Mutations in *Pisum*

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(With 5 Textfigures)

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INTRODUCTION

In 1925 the writer (4, pp. 450—453) summarized the literature on mutations in *Pisum*. Some of the variations, described by several investigators, leave some doubt as to whether really mutation had occurred. Others, however, are most probably mutations. More recently Delwiche and Renard (1) ascribed two variations to mutation: the "pitcher-leaved variation" which was lethal and an "emerald chenille mutation". About the occurrence of the characteristic "sterile" Sverdrup (3, p. 226) states that it ". . . appeared in 1914 in a crop of the variety Duke of Albany . . . ". It may be that this is another instance of mutation, but this possibility was not discussed by the author.

During nine years of genetic investigations in *Pisum* the present writer observed a number of variations, not due to environmental factors. Some of them were shown to be caused by spontaneous crossing (6, pp. 353—357; 7, pp. 244—248), a few, however, were caused by mutation. One of these was described before (7, p. 243), the others will be dealt with in the present paper.

THREE OR MORE FLOWERS PER PEDUNCLE

By far the most varieties of *Pisum* have either 1, 1—2 or 2 flowers per peduncle. A few varieties are known which have 3 or 4, seldom 5 or even 6 flowers per peduncle. There is a clear distinction between varieties having 1 or 2 flowers and those having 3 or more. Vilmorin found a monofactorial difference between the two characters mentioned, 3 or more being recessive. There may be, however, a rather great modification and plants belonging to the recessive class may possess more peduncles with 1 or 2 flowers than with 3 or more. For literature see 4, p. 411.

In 1923 the writer crossed the two varieties "Mangetout tardif à cosse jaune" and "Pois sans parchemin beurre" — kindly sent to him by Mr. A. MEUNISSIER at Verrières-le-Buisson, France — with the primary object to study pod membrane. The cross-number is 8. Pedegree cultures of the parental lines together with the F_2 results pointed out that the Pois sans parchemin beurre was not homozygous with regard to some of the pod characters. Therefore the study of these characters in the cross in question was not continued and the study of the whole cross would have been dropped, had not F_2-plants appeared with 3 or more flowers per peduncle. The progenies of the two F_1-plants segregated as indicated in table I.

Table I

F_2-group	1—2 fl. p. ped.	3 or more fl. p. ped.
8—1	33	13
8—2	22	3
total F_2	55	16
expected acc. to 3 : 1	(53·25)	(17·75)

None of the parental varieties nor their pedegrees had more than 2 flowers per peduncle and Mr. A. MEUNISSIER informed me that in the ancestry of the two varieties the character "3 or more flowers" had never occurred. On account of the F_2-segregation according to a 3 : 1 scheme the occurrence of triplets cannot be explained by ascribing it to the effect of crossing. However, the number of F_2-individuals was small and therefore an F_3 was grown to see whether the monofactorial difference would be confirmed.

Out of 13 recessive F_2-plants 9 bred true, the remaining 4 breeding true with a few exceptional plants which in F_4 gave families consisting of plants with for a great part peduncles with 2 flowers; every F_4 plant, however, had at least one peduncle with 3 flowers. Out of 15 F_2-plants with the dominant character 5 bred true and 10 segregated in the ratio 115 : 44 with an expectation of (119·25) : (39·75).

These results confirm the monofactorial character of the segregation. However, the results with the recessive character suggest the action of one or more modifying factors. Some lines with a tendency to form an average of 4 flowers per peduncle were selected. Others gave a high frequency of 2 flowers per peduncle. Five or 6 flowers were only observed in the former lines. The monofactorial difference is therefore the difference between "never 3 flowers" and "at least partly 3 or more

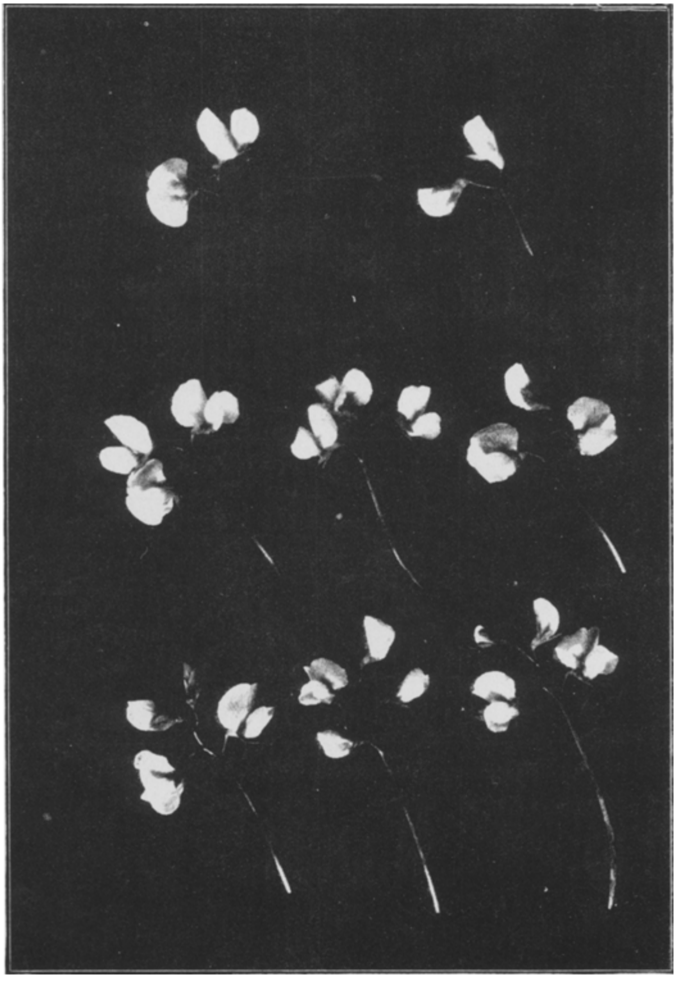

Fig. 1. Top-row: Typical inflorescences of parents of cross 8. Second and third row: Inflorescences of lines appeared in the progeny of cross 8

flowers". Plants of the latter type may have a larger or smaller percentage of double or single inflorescences.

In fig. 1 the parental inflorescences are pictured on the top row, some of the segregated types are shown on the two next rows.

We cannot explain the occurrence of 3 or more flowers per peduncle in this cross but by mutation. Evidently the two F_1-plants were heterozygous for the character in question and the mutation may therefore have taken place in the F_1-plants. It sounds more plausible, however, that one of the parents has formed mutated gametes: the seeds from which the F_1-plants arose, came from one and the same crossing. If this hypothesis is correct, it is nothing but accidental that the mutation has been observed in a cross.

A DOMINANT BUD-MUTATION OF A MEMBRANE-FACTOR

The strongly developed sclerenchymatous membrane at the innerside of the pod-wall, as found in the greater part of the varieties of *Pisum*, is determined by the presence of two factors, symbolized by *P* and *V*. In the absence of both factors there is no membrane at all. According to RASMUSSON (2, pp. 46—58) absence of *P* in the presence of *V* gives a stripe of rather strong membrane along each seam, especially along the dorsal one. WELLENSIEK (6, pp. 341—342) observed that *P* alone gives a thin membrane covering the whole innerside of the pod-wall. This was confirmed by RASMUSSON. *PPVV*-types have smooth pods which are unedible, the other three types have inflated edible pods and are "sugar-peas".

In 1922 the F_2 was grown of a cross $PPVV \times PPvv$ which, in accordance with the above theory, consisted of 75% strong membranous plants and 25% thin membranous plants. The monofactorial character of the segregation was confirmed in F_3. The cross in question is cross 4, as described before (5, p. 26). The recessive *PPvv*-type which was already constant in 1923, bred true in 1924. In 1925, however, one plant out of a family of 30 showed a remarkable variation in so far as it had both smooth pods and constricted ones. As fig. 2 shows, the two lower branches had constricted pods only, the main branch — second from the right on the picture — had smooth pods only, while the second-from-the-left branch had one constricted and for the rest smooth pods. The last mentioned branch is enlarged in fig. 3. I draw the attention to the fact that the differences in question are very clear and that classification is done without the least difficulty.

The seeds of each individual pod were harvested separately. The progeny consisted of 130 plants and contained all three classes: smooth-podded plants, constricted-podded plants and mosaic ones like the mother.

The following table II gives the detailed results, wherein the right branch of fig. 2 is indicated as I, the left one as II, the second from the left as III and the second from the right as IV; furthermore "smooth" stands

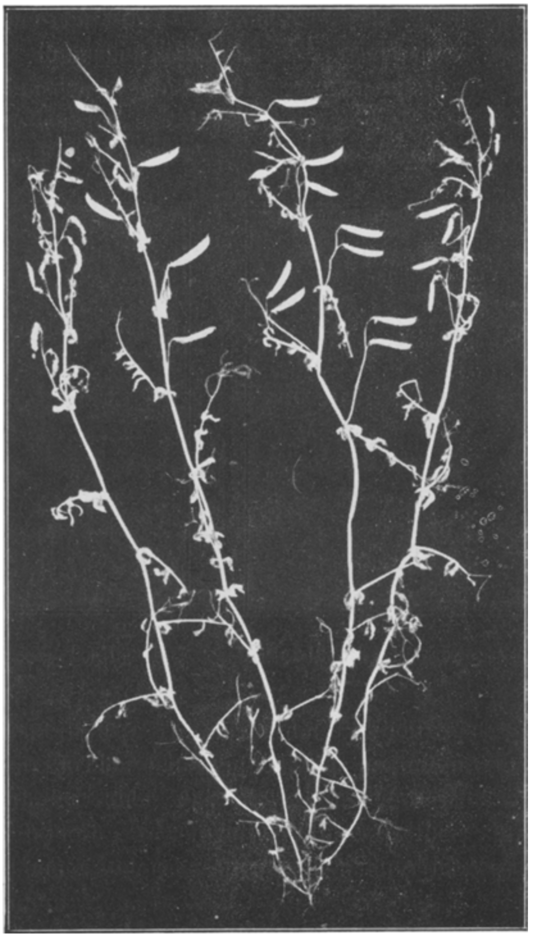

Fig. 2. Mosaic plant with both smooth and constricted pods, appeared in a pure line with constricted pods

for "smooth-podded plants" and "constricted" for "constricted-podded plants".

We see from this table that there is no evident relation between the type of pod and its progeny. The offspring of some representatives of the three types in the 1926-material was grown in 1927 and gave the results, put together in table III.

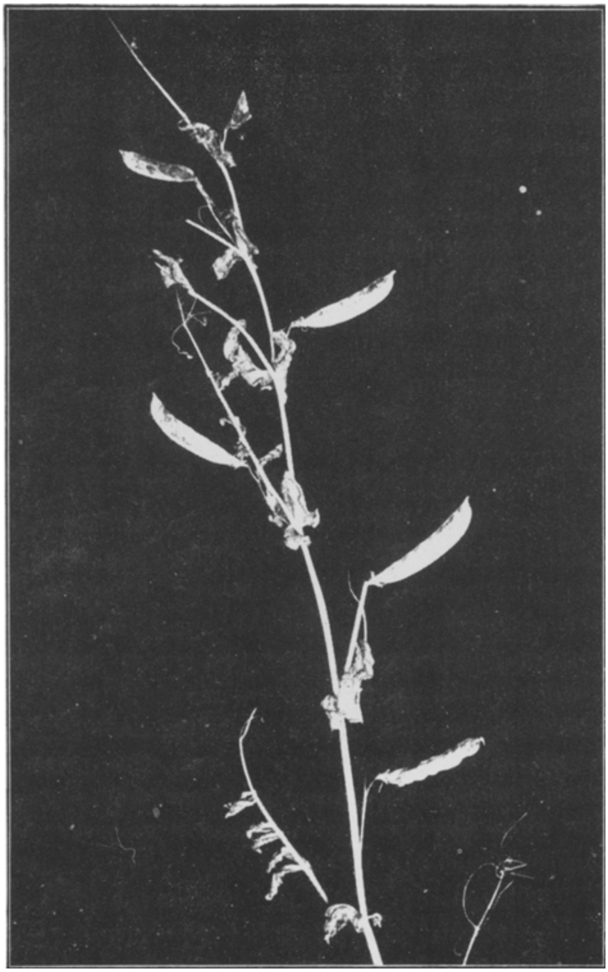

Fig. 3. Part of fig. 2 enlarged, showing constricted and smooth pods on one branch

We see that in 1927 the relative number of "smooth" plants has increased as compared with 1926, both among the progenies of smooth pods and of constricted ones. No constant "smooth" lines had appeared yet, however. In 1928 progenies were grown of 8 "smooth" plants and

Table II

Progeny of	"smooth"	"constricted"	"mosaic"
I, 8 constricted pods	2	29	2
II, 8 " "	1	24	2
III, 1 " "	0	3	0
III, 4 smooth pods[1])	0	19	0
IV, 11 " "[1])	4	37	7
total	7	112	11

[1]) 1 pod did not yield seed.

Table III

Progeny of	"smooth"	"constricted"	"mosaic"
4 "smooth" plants	0	11	0
	17	24	0
	2	15	0
	15	50	0
total	34	100	0
2 "constricted" plants	21	21	0
	3	28	0
total	24	49	0
4 groups of smooth pods from mosaic plants	1	20	0
	18	29	0
	13	14	0
	20	22	0
total	52	85	0
4 groups of constricted pods from mosaic plants, corresponding to the 4 former groups	10	30	0
	1	4	0
	6	33	0
	15	12	1
total	32	79	1

of the one mosaic plant, all belonging to the family which in 1927 contained the relatively largest number of "smooth" plants. Four of the "smooth" plants bred true; the numbers in these groups are 40, 56, 45, 50. The other 4 segregated in "smooth" and "constricted" in the ratios 35 : 3; 27 : 5; 33 : 14; 22 : 8; with a total of 117 : 30. The third mentioned line had 1 mosaic plant.

The smooth pods of the mosaic plant yielded 25 "smooth" : 37 "constricted" plants, the constricted pods of same gave 20 "smooth": 12 "constricted" : 1 mosaic plant. An inflorescence of this mosaic plant, containing a smooth and a constricted pod, is pictured in fig. 4.

When we exclude the offspring of the mosaic plant, the above figures suggest a monohybrid Mendelian ratio. The ratio of true breeding to segregating lines of 4 : 4 would have been expected to be (2·7): (5·3). The ratio in the segregating lines of 117 : 30 corresponds to an expectation of (110·25) : (36·75). However, the family, from which the group in question has arisen, must also have consisted of 75 % "smooth": 25 % "constricted" plants, if there would have been a simple Mendelian segregation. Actually it consisted of 35 "smooth" : 34 "constricted": 1 mosaic plant, while it was the offspring of a mosaic plant itself. Therefore we cannot decide with certainty how the constant lines have arisen, but the fact that they were found is important enough.

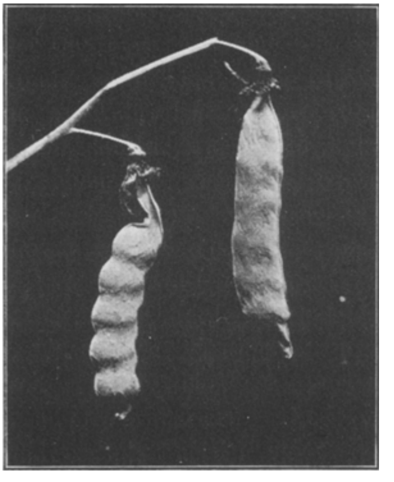

Fig. 4. Smooth and constricted pod on one peduncle of a mosaic plant

Summarizing, we see that after three years of selection from a mosaic plant which had appeared in a pure line, some lines have been obtained, differing from the original line in the possession of a dominant character. Consequently the original mosaic plant must have been a dominant bud-mutation, in which factor v has changed into V.

No regularity could be detected as to the character of the pods of the bud-mutation and of their offspring. Therefore some mutated gametes must have occurred in unchanged vegetative parts of the plant and mutated vegetative parts must partly have given rise to unchanged gametes. When all mosaic plants in the offspring of the original bud-mutation are again bud-mutations, there has been a rather high frequency of change. This would suggest that factor v is rather unstable and a support for this hypothesis is formed by the following observation.

"Reuzenboterpeul" is a variety of the genotype *PPvv*. In 1927 a pure line of this variety had been under observation for 6 years, during which period it had kept perfectly constant. In the year mentioned, however, one plant had pods with a strong membrane. The progeny consisted of 24 plants which all had smooth pods with a strong membrane. At the left of fig. 5 part of a normal Reuzenboterpeul-pod is pictured; at the right, part of the smooth type of pod with a strong membrane is shown. Spontaneous crossing cannot have caused the variation, because no segregation occurred and, moreover, spontaneous crossing is highly improbable, because the original line is characterized by two striking recessive characters, namely strongly curved pods with a very thick pod-wall. These characters reappeared typically in the new line with smooth pods. Therefore mutation is evident in this case also and it is remarkable that, although the mutation is dominant, it was immediately constant. The mutated factor is the same in this case as in the bud-mutation.

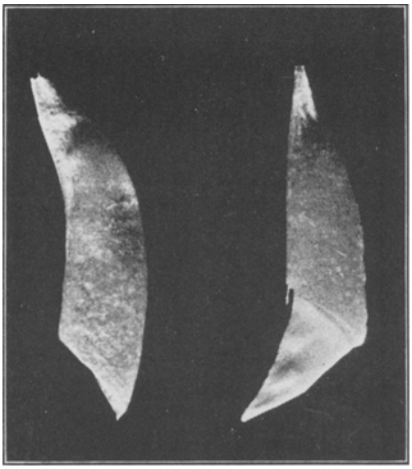

Fig. 5. Left: Pod of "Reuzenboterpeul" with unvisable thin membrane Right: Pod with strong membrane, occurred in "Reuzenboterpeul"

Mr. A. R. ZWAAN, the breeder of the Reuzenboterpeul, informed me that it is rather hard to keep the variety free from smooth-podded plants. If these are caused by mutation like in the cases described above, perpetuated selection will be necessary to keep the variety constant.

Finally I draw attention to MEUNISSIER's statement (see 4, p. 452) that he often found plants bearing both smooth and constricted pods. Evidently he did not enter into a detailed study of these plants, however.

SUMMARY

Two mutations in *Pisum* are described:

1. The occurrence of "three or more flowers per peduncle", which is a recessive character.

2. The occurrence of constant lines with the dominant character "smooth pods", found in the progeny of a mosaic plant which had both smooth and constricted pods and which itself has arisen in a pure line with constricted pods.

Additional Note. After this paper had gone to the press, my attention was drawn to KAZNOWSKI's publication "Studja nad grochem (*Pisum* L.)", appeared in Mém. Inst. nat. Polonais d'écon. rurale 7 p. A, 1926: 1—91, in which paper three cases of mutation in *Pisum* are described (cp. pp. 81—84, 91).

Wageningen, Oct. 31, 1928

Literature cited

1. DELWICHE, E. J. and EARL RENARD, Mutations in the Pea. J. Her. **17**, 1926: 105—106.
2. RASMUSSON, J., Genetically changed linkage values in *Pisum*. Hereditas **10**, 1927: 1—152.
3. SVERDRUP, ASLAUG, Linkage and independent inheritance in *Pisum sativum*. J. Gen. **17**, 1927: 221—251.
4. WELLENSIEK, S. J., Genetic monograph on *Pisum*. Bibliographia Genetica **2**, 1925: 343—476.
5. WELLENSIEK, S. J., *Pisum*-Crosses I. Genetica **7**, 1925: 1—64.
6. WELLENSIEK, S. J., *Pisum*-Crosses II. Genetica **7**, 1925: 337—364.
7. WELLENSIEK, S. J., *Pisum*-Crosses III. Genetica **11**, 1928: 225—256.