ± 0.04	0.75 ± 0.18	0.30 ± 0.12	0.44 ± 0.19	1.35	0.10 - 0.25
Pop. 4 (Mn 494-All x L 1532)	0.64 ± 0.03	0.07 ± 0.03	0.74 ± 0.07			5.66	0.10 - 0.25
Root volume							
Pop. 1	21.50 ± 0.87	11.27 ± 0.83	4.11 ± 2.01			0.97	0.75 - 0.90
Pop. 2	44.89 ± 3.18	9.52 ± 1.46	-7.40 ± 3.61	-12.17 ± 3.74	-1.13 ± 5.41	0.12	0.90 - 0.95
Pop. 3	6.52 ± 1.96	4.68 ± 0.59	12.06 ± 3.18	5.34 ± 2.02	5.89 ± 2.42	1.23	0.25 - 0.50
Pop. 4	10.07 ± 0.51	1.48 ± 0.50	12.77 ± 1.10			6.82	0.05 - 0.10
Root to shoot weight ratio							
Pop. 1	0.66 ± 0.04	0.19 ± 0.04	-0.04 ± 0.08			0.89	0.75 - 0.90
Pop. 2	0.54 ± 0.02	0.04 ± 0.02	-0.11 ± 0.03			0.77	0.75 - 0.90
Pop. 3	0.28 ± 0.01	0.01 ± 0.01	-0.04 ± 0.02			2.03	0.50 - 0.75
Pop. 4	0.23 ± 0.01	0.08 ± 0.01	-0.06 ± 0.02			0.92	0.75 - 0.90

^aSignificance of each gene effect estimate can be determined by t-test procedure, where value of t is found by dividing each estimate by its SE.

^b[m] = mean effect, [d] = additive gene effect, [h] = dominance gene effect, [i] = additive x additive gene effect, [j] = additive x dominance gene effect. Dominance x dominance gene effect [l] is not included because the estimate is not significant in all cases.

^cχ² denotes Chi-square value for testing goodness of fit of model; P denotes probability level.

were made to adjust the values using a common weighting factor for all generations, but was found not to have changed the estimates significantly. Likewise, due to the same reason, estimates of epistasis for these two traits in Population 2 were negative. However, only additive x additive epistatic parameter [i] was significant for both traits. In Population 3, both additive x additive [i] and additive x dominance [i] epistatic effects were significant for root weight and volume.

An additive-dominance model was adequate in explaining the variability in root to shoot weight ratio in all four populations (Table 3). However, the importance of the genetic parameters in the control of this trait was not consistent with populations, and therefore, inconclusive.

Simple correlation coefficients among the root characteristics, and between the root and other plant characteristics are presented in Table 4. In all populations, root weight and volume were highly correlated (r values ranged from 0.832 to 0.963). Similarly, high correlations were also found by Veitenheimer (1981) who utilized diverse pea genotypes in the study. No consistent correlation was found between root to shoot weight ratio and size of the root system. Root to shoot weight ratio was positively correlated with root weight in Populations 3 and 4 ($r = 0.345$ and $r = 0.424$, respectively), but was not correlated in Populations 1 and 2 ($r = 0.076$ and $r = 0.248$, respectively). Similarly, root to shoot weight ratio was correlated with root volume in Populations 2 and 4 ($r = 0.305$ and $r = 0.360$, respectively), but was not correlated in Populations 1 and 3 ($r = -0.011$ and $r = 0.006$, respectively).

In all populations, in general, correlations of root weight and volume with all shoot characteristics measured were positive, except for the correlations between root weight and number of branches in Population 3, and between root volume and number of branches in Population 4, which in both cases were not significant (Table 4). This indicates that, in general, plants with larger and heavier root systems had larger and heavier shoots and larger total leaf area than those with smaller and lighter root systems, although exceptions were found. As expected, root to shoot weight ratio was negatively correlated with shoot weight in all populations. Number of days to flowering in Populations 1 and 2 was highly,

positively correlated with root weight and volume, indicating that, in these populations, plants that flowered earlier had smaller root systems than those that flowered later. In contrast, however, in Population 4, days to flowering was highly, negatively correlated with root weight and volume. In Population 3, days to flowering was positively correlated only with root volume, but not correlated with root weight. Days to flowering was negatively correlated with root to shoot weight ratio in Populations 3 and 4, but was not correlated in Populations 1 and 2.

CONCLUSIONS

The significant additive and dominance effects for root weight and volume showed the importance of these parameters in the genetic control of these two characteristics, although epistatic effects were also important in some populations. Large additive effects and high heritability estimates indicated that selection for superior lines with large root systems should be effective. Maximum utilization of additive effects can be obtained by selection after each generation of selfing. Selection procedures using any kind of non-destructive methods like the use of hydroponically grown plants or partial root harvest, and simultaneously selecting for other desirable traits could be employed. Selections may be delayed until later generations in populations where additive x additive gene effect is important. The tendency of the larger root systems to be associated with later flowering plants was not absolute, thus, effective selection for plants with large root systems but without concomitant lateness should be possible.

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TABLE 4

Simple correlation coefficients between pairs of root characteristics and between root and other plant characteristics measured at flowering in four pea populations

	RV	RSWR	SW	LA	NN	NB	DF ^a
Population 1							
(Sprite x L 1482)							
RW	0.963** ^b	0.076	0.773**	0.543**	0.821**	0.425**	0.745**
RV		-0.011	0.798**	0.584**	0.765**	0.471**	0.653**
RSWR			-0.492**	-0.545**	-0.181	-0.502**	-0.139
Population 2							
(DSP x L 1073)							
RW	0.930**	0.248	0.846**	0.790**	0.813**	0.479**	0.793**
RV		0.305*	0.750**	0.694**	0.694**	0.549**	0.638**
RSWR			-0.272*	-0.321*	0.021	-0.182	0.091
Population 3							
(Mn 108 x L 1254)							
RW	0.832**	0.345**	0.610**	0.658**	0.413**	0.205	0.147
RV		0.006	0.659**	0.728**	0.496**	0.290*	0.312*
RSWR			-0.451**	-0.357**	-0.473**	-0.343*	-0.577**
Population 4							
(Mn 494-All x L 1532)							
RW	0.936**	0.424**	0.735**	0.621**	0.523**	0.275*	-0.592**
RV		0.360**	0.715**	0.664**	0.467**	0.259	-0.522**
RSWR			-0.275*	-0.260	-0.101	-0.139	-0.484**

Correlation coefficient differs significantly from zero based on the 0.05 or 0.01 level of probability, respectively.

^a RW = root weight, RV = root volume, RSWR = root to shoot weight ratio, SW = shoot weight, LA = leaf area, NN = number of nodes on main stem, NB = number of branches, DF = days to flowering.^b All correlation coefficients are based on 58 F₂ individuals.

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