OVULE MORTALITY IN GRAM (*CICER ARIETINUM* L.)

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I. Introduction

IN the course of an investigation on seed-setting in gram (*Cicer arietinum* L.) the writers observed that some pods contained a number of shrivelled-up and undersized seeds, presumably as a result of the failure of some ovules to get fertilised or to develop normally after fertilisation. As this has an important bearing on yield, a study of the productive capacity of the plant in terms of the number of ovules produced and the number which develop into mature seeds was taken up. The work was conducted at Pusa in 1937–38.

II. Material and Methods

Twenty-eight varieties of gram were selected for the study, the selection being based on peculiarities of seed-setting observed in the previous season.

These varieties could be classified into the following six classes on the basis of their seed-setting behaviour :—

1. Varieties predominantly one-seeded .. 1*, 4, 38, 39, 42 and 29.
2. Varieties predominantly two-seeded .. 9, 17, 25, 53, 57, 64.
3. Varieties with three-seeded pods .. 47 and 58.
4. Varieties with three and four-seeded pods .. 76, 82, 83, 84.
5. Varieties with a relatively low number of empty pods .. .. .. 12, 60, 61, 73, 74.
6. Varieties with a relatively high number of empty pods .. .. .. 3, 13, 20, 22, 30.

A maximum of two hundred pods of a fair size were collected from ten randomly selected plants of each variety. They were of all ages but the distinction between the developing and aborted ovules was clear.

III. Variation in the Production of Ovules

The variation in the number of ovules per pod which was observed, is given in Table I. The maximum number of ovules found in a pod is four (with but one exception where five ovules were found) but this is not common. Two-ovule pods are the most numerous; three-ovule pods are also common but pods with a single ovule are rare. All variations in the number of ovules per pod may be found within the same variety, but the proportion in which the different ovule groups occur is evidently a varietal characteristic. Some varieties show a predominance of one particular ovule group while in others another ovule group may be more common, *e.g.*, varieties numbers 82, 83 and 84 have more than 20 per cent. of four-ovule pods, whereas in the other varieties the proportion of four-ovule pods is very low. Again, in eleven varieties, two-ovule pods form over 90 per cent. of the total.

It is interesting to note that three- and four-ovule pods are more widely distributed among the varieties than would be suspected from a study of seed setting alone. In the seed-setting studies which were conducted by us (not reported here) varieties 82, 83 and 84 gave a few four-seeded pods but the present study of ovule production shows that the four-ovule group occurs in 18 out of the 28 varieties examined. Similarly three-ovule pods were found in all the 28 varieties.

* The numbers refer to the varieties of gram bred at the Imperial Agricultural Research Institute. Thus variety 1 represents Imperial Pusa 1, and so on. They have been described by Howard, Howard and Khan (1915) and by Shaw and Khan (1931).

TABLE I
Variation in the Production of Ovules in Selected Varieties of Gram

Variety	Number of pods				Total pods	Percentage of pods			
	With 1 ovule	With 2 ovules	With 3 ovules	With 4 ovules		With 1 ovule	With 2 ovules	With 3 ovules	With 4 ovules
1	..	94	6	..	100	..	94·0	6	..
3	6	168	24	2	200	3	84·0	12	1
4	1	87	10	2	100	1	87·0	10	2
9	..	161	39	..	200	..	80·5	19·5	..
12	22	151	27	..	200	11	75·5	13·5	..
13	..	91	8	1	100	..	91·0	8·0	1
17	1	190	8	1	200	0·5	95·0	4·0	0·5
20	..	182	18	..	200	..	91·0	9·0	..
22	..	173	17	..	190	..	91·0	9·0	..
25	6	85	94	15	200	3	42·5	47·0	7·5
29	..	67	106	27	200	..	33·5	53·0	13·5
30	..	108	85	7	200	..	54·0	42·5	3·5
38	1	59	19	1	80	1·3	73·7	23·7	1·3
39	..	182	17	1	200	..	91·0	8·5	0·5
42	..	99	1	..	100	..	99·0	1·0	..
47	2	101	82	15	200	1·0	50·5	41·0	7·5
53	1	71	25	3	100	1·0	71·0	25·0	3·0
57	1	195	4	..	200	0·5	97·5	2·0	..
58	2	135	56	7	200	2·0	62·5	28·0	3·5
60	12	178	10	..	200	6·0	89·0	5	..
61	..	166	32	2	200	..	83·0	16·0	1
64	1	45	3	1	50	2·0	90·0	6·0	2·0
73	..	74	16	..	90	..	82·0	18·0	..
74	1	180	19	..	200	0·5	90·0	9·5	..
76	..	190	9	1	200	..	95·0	4·5	0·5
82	..	22	116	62	200	..	11·0	58·0	31·0
83	..	52	101	46+1*	200	..	26·0	50·5	23·5+0·5*
84	..	20	68	42	130	..	16·1	52·3	32·3
Total	57	3326	1,020	236+1	4640	1·23	71·68	21·99	5·1

* One pod had 5 ovules.

An analysis of ovule production in these varieties suggests that the latter differ in their inherent capacity to produce a high number of ovules. Only some varieties are able to produce four ovules per pod; even in these varieties the high level of ovule formation is limited to a certain proportion of the total number of pods produced.

IV. Abortion of Ovules

Many more ovules are produced than develop into seeds. The total figures for all the types are given in Table II.

TABLE II

Abortion of Ovules in Varieties of Gram

No. of varieties	No. of ovules aborted	No. of ovules set	Total No. of ovules initiated	Percentage setting	Percentage sterility
28	3,919	6,799	10,718	63·44	36·56

Taking all the varieties into consideration, only sixty-three out of a hundred ovules develop into seeds. But different varieties show different degrees of setting. The percentage setting* was found to vary from 50·4 per cent. in variety 39 to 85·9 in variety 20. This is a very wide variation and the ability to develop seed seems to be a varietal character. The four-ovule types are among the lowest setters (52–54 per cent.). Thus high ovule production does not mean high setting and hence types characterised by a high number of ovules per pod are not necessarily varieties of economic value. The so-called *Kabuli*† types are also low setters.

V. Setting in the Several Ovule Groups

The details of setting are presented in Table III.

The pods in each type were classified into two-, three- and four-ovule classes and the percentage of setting was calculated for each class. In some varieties the number of three- and four-ovule pods were too few for calculation of percentages. The percentage of setting is highest in the two-ovule group. It is less in the three-ovule group and least in the four-ovule group. Percentage setting in the one-ovule group was not calculated, the numbers being too few.

* Kadam *et al* (1938) noted that the average setting in about twenty types of gram studied by them was about 53 per cent.

† We are informed by Dr. B. B. Mundkur, member of the Agricultural Delegation that visited Afghanistan in 1939, that gram is not grown anywhere around Kabul. The only area where it is grown on a small scale in Afghanistan is in the Laghman and Jalalabad valleys between the Sulaiman Mountains and the Hindukush Range.

TABLE III

Comparative Setting in the 2-, 3- and 4-Ovule Groups and in all the Pod Groups Combined

Variety	Total No. of ovules	% setting in all groups	% setting in the 2-ovule pods	% setting in the 3-ovule pods	% setting in the 4-ovule pods
1	206	58·73	59·57	50·0*	..
3	422	52·61	55·37	37·50	37·50*
4	213	62·44	64·37	56·70	37·50*
9	439	65·37	67·70	59·70	..
12	405	67·66	69·20	53·09	..
13	210	80·95	82·96	66·70*	75·00*
17	409	70·66	70·26	75·00	75·00*
20	418	85·88	87·10	77·70	..
22	397	72·54	73·69	65·92	..
25	518	60·61	70·60	58·16	40·00
29	560	55·18	66·42	53·46	46·30
30	499	64·54	74·99	56·85	53·67*
38	180	57·66	64·40	52·62	50·00 *
39	419	50·36	51·93	39·21	50·00*
42	201	55·22	55·55	33·30*	..
47	510	63·52	69·79	60·98	52·84
53	230	68·26	75·36	57·33	40·67*
57	403	72·95	73·58	50·00*	..
58	468	59·19	63·33	54·17	46·41*
60	398	62·05	62·90	46·67	..
61	436	67·20	70·49	56·23	62·50*
64	104	67·30	68·90	55·56*	50·00*
73	196	64·79	70·94	46·67	..
74	418	69·85	70·55	64·91	..
76	411	76·50	79·21	66·67*	50·00
82	640	52·81	72·73	55·75	45·15
83	596	62·85	66·34	52·16	46·56
84	412	54·24	75·00	57·85	45·83

* Based on less than 30 ovules.

In the four-ovule group it is usually below 50 per cent. There is thus a far greater waste of plant material in the three- and four-ovule classes. The two-ovule pods even among the four-ovule varieties like 82, 83 and 84 show a high percentage of setting (66-79 per cent.). Within the two-ovule group there is great variation, being 51·9 per cent. in variety 39 and 87·1 in variety 20. Considering the setting in all the groups, wide variations have been found, ranging from 50·4 in variety 39 to 85·9 in variety 20.

VI. Abortion in Relation to the Position of the Ovule in the Pod

In the pod the ovules are arranged in a linear fashion one below the other. The ovule nearest the stigmatic end has been referred to in this study as the topmost or first ovule, the one below being the second ovule, and so on. The abortion of ovules in relation to the position occupied by them in the pod was studied and the results are given below.

The two-ovule group.—It is not always that both the ovules in a pod develop into seeds. Out of 3,326 pods examined only in 1,270 or 38 per cent. of the cases did both the ovules develop. In nine cases both the ovules failed to develop. In general, only one of the ovules develops, the other being aborted. In all the varieties combined there were, 2,047 pods of the two-ovule group in which only one of the two ovules had developed. Of these, in 942 pods the first ovule and in 1,105 pods the second ovule was aborted. The first position therefore appears to be slightly more favourable. Studying the varieties individually it was found that in eight the abortion at the first ovule position was greater and in three varieties the abortion was equal in the two positions. The distribution of the fertile ovule in two-ovule pods is perhaps really at random.

The three-ovule group.—There were 1,020 pods in this group.

In the case of these three-ovule pods, the third or the bottommost position is definitely at a disadavantage. The abortion in each position, in all the types combined, is as follows:—

Abortion in first ovular position	..	324
Abortion in second ovular position	..	348
Abortion in third ovular position	..	673
Total number of aborted ovules	..	1,345

Abortion thus appears to be nearly equally distributed in the first two positions, but the third position definitely predisposes to abortion. It may be noted in passing that in 58 pods or nearly 6 per cent. of the pods, it was only the third ovule that developed, to the exclusion of the first two. In 94 pods all the three ovules were found to have developed.

The four-ovule group.—The number of pods belonging to this group was only 236 and these were restricted in their distribution. Out of a possible 944 ovules only 435 or 46 per cent. developed and 509 failed to mature. The 509 undeveloped ovules in this group were distributed as follows :—

Abortion of first ovule	88
Abortion of second ovule	92
Abortion of third ovule	148
Abortion of fourth ovule	181
Total number of aborted ovules ..	509

In the matter of abortion the first and second ovules seem to fall into one group and the third and fourth ovules into another. The fall in fertility from the first to the second ovular position is almost imperceptible but from the second to the third is sudden and from the third to the fourth is only somewhat less so.

VII. *Discussion*

Ovule Production and Setting.—In this investigation an attempt has been made to study the factors influencing seed production and to examine the variations in the production of ovules which ultimately make up yield. Ovule mortality has been shown to be a very important factor which is significant in yield studies. Though four seeds per pod may theoretically be expected this is seldom realised in practice, and only about 60 per cent. of the ovules develop into seeds. Varietal differences have been found in ovule production. Increased production of ovules is however no indication of better setting and in fact the processes of production of ovules and their development into seeds appear to show an inverse relation, as shown in Table IV.

Harris (1913) also found an inverse ratio between ovule production and seed production in *Phaseolus vulgaris.*

A small number of ovules in the pod seems to favour better development. Taking the two-ovule group, we find in each variety wide variation ranging from 51·9 in variety 39 to 87·1 in variety 20 which suggests the existence of genetic factors. The present study reveals that there are two separate phenomena—the production of ovules, the capacity to develop them into seeds—which are probably genetic in basis.

The position of the fertile ovule.—Woodworth (1930) working on abortive seeds in soybeans found that the tip seed rather than the basal one has the better chance of development and concludes that seed development " may

TABLE IV

Percentage of Setting in Different Varieties of Gram

Group	Variety	Average No. of ovules per pod	Percentage of setting
4-ovule pods	29	2·8	55·18
	82	3·2	52·81
	83	3·0	52·85
	84	3·2	54·24
Many 3-ovule pods	25	2·6	60·61
	47	2·6	63·52
2-ovule pods only about 75 per cent.	12	2·0	67·66
	38	2·3	57·66
	53	2·3	68·26
	58	2·3	59·19
2-ovule pods above 90 per cent.	17	2·0	70·66
	20	2·1	85·88
	22	2·1	72·54
	42	2·0	55·22
	57	2·0	72·95
	76	2·1	76·50

be the expression of a general principle of reproductive development prevailing in plants". He does not consider nutrition to be the primary factor concerned in these differences. In the case of gram also the available evidence indicates the greater fertility of the tip ovules. In Table V the figures for

TABLE V

Position of the Aborting Ovule in Different Ovule Groups

Ovule group	Number of pods in which				Total No. of pods in the group
	The 1st ovule is aborted	The 2nd ovule is aborted	The 3rd ovule is aborted	The 4th ovule is aborted	
2	951	1,114	..	..	3,326
	*29**	*34*	..	..	
3	324	348	673	..	1,020
	32	*34*	*66*	..	
4	88	92	148	181	236
	37	*39*	*63*	*77*	

* The figures in italics give the percentage of pods with aborted ovules.

the number of pods in which the ovule is aborted in each position are summarised.

The ovules at the first two positions seem to stand an equal chance of fertilization. The diminution in fertility from the second to the third ovule position is sudden. The third ovule is infertile in 66 per cent. of the pods in the three-ovule group and 63 per cent. of the pods in the four-ovule pods. The fourth ovule is infertile in 77 per cent. of the pods. There is thus apparent a gradual decline in fertility from the first to the fourth ovular position. But the first two positions are more nearly alike and stand in the same class. The two lower ovule positions form another group.

Sterility, though greater in the lower positions, is by no means confined to them. There is considerable sterility in the first two positions. In the three-ovule group, in 5·7 per cent. of the cases (58 out of 1,020) only the third ovule develops, to the exclusion of the first two, and in the four-ovule pods, 11 per cent. of the pods (26 out of 236) show sterility of the first two positions.

Factors governing different growth rates of pollen tubes may be present, but this does not appear likely as in many cases ovules in the lower position develop to the exclusion of those in the first position. It is possible that " feeble incompatibility" factors may operate bringing about the abortion of ovules before or after fertilization.

Suppression of ovules.—The varietal differences in ovule production strongly suggest the operation of a genetic tendency for the gradual reduction in the number of ovules per pod. Though four ovules are not rare and three ovules are common, two ovules are the rule and the working out of this principle of reduction is further illustrated by the occasional production of one-ovuled pods.

Thompson (1929) has shown from a study of vasculation that this (reduction) is a phylogenetic tendency exhibited by the *Leguminosæ* as a whole. He has, in particular, drawn attention to the low ovule production in the family. Thus, out of 400 genera examined, there is but a single ovule in 28 genera while in 101 other genera, which includes *Cicer*, there are 1, 2 or few ovules. He concludes that " the gynaecium is unstable in both legume number and fertility".

Ovule abortion.—There are two aspects to this tendency for sterilisation; one is the complete elimination of ovules, the other is their abortion. The one represents the complete working out of the other tendency.

It is difficult to suggest an explanation for the failure of these ovules to develop. Defective pollen tube growth does not appear to be a reason. Though fertility is far less in the lower positions, the fact that in some cases only the ovules at the lower positions develop eliminates the possibility of defective pollen tube growth being the factor concerned.

Bradbury (1929), Dorsey (1919), Tukey (1933 and 1936) and Harrold (1935) studied ovular abortion in the stone fruits. They conclude that there is an abortion of the embryo or the embryo-sac and this is accompanied by a lack of proper nutrition. This explains *how* the failure of development comes about but not *why*. Martin (1915) attributes the abortion of ovules in alfalfa " to the fact that a few ovules monopolise the food supply". If it is merely a question of competition, either the lower ovules, which are nearer the sources of nutrition must develop, or the first ovule which is nearest the stigma and which may be expected to be fertilised first and thus get a start over the others must develop. The facts of ovule abortion do not support this. There are many cases of first ovule abortion and abortion in the lower positions is the greatest. Lack of nutrition as a probable explanation of ovule mortality has not been favoured by many investigators. Cooper *et al* (1937) studying ovule mortality in alfalfa agree with Kraus (1915) and consider that " the failure of conduction is the result rather than the cause of the failure of the growth of these parts". This is also in keeping with the known processes of vascular development of the leguminous carpel, where the greater part of the conducting tissue of the legume is laid down after, and in response to, fertilisation (Thompson, 1929). Maheswari (1931) thinks that the degeneration which commonly occurs in the embryo-sacs of *Albizzia lebbek* bears no causal relation to the nutritional disturbances but represents an inherent tendency. Mangelsdorf (1926) has shown that to obtain normal seed in maize 18 dominant factors must be present. Woodworth (1930) also concludes that the occurrence of abortive seeds in soybeans is largely a genetic problem.

In the case of gram, the failure to develop all the ovules appears to be the expression of a type of self-incompatability known as " reduced seed production". Our data do not permit any theorising but the known facts of ovule abortion support the view that it is fundamentally genetic in nature, though environmental factors also come into play.

VIII. Summary

1. The number of ovules per pod varies from one to four, and is a varietal character.

2. There appears to be a tendency in this crop plant for a gradual reduction in the number of ovules per pod.

3. All the ovules do not develop into seeds and the capacity to develop the ovules into seeds also varies considerably. It is higher in some varieties than in others. It is also higher in the two-ovule pods than in the three- and four-ovule pods.

4. Varieties which produce a larger number of ovules per pod are not necessarily those which set a high proportion of seeds.

5. The two ovules nearest to the stigma stand a better chance of development than those at the third and fourth positions.

6. It is suggested that the production of ovules as well as the capacity to develop them into seeds is due primarily to inherent causes, and, as such, is capable of genetic elucidation.

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