INHERITANCE AND LINKAGE DATA OF SOME CHARACTERS IN PEAS (*PISUM SATIVUM*)*

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(With Plate 2)

Descriptions of six mutants in peas (*Pisum sativum*) and the data available on their inheritance and linkage relations are presented herein. The first mutant was obtained from a seed company; the other five were harvested from experimental plots and increase fields grown at the Washington Agricultural Experiment Station, Pullman, Washington.

Screwball

Screwball, a true-breeding recessive mutant, appeared in the Alderman variety of peas at the Pea Breeding Station of Associated Seed Growers, then located at Hamilton, Montana. Screwball plants are dwarf with crinkled leaves which are more rigid than normal. The surface of the leaves is dull and lustreless, and may be covered with a whitish bloom. A screwball plant is shown in Pl. 2. All plants in Pl. 2 were grown in the field and were 5 weeks old when photographed.

Two F_2 seedling populations from normal × screwball crosses segregated 310 normal and 121 screwball plants. χ^2 for goodness of fit to a 3:1 ratio was 2·16 ($P=0{\cdot}14$). This indicates that the inheritance of screwball is governed by a single gene pair, which is herein designated by the symbol **Sb sb**. Because screwball plants are dwarf, they are more subject to environmental adversities than are normal plants. Thus, counts made when the plants are mature often exhibit an increased ratio of normal to screwball phenotypes. For this reason the above segregation ratio includes only those counts made in the seedling stage. Seedling counts also were made in segregating F_3 lines of two crosses with the result of 2313 normal and 629 screwball plants. χ^2 for goodness of fit to a 3:1 ratio was 20·56, $P=6\times10^{-6}$. Data were available on the germination of one of these two crosses. Germination was 71 % among 1396 seeds of the homozygous normal F_3 lines and 62 % among 471 seeds of homozygous screwball F_3 lines. Thus differential germination of the various classes of seed may be the explanation for the deficiency of screwball plants in the segregating F_3 lines.

Linkage of **sb** for screwball with the gene pair **I i** for cotyledon colour was found in 1947. The gene **I** for yellow cotyledons is dominant to the gene **i** for green cotyledons. Since cotyledon colour is determined by the genetic constitution of the embryo, the F_2 phenotypes occur among the seed produced on the F_1 plant. Screwball plants can be easily distinguished in the seedling stage, so it was relatively easy to study the linkage relations of **sb** and **i**, since F_3 data could be obtained without growing the F_3 plants to maturity. Linkage data were obtained each year from 1947 through 1950, and include F_2 data from six and F_3 data from two crosses. Counts made on F_3 lines segregating for both gene pairs in the coupling phase are included with the F_2 data in Table 1.

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A recombination value of 11·6 ± 0·5 % was calculated by Fisher's scoring method (Kramer & Burnham, 1947) from the combined data. A heterogeneity χ^2 of 8·57 for 5 degrees of freedom ($P = 0·10–0·20$) indicated that the data could be considered homogeneous and hence suitable for combining.

The gene **d** for absence of colour in the leaf axil has been reported to be linked with **i** with about 43 % recombination (Winge, 1936; Rosen, 1944). The gene **D** exhibits an effect only in the presence of the gene **A**, a basic gene for anthocyanin. The strain No. 677 with the genotype **A A d d i i Sb Sb** was obtained from Dr Herbert Lamprecht of

Table 1. *Data on the linkage of* **sb** *and* **i**

F_2 data

	Coupling phase		Repulsion phase	
	I	**i**	**I**	**i**
Sb	2847	207	230	116
sb	187	671	95	4

F_3 data, coupling phase

	I I	**I i**	**i i**
Sb Sb	75	18	1
Sb sb	28	134* 3†	18
sb sb	2	14	

* Genes in coupling phase in F_2 plants.
† Genes in repulsion phase in F_2 plants.

Table 2. *F_2 data on the linkage of* **d** *with* **i** *and* **sb**

	Factor pair		No. of plants: D		d			
Phase	Y	y	Y	y	Y	y	Sum	Percentage recombination
Coupling	**I**	**i**	139 (137·0)*	41 (43·0)	49 (51·0)	18 (16·0)	247	47 ± 4·6
Repulsion	**Sb**	**sb**	343 (336·9)	82 (88·1)	104 (110·2)	35 (28·8)	564	55 ± 3·0

* The numbers in parentheses are the number of plants expected on the basis of independent inheritance.

Table 3. *Data from repulsion crosses on the linkage of* **fa** *with* **sb** *and* **i**

	Fa Fa	**Fa fa**	**fa fa**
Sb Sb	7 (9·0)*	25 (25·4)	16 (13·5)
Sb sb	15 (13·0)	37 (36·6)	17 (19·5)

χ^2 for independence = 1·54, $P = 0·30–0·50$.

	I I	**I i**	**i i**
Fa	89 (90·8)	146 (147·1)	27 (24·1)
fa	24 (22·2)	37 (35·9)	3 (5·9)

χ^2 for independence = 2·01, $P = 0·30–0·50$.

* The numbers in parentheses are the number of plants expected on the basis of independent inheritance.

Sweden. F_2 populations of no. 677 × screwball were grown in 1949 and 1950. Those grown in 1949 segregated for **d** and **sb**, while those grown in 1950 also segregated for **i**. These data are given in Table 2.

Recombination values were calculated by the product method (Immer & Henderson, 1943). Because of the small population no definite conclusions can be drawn as to whether or not **d** and **i** are linked. The recombination percentage of 55 ± 3·0 between **d** and **sb** indicates that if **d** and **i** are on the same chromosome, **sb** may be on the opposite side of **i** from **d**.

Winge (1936) reported 44 % recombination between **i** and the **fa** gene for fasciated stem. Data obtained on the linkage of **fa** with **sb** and **i** are given in Table 3. Screwball plants were not classified for **fa** because it was difficult to do so accurately. **sb** and **fa** do not appear to be linked (χ^2 for independence $=1{\cdot}54$, $P=0{\cdot}30$–$0{\cdot}50$), but the population of 117 plants is too small to provide conclusive evidence. **fa** and **i** also appear to be inherited independently with a χ^2 for independence value of 2·01 ($P=0{\cdot}30$–$0{\cdot}50$) for a population 326 plants.

YELLOW-GREEN

Yellow-green seedlings are a uniform yellowish green colour when they emerge, but become greener as they grow older. Although the seedlings are easy to distinguish, particularly in the field, the older plants are often difficult to detect because they are only slightly lighter green and slightly smaller than normal plants.

Yellow-green was found among the progeny of a single Alaska plant. Of 81 plants grown from seed of this original plant, 67 were normal and 14 were yellow-green. F_1 plants of crosses between yellow-green and normal plants are normal in appearance. F_2 populations segregated 757 normal to 160 yellow-green plants. This is a poor fit to the expected 688 normals and 229 yellow-greens if the character is monofactorially inherited. A possible explanation for this discrepancy may be that all the counts were made when the plants were harvested instead of in the seedling stage. The yellow-green plants were staked or tagged as seedlings, but because they are not so vigorous nor so large as normal plants, they are more likely to be covered up or cut off during cultivation,

Table 4. *Data from coupling crosses on the linkage of* **yg** *and* **a**

F_2 data

	A	**a**
Yg	701	52
yg	29	150

F_3 data

	A A	**A a**	**a a**
Yg Yg	69	25	6
Yg yg	19	148	28
yg yg	0	6	

or overlooked at harvest. Of 277 normal F_2 plants tested in F_3, 98 were homozygous and 179 heterozygous, a good fit ($\chi^2=0{\cdot}53$, $P=0{\cdot}44$) to a 1:2 ratio. Thus it appears probable, even though the F_2 segregation is not a good fit to a 3:1 ratio, that yellow-green is governed by a single gene pair, for which **Yg yg** is the suggested symbol.

Evidence of linkage between **yg** and **a** was found in 1949. Data on the linkage of these genes were obtained from F_2 and F_3 populations and are given in Table 4.

A recombination value of $11{\cdot}2 \pm 0{\cdot}9\%$ was calculated by Fisher's scoring method as best fitting the combined data. A heterogeneity χ^2 of 11·29 for 3 degrees of freedom ($P=0{\cdot}01$) indicated the data to be somewhat heterogeneous. Most of the large χ^2 value was due to the segregation of the 34 **Yg a** F_3 lines. Six of these lines were homozygous for yellow-green which would indicate somewhat more crossing-over than did the other data.

YELLOW-GREEN 2

Yellow-green 2 appears as a normal seedling immediately after emergence. However, in approximately a week the green colour changes to yellowish green with parts of the plant sometimes almost pure yellow. As the plants grow older their foliage again becomes greener, and they mature and produce seed.

Yellow-green 2 was found in the second generation grown from Alaska seed which was irradiated with 40,000r. of X-rays. The plants breed true, and F_1 plants from crosses with normal plants are normal in appearance. Five F_2 populations grown from 721 seeds segregated 518 normal to 121 yellow-green 2 plants. On the basis of a 3:1 ratio, the ratio expected is 479:160. A test for goodness of fit gave a χ^2 value of 12·7 ($P=0{\cdot}0004$). Although there is a definite deficiency of mutants in the F_2, it appears likely that the inheritance of yellow-green 2 is governed by a single gene pair. Data given in Table 5 indicate that yellow-green 2 is inherited independently of the genes **a** and **r**.

Table 5. *F_2 data on the linkage of yellow-green 2 with* **a** *and* **r**

		No. of plants						
	Factor pair	Normal		Yellow-green 2			χ^2 for inde-	
Phase	**Y y**	**Y**	**y**	**Y**	**y**	Sum	pendence	
Coupling	**A a**	170 (173·0)*	73 (70·0)	35 (32·0)	10 (13·0)	288	†	
Repulsion	**R r**	112 (112·8)	41 (40·2)	31 (30·2)	10 (10·8)	194	0·11	0·50–0·95

* The numbers in parentheses are the number of plants expected on the basis of independent inheritance.
† Deviations are in the opposite direction from those which would be obtained if due to linkage.

Elongate

Two elongate plants were found in an F_3 line of an Idaho White × Idabelle cross. These plants are similar but not identical in appearance to the 'rabbit-ear rogues' which occur in many varieties of garden peas. The stipules and leaflets are longer and narrower than those of normal plants as shown in Pl. 2.

F_1 plants from the cross elongate × normal are normal in appearance. Elongate plants breed true. Twelve F_2 populations produced 1511 normal plants and 227 elongate plants, a significant deviation from a 3:1 ratio. Of 65 F_3 lines, 28 consisted of normal plants only and 37 segregated for normal and elongate. Significant deviations from 3:1 ratios due to

Table 6. *F_2 data on linkage of elongate with other factors*

		No. of plants						
	Factor pair	Normal		Elongate			χ^2 for inde-	
Phase	**Y y**	**Y**	**y**	**Y**	**y**	Sum	pendence	P
Coupling	**A a**	400 (405·2)*	149 (143·8)	62 (56·8)	15 (20·2)	626	†	
Repulsion	**Bl bl**	226 (232·1)	60 (53·9)	41 (34·9)	2 (8·1)	329	6·51	0·01
Repulsion	**Fa fa**	161 (162·2)	45 (43·8)	24 (22·8)	5 (6·2)	235	0·33	0·50–0·95
Repulsion	**Gp gp**	156 (156·3)	40 (39·7)	21 (20·7)	5 (5·3)	222	0·02	0·50–0·95
Repulsion	**I i**	218 (218·5)	87 (86·5)	37 (36·5)	14 (14·5)	356	0·03	0·50–0·95
Repulsion	**K k**	155 (155·2)	44 (43·8)	22 (21·8)	6 (6·2)	227	0·01	0·50–0·95
Repulsion	**R r**	265 (267·6)	118 (115·4)	48 (45·4)	17 (19·6)	448	0·58	0·30–0·50
Repulsion	**St st**	216 (212·6)	66 (69·4)	29 (32·4)	14 (10·6)	325	†	

* The numbers in parentheses are the number of plants expected on the basis of independent inheritance.
† Deviations are in the opposite direction from those which would be obtained if due to linkage.

a deficiency of recessives have been reported for numerous mutations by Gustafsson (1938) and Moh & Smith (1951). Gustafsson postulated that the aberrant segregations resulted from gametic elimination. Moh & Smith considered several mechanisms for such aberrant ratios. One was that some mutations might be the result of, or closely associated with, deficiencies or other aberrations, or possibly with pleiotropic effects that reduced the transmission of chromosomes containing the mutant genes. They pointed out that certain kinds of chromosomal aberrations could produce an excess or a deficiency of any particular genotype.

Data obtained from F_2 populations on the linkage relations of elongate with various genes are given in Table 6. Except for inconclusive evidence in the case of **bl**, elongate appears to be inherited independently of all the genes studied.

GREEN AND YELLOW

Green and yellow was found in a field of First and Best which was the fourth increase of an individual plant selection. This character is a chlorophyll deficiency in which a large part of the foliage has irregular, narrow, green and yellow stripes, with the veins yellow and the areas between the veins green. At the growing tip the leaves may be almost entirely yellow, but as the leaves grow older they approach the normal green colour.

Green and yellow produces a limited amount of seed which does not breed true. Of 73 F_1 plants grown from crosses between normal and green and yellow plants, 38 were normal and 35 green and yellow. Both normal and green and yellow F_1 plants resulted, regardless of whether the female parent was normal or green and yellow. The normal F_1 plants bred true for normal; the green and yellows segregated for normal, green and yellow, and albino. During the last four years, 603 seeds harvested from green and yellow plants have produced 228 normal, 314 green and yellow, and 21 albino plants. The normals bred true for normal, the green and yellows segregated, and the albinos died as seedlings. It appears that green and yellow may be due to a dominant mutation which is lethal when homozygous. If so, this mutation is of special interest because of the rarity of dominant mutations. As indicated above, Moh & Smith (1951) have suggested mechanisms by which deviation from a 1:2:1 ratio could be accounted for.

SHINY SPOTS

Several new mutant plants were found in an F_3 line of the cross Blackeye × screwball. This F_3 line was homozygous for the yellow cotyledons of Blackeye and segregated for screwball. The mutant character was named 'shiny spots' because of the appearance of irregular shiny areas on the leaves. The plants are dwarf with the leaves abnormally curled and bent. Shiny spots breeds true and produces normal F_1's when crossed with normal plants.

SUMMARY

Descriptions of six apparently new mutants in peas and the available data on their inheritance and linkage relations are given. Screwball is a dwarf plant with curled, crinkled leaves. Its inheritance appears to be governed by a single recessive gene, **sb**, which is linked to **i** with $11{\cdot}6 \pm 0{\cdot}5\%$ recombination.

Yellow-green plants emerge as uniform yellowish green seedlings which become greener as they grow older. The inheritance of yellow-green appears governed by a single recessive gene, **yg** which is linked to **a** with $11{\cdot}2 \pm 0{\cdot}9\%$ recombination.

Yellow-green 2 emerges as a normal seedling, but in approximately a week the green colour changes to a yellowish-green with parts of the plant sometimes almost pure yellow. Later the foliage again becomes greener. Inheritance is probably governed by a single recessive gene which appears to be inherited independently of **a** and **r**.

The mutant elongate is similar but not identical in appearance with 'rabbit-ear rogues.' Elongate plants breed true and produce normal F_1 plants when crossed with normal plants.

On the basis of a 3:1 ratio, a definite deficiency of elongate plants occurred in the F_2 populations. Elongate appears inherited independently of **a**, **fa**, **gp**, **i**, **k**, **r**, and **st**. Evidence with **bl** was inconclusive.

Green and yellow is a chlorophyll deficiency in which a large part of the foliage has irregular, narrow, green and yellow stripes. Near the growing tip leaves may be practically yellow, while older leaves are often almost entirely green. It appears that green and yellow may be due to a dominant mutation which develops a lethal white seedling when homozygous.

Shiny spots is a dwarf with the leaves abnormally curled and bent. The name arises from the small irregular spots on the leaves. This mutant breeds true and produces normal F_1 plants when crossed with normal plants.

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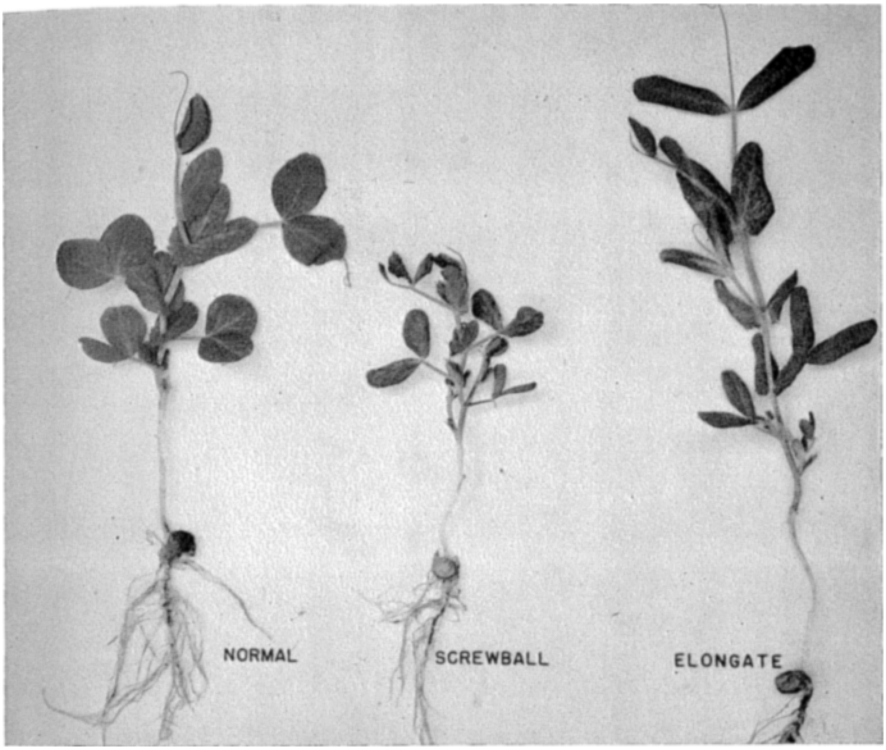
EXPLANATION OF PLATE 2

Representative normal, screwball, and elongate plants. Grown in field and photographed when five weeks old.


NORMAL
SCREWBALL
ELONGATE