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Dominance, Overdominance and Epistasis in *Pisum sativum* L.

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Summary. Dominant genes are the main cause of the heterosis induced by fasciated mutants of different lines of *Pisum sativum*. Most of these cases were originally interpreted by different authors as examples of monogenic overdominance. Several not-closely-linked genes appear to have mutated simultaneously in most of the fasciated lines. Although fasciation itself is recessive, other mutant characters, such as lateness, increased stem length (number and length of internodes) and, in part, seed production per plant, show dominant inheritance. The latter two features are, however, to a considerable extent suppressed in the fasciated lines by unfavourable gene-interactions (epistasis). Crossing these lines with non-fasciated ones shows that the epistatic genes are recessive and the dominant genes are then no longer hindered in their action. By eliminating the epistatic genes from the genomes of fasciated lines by recombination, the heterosis phenomenon has been fixed on six independent occasions for different lines. The *fasciata* genes themselves were found to be the most probable cause of these cases of recessive epistasis. The question whether different kinds of fasciation affect heterosis differently is examined. Recessive epistasis and dominance explain most of the quantitative distinctions between the different hybrids. In addition, one example of heterosis between non-fasciated lines is given and the possible meaning of the overall results for plant breeding and population genetics is mentioned.

Key words: *Pisum sativum* – Fasciation – Epistasis – Dominance of lateness, length and yield – Overdominance

Introduction

Several experimentally obtained or spontaneously arisen fasciated pea mutants cause an extraordinary strong heterosis in various vegetative and generative characters when crossed with their initial lines, other varieties or different mutants (Lamprecht 1952; Gottschalk 1970, 1976, 1977; Gottschalk and Milutinović 1973a, b). These findings were originally interpreted as cases of overdominance: on account of strongly deviating F_3-segregation, Lamprecht (1952) discussed mono- and digenic heterosis, considering a heterotic effect of the *fasciata* alleles in the heterozygous state as "almost sure". But he did not repeat this point of view in the voluminous summary of his work in 1974. Gottschalk (1970, 1976) and Milutinović (1972) suggested essentially monogenic overdominance. Again the *fasciata* genes were thought to be of major importance, but the possibility of polygenic overdominance was still considered possible by all workers in the field.

Most of the fasciated mutants used for the crosses have a rather complicated genotypic constitution: they are homozygous for up to 16 different mutant genes – of which at least 3 seem to cause different kinds of stem-fasciation. The action of most of these genes is not discernible in the fasciated forms. They are hypostatic and become effective only if the respective epistatic genes have been eliminated from the genomes (Gottschalk 1977, 1981a, b; Gottschalk and Bandel 1978).

It was therefore not possible to state *prima facie* whether the heterotic effects observed in the F_1-hybrids were due to the influence of one or several genes for fasciation or to an unknown number of other mutant genes of the fasciated parents. Neither was it clear whether the increased vigour of the hybrids was due to heterozygosity per se as it could as well have been caused by dominance of hypostatic genes of the fasciated mutants. Furthermore, a combination of the two possibilities just mentioned with positive gene interactions as defined by Fisher (1978) could have been the reason for the hybrid vigour.

In order to obtain more information and to solve the problems involved, fasciated recombinants of less

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complicated constitutions were crossed with the non-fasciated mother variety and the behaviour of the following generations, including backcrosses, was studied. The results obtained so far point to recessive epistasis of the *fasciata* genes and dominance of lateness, length and yield as the main cause of the heterotic effects in nearly all the cases studied.

Materials and Methods

Ten X-ray induced mutants of the variety 'Dippes Gelbe Viktoria' (=DGV=initial line=IL) of *Pisum sativum* and eight recombinants are considered in the present paper. In addition, one non-fasciated and three fasciated mutants of other collections, as well as a commercial fasciated fodder pea variety and the wild form *Pisum arvense*, were included in the investigations. The number of mutant genes (or alleles respectively) present in their genomes in relation to 'Dippes Gelbe Viktoria' is presented in the brackets following the various genotypes.

For some fasciated forms the final number may not yet have been achieved as a few genes could be closely linked and thus would have shown segregation only in a very numerous F_2 generation. On the average, 200–300 F_2 plants of each cross were evaluated in 1979–1981. The following genotypes were used:

(a) Strongly fasciated mutants: 33 A (4), 489 C (16)
(b) Linearly fasciated mutants: 123 (12), 251 A (12)
(c) Linearly fasciated recombinants:

R 661 (1): derived from 489 C × 26
R 859 (2): derived from 123 × R 46 C
R 893 (4): derived from 'Ornamenta' × R 46 C
R 875 (5): derived from 251 A × 137
R 710 (5): derived from *cochleata* 5137 × 489 C

(d) Weakly fasciated recombinants with stem bifurcation:

R 161 (1): derived from 489 C × 1201 A
R 177 (2): derived from 489 C × 1201 A (small seeds and full penetrance for stem bifurcation: homozygous for genes *sg* and *bif-1*)

(e) Non-fasciated recombinant: R 46 C (2): derived from 46 A × 1201 A (early flowering, stem bifurcation – genes *efr* and *bif-1*)

(f) Other mutants including the genotypes used for the crosses which gave rise to the recombinants:

26 (1): extremely shortened internodes
46 A (1): early flowering (gene *efr*)
137 (1): reduced chlorophyll content; chlorotica
176 A (1): reduced size of leaves, flowers, pods and grains (gene dim-1)
1001 (1): increased seed size
1201 A (1): dichotomously bifurcated stem (gene *bif-1* with unstable penetrace)

(g) Genotypes from different collections:

Non-fasciated:

- The *cochleata* mutant with reduced stipules and certain flower anomalies from Wellensiek's collection in Wageningen (6 genes) and its initial line 'Dominant' (Wellensiek 1959, 1962)

Strongly fasciated:

- The commercial fodder pea variety 'Ornamenta' developed by means of a spontaneous fasciated mutant (Scheibe 1965; Gottschalk and Bandel 1978; Gottschalk 1981a; 14 genes)
- Mutant I/74, II/87, and VI/10 with 4, 4, and 7 mutant genes in relation to 'Dippes Gelbe Viktoria' respectively; from Vasileva's collection in Sofia, and their mother varieties 'Ramonski', 'Raman' and 'Urojaini'.

(h) *Pisum arvense* (no F_2-segregations studied as yet). The material was obtained from the Botanical Garden Tübingen.

Realistic diagrams of the relationships were difficult to obtain. Due to a lack of space, most of the recombinants derived from the heterotic hybrids had to be grown on an ecologically different field: on Venusberg (Bonn) all the mean values were shifted in favour of DGV, which showed 117.49% height and 233.02% seed number in 1979 compared to the mean values of DGV (=100%) on the experimental field in Bonn, Carl-Troll-Straße (5 control groups on each field). For height the extreme ratio of 100:134.51 was found 1980. To compensate such differences, hybrids and recombinants with 200% height of DGV at Carl-Troll-Straße would have to show about 270% height of the mother variety from that field (and even higher values for seed production per plant) to reach the same ratio on Venusberg, which was not the case.

We have, nevertheless, given the real comparative values of each field respectively and then added the approximate relative values in dotted lines for Carl-Troll-Straße, where most of the F_1's had grown. Basis were the relations found between DGV, 489 C, and 489 C × DGV, from which lines and hybrids we had extensive materials on both experimental fields. The solid lines have to be substracted for Venusberg in Figs. 3 and 4. Although no clear gene-ecological differences can be given at present for most of the different lines and hybrids, the dotted lines seem to convey a more realistic picture in several cases than the comparative values given. According to all experiences made on both fields, there is also an advantage: the principle proved to be the same under the different ecological conditions.

So far some 15,500 plants have been investigated for this project (more than 40 different F_1 hybrid stocks with double repetition of a few outstanding cases and segregation and selection from F_2 to F_5 – including backcrosses and their segregations). For developing the pure recombinant lines, Gottschalk had already spent many years of study and selection of several thousand plants before this work started. A part of my studies is presented in the following text.

Results

(a) Flowering and Ripening Period

Nearly all the fasciated mutants and recombinants causing heterosis in plant height and seed production were delayed in flowering and ripening, usually about 5 to 10 days. The only exception from this rule was the fasciated recombinant R 710 which was some 5 days earlier than 'Dippes Gelbe Viktoria'. For yet unknown reasons this is the only case where the acceleration also showed dominant inheritance. Heterosis in height and yield was still strong in the hybrids, but lowered in comparison to the late lines (Figs. 3, 4). In general, we got several transgressive recombinants in the F_4,

derived from crosses with late forms which were as early in flowering and ripening as DGV, so that the F_1-heterosis phenomenon could largely be fixed in non-late lines (see, for example, the long recombinants derived from 489 C×DGV and 251 A×DGV in Figs. 3, 4). Yet none of the hybrids and/or recombinants was earlier than its better parental form. Thus, no heterosis was achieved in this character.

(b) Stem-Fasciation

At least three, possibly four different kinds of stem fasciation are available in our Pisum material which appear to be caused by different *fasciata* genes of a polymeric group. Representatives of three kinds of fasciation were crossed with non-fasciated genotypes in order to solve the question whether the heterosis-phenomenon observed in former crosses was really due to heterozygosity in the *fasciata* alleles.

Among them were the mutants 33 A, II/87, and the recombinants R 161, R 661, R 859 and R 893 (Figs. 3, 4). The respective F_1-hybrids did not show heterosis. R 177 did not induce heterosis in height and its increased number of seeds per plant is largerly a compensation of the reduced seed size. The mutants and recombinants represent all three kinds of fasciation. Moreover, some very small (short II/III, see below), non-fasciated recombinants proved to be heterozygous, segregating even smaller, fasciated lines in the following generations. These small types had given no hint of heterosis. Strongly fasciated forms normally inducing hybrid vigour when crossed with their mother line did not induce heterosis when crossed with homozygous lines already as tall as the heterotic hybrids. And, eventually, F_3-segregation results (see below) after selection of the tallest and most vigorous F_2-plants were contrary to all expectations possible on the hypotheses that the heterosis was induced by heterozygosity in *fasciata* genes. It is to be concluded from these findings that the *fasciata* genes studied so far are neither the cause of the heterosis observed in distinct crosses nor do they contribute to it. Thus, we have to look for a different genetic mechanism for interpreting our findings.

(c) Plant Height

In nearly all cases where a pronounced heterosis effect occurred in the material, the mean number and length of internodes of the fasciated genotypes were increased in comparison with the mother variety 'Dippes Gelbe Viktoria' (first measurements by Milutinović 1972). A characteristic feature of the strongly fasciated genotypes is, however, a specific growth anomaly (Fig. 1). The upper internodes are extremely shortened and the distance between the nodes is generally rather irregular in all the fasciated forms: Several nodes are only a few millimeters apart and some internodes seem to be simply skipped so that one could imagine the length of these internodes is longer in the F_1 as a result of the action of alleles for normal stem growth contributed by DGV. But fasciation itself implies an increase in the number of leaves and flowers, and the overall increase in these features cannot necessarily be equated with missing internodes due to growth disturbance (details last published by Grupe 1956). It is, nevertheless, interesting that the fasciated mutants inducing heterosis usually show a few very long interstitial internodes which are just as long as the longest (middle) internodes of the heterotic F_1 plants (Table 1; Fig. 2). Fasciated forms not causing heterosis did not show this character. No anomalies are observed in the F_1 hybrids derived from crosses between fasciated and non-fasciated genotypes. The *fasciata* genes are recessive and an undisturbed development of the internodes is possible under the influence of the dominant alleles of the initial line or other normal lines.

As pointed out above, at least two different hypotheses could be invoked for the elongation and increased number of the internodes in the heterotic F_1 hybrids: heterozygosity *per se* (the *fasciata* genes are

Fig. 1. **Fig. 2.**

Figs. 1 and 2. 1 Growth anomaly of a strongly fasciated mutant. The reproductive organs are concentrated at the end of the stem. The upper part of the stem is broadened, the distances between the internodes irregular and the number of the leaves increased. **2** From left to right: Mutant VI/10, DGV, and F_1 Mutant VI/10×DGV. The mutant already shows a few very long internodes (arrows). It appears that fasciation hinders the full growth as we find it in the F_1 by shortening the upper part of the stem

Table 1. Examples for mean length of the longest internodes in cm (and %) of the initial line 'Dippes Gelbe Viktoria' (Venusberg 1980)

Compare figure				
	Mutant 489 C and recombinant R 875 cause heterosis	DGV	10.10 cm	(100%)
		489 C	15.06 cm	(149.11%)
		F_1 489 C × DGV	15.53 cm	(153.76%)
		Tall recombinant (from 489 C × DGV)	14.54 cm	(143.96%)
		R 875	14.51 cm	(143.66%)
		Tall recombinant (from R 875 × 1001)	15.21 cm	(150.59%)
	Recombinants do not cause heterosis	R 661	10.13 cm	(100.30%)
		R 161	9.45 cm	(93.56%)
		R 177	11.12 cm	(110.10%)

already excluded from this possibility) or dominance of genes for plant height hypostatic to other mutant genes in the respective *fasciata* lines. The answer was given by homozygous non-fasciated recombinants derived from crosses between fasciated genotypes and 'Dippes Gelbe Viktoria' which were exactly as tall as the F_1 hybrids (Fig. 3), and which proved to be fully dominant over the shorter initial line (details under subheading selection).

As different degrees of hybrid vigour depend on different *fasciata* lines, there can be no doubt that the respective genes for increased plant height in the hybrids and recombinations are derived from the fasciated parents of these crosses. Yet they cannot express their full action there so that the plants of the fasciated mutants are considerably shorter than those of the hybrids and of the long-stemmed non-fasciated recombinants. This is understandable only if we assume the presence of a group of epi- and hypostatic genes in the genomes of the fasciated mutants. The genes for long internodes just mentioned are suppressed in their action to a considerable extent by other mutant genes. The latter ones are epistatic to the former ones; moreover, they are recessive to the corresponding alleles of the initial line.

Thus, the findings obtained become understandable by assuming a case of recessive epistasis, for which the *fasciata* genes are the most likely candidates because:

(1) As already mentioned, the *fasciata* alleles cause growth anomalies shortening several internodes (but never elongating them in comparison with the tall recombinants).

(2) Heterozygotes segregating in nothing but one fasciata gene are as tall as the related non-fasciated homozygous lines, but the fasciated lines are shorter.

(3) Originally tall lines are shortened by fasciation.

(4) Length of fasciated forms is more labile under different climatic conditions (sometimes manifesting different kinds of stem fasciation) than that of long non-fasciated recombinants (Gottschalk and Kaul, 1975, 1980). This was essentially repeated in a test with heterotic hybrids and their tall recombinants in relation to the fasciated line under at least

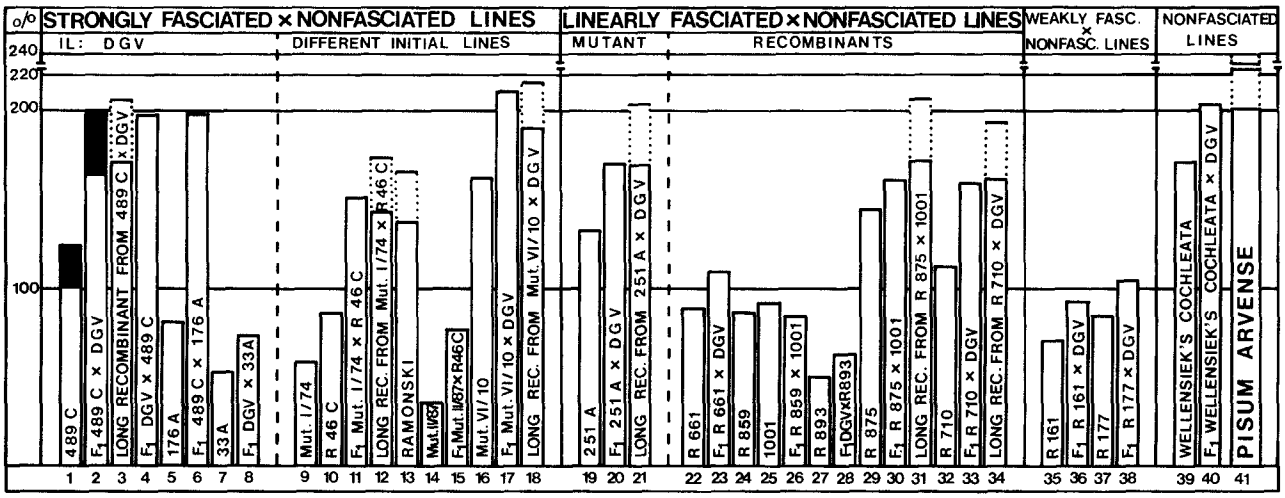

Fig. 3. Height of different *Pisum* lines, hybrids, and recombinants in per cent of DGV. For explanations of black and dotted lines see materials and methods

three different climatic conditions (phytotron, growth chamber, greenhouse and experimental fields, Bonn).

(5) The other genes segregating from hybrids of the cross 489 C×DGV and others do not, as far as is known, cause the above mentioned features in the presence of the genes for long internodes.

There can be no doubt, then, that the *fasciata* genes affect length negatively (see also Lamprecht 1974, p. 315). We cannot, however, exclude at present additional epistatic gene-interactions between, perhaps, the *fasciata* genes and other mutant genes in the fasciated lines.

The result of dominant inheritance in the polygenic characters of increased number and length of internodes is in agreement with the findings obtained by other authors such as Mendel (1866), Keeble and Pellew (1910) and Lamprecht (1974). According to Lamprecht certain tall lines were even overdominant in length. The author mentions slight overdominance wherever heterozygosity for the gene pair Le/le for plant height occurred, a point which we, however, could not yet establish.

(d) Seed Production

The average increase in number of seeds per plant seems to be the most spectacular feature in the heterotic F_1 hybrids (Fig. 4). Even if one considers that the thousand grain weight is often reduced by about 20%, an overall increase for the character "seed weight per plant" up to 200% of the control values of 'Dippes Gelbe Viktoria' is a remarkable result.

As seed production is a feature resulting from many components, we tried to genetically analyze the most important ones for our problem:

(1) Number of fertile nodes (including first fertile node and average internode length. There are interactions between the latter two features and seed production – timing of hormone concentrations in different plant parts and shading of leaves being involved).

(2) Number of fertile branches (with fertile nodes as above).

(3) Number of pods per plant (normally sum total of the number of fertile nodes×2).

(4) Seeds per pod with sum total of seeds.

(5) Grain size.

Gene interactions and recombination including dominant, intermediate, and/or recessive inheritance of the different components for seed production is to be expected, free recombination somewhere reaching its physiological limits.

The number of fertile nodes was raised in the hybrids (the main stem as well as the number of fertile branches being involved). DGV showed a mean number of 24.04 internodes (always counted from the first node of the primary leaves) and – to take one important example – F_1 489 C×DGV had 29.11 internodes – about the same number as several recombinants derived from these and other hybrids. One cannot, however, simply add five fertile nodes for the hybrid, because the first fertile node in the IL was the 14^{th} whereas in the hybrid it was the 19^{th} (always ± 1; this is a very constant feature). The mean number of fertile nodes of the main stem was 8.15 in the IL and 9.95 in

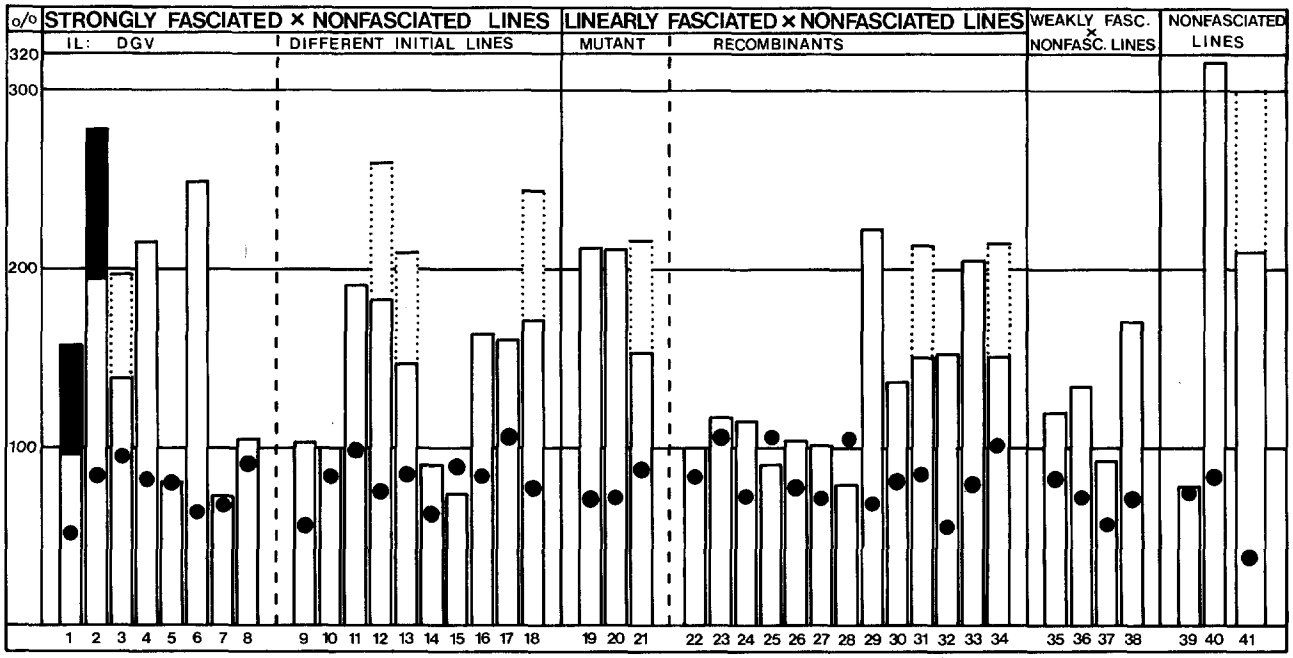

Fig. 4. Seeds per plant (□) and thousand-grain-weight (●) in per cent of DGV. For explanation of the solid and dotted lines see materials and methods. No marked differences were found in the thousand-grain-weight of the same lines on different fields. For identification of the different lines and hybrids compare serial numbers of Fig. 3

the hybrid. In the IL normal development of pods was evidently not possible on all its nodes above the first fertile one. The mean number of fertile branches was 0.85 (IL) and 2.26 (hybrid), the average number of pods per branch being 3.47 and 5.98 respectively. Lateness in flowering and ripening was dominant, because in the hybrids the higher number of sterile nodes (late parent) was dominant over the one with the lower number (early parent) (compare H. and O. Tedin, 1923). It was possible to raise the number of fertile nodes in recombinants having about the same number as the tall hybrids, but with the fourteenth node being the first fertile one. So in this feature the heterotic hybrids were even surpassed by some recombinants with 11–13 fertile nodes on the main stem.

Seed production depends partly on the number of fertile nodes and well-developed internodes. High number and long internodes are dominant over small number and short internodes. Both the dominant characters are present in a hypostatic state in many fasciated lines (see above). Thus raised seed production is partly inherited dominantly in the hybrids in correlation with these characters. The number of seeds per pod was some 20% higher in the hybrids than in the IL compensating the lowered TGW which latter showed intermediate inheritance. Details in Fig. 4.

So far a study of branching, a feature very easily influenced by environmental factors (Lamprecht 1950, 1974), showed contradictory results. In 1980, recombinants showed the same type of increased branching as the best heterotic F_1's. In 1981 the latter surpassed the former in one case. Heterozygosity in certain gene pairs and/or special gene interactions in the hybrids cannot yet be fully excluded for this character. Moreover, the question whether the findings obtained are exclusively due to nuclear genetic components or whether extranuclear factors are also involved in the same case may be raised:

Reciprocal crosses of 'Dippes Gelbe Viktoria' × mutant 489 C and mutant 489 C × 'Dippes Gelbe Viktoria' led in former investigations to differences in the seed production of the hybrids (Milutinović 1972) though not in height. The new results agree with these findings. But for a final analysis reciprocal crosses should be repeated with more extensive material.

(e) Segregation

F_2-segregation after crossing fasciated with non-fasciated genotypes is generally rather complicated: As quoted above, in several fasciated mutants causing heterosis, up to 16 genes seem to have mutated simultaneously (Gottschalk 1977, 1981a). A few of them are dominant, but most of them have mutated to the recessive state. Tables showing segregations of different crosses have been published several times (Gottschalk/Milutinović 1973b; Bandel and Gottschalk 1978b; Lönnig 1980) so that the following example of a cross with a fasciated recombinant of less complicated genetic constitution may suffice to convey a notion of the problems involved.

F_2 R 875 × 1001 phenotype	
– very tall	143
– tall, linearly fasciated	34
– tall, linearly fasciated, bifurcated	5
– IL	2
– short I (about half as long as the IL)	26
– short I, linearly fasciated	6
– short I, linearly fasciated, bifurcated	1
– 1001	6
	223

Segregation in F_3, comprising another 316 plants, added 'tall bifurcated' and 'short II' (about a quarter as long as the IL). Two families (each the descendants of one selected F_2-plant) of a further 57 plants consisted of tall ones only.

A simple 3 : 1 segregation in F_2 for height is prevented by the following facts:

(1) hypostasis of short I/II/III

(2) interactions between the genes for height and the different alleles for fasciation, single or in combination

(3) recombination of number and length of internodes (Lamprecht 1974).

In case of dominance of the tall, non-fasciated lines we would, nevertheless, expect a clear majority of these forms in relation to the others (as demonstrated above). This has been found in almost all cases comprising thousands of plants.

On the other hand, there were no tall plants in all the segregations of fasciated mutants and recombinants not causing heterosis, which would not be self-evident if this feature were recessive as short I/II and III.

(f) Selection and Further Segregations

The majority of tall plants of our F_2-families had already led to the hypothesis that dominant genes hypostatic in fasciated mutants would be one important cause of the heterosis observed (Lönnig 1980). Provided that only a few not-closely-linked genes were involved, recurrent selection could be expected to yield the following results:

(1) Homozygous recombinants derived from heterotic F_1 hybrids showing the same increased number and length of internodes as the F_1 as well as increased number of seeds per plant.

(2) Such lines when crossed with DGV would show dominance for height and seed production.

Table 2. Number of F_3-families with the ratios of the different segregation groups

F_3	Numbers of families	Segregation in fasciated and non-fasciated forms	Only non-fasciated plants, segregation in long and short ones	Only tall non-fasciated plants
R 875 × 1001	10	7	1	2
489 C × IL	9	5	2	2
251 A × IL	12	6	4	2
R 710 × IL	12	6	3	3
Bul I × 46 C	6	5	1	0
Bul VI × DGV	13	9	2	2
	62	38	13	11

We always chose the tallest and vegetatively and generatively the best developed F_2 plant, which gave the following F_3 results:

The ratio of the families segregating fasciated plants to the rest is 1.58 : 1 (38 : 24). But if any of the *fasciata* alleles in a heterozygote state were responsible for the visible hybrid vigour, all the F_3 families (62 : 0) should have segregated fasciated plants. Assuming a simple 3 : 1 F_2-segregation of the non-fasciated to fasciated plants (which is in agreement with the overall results obtained) ⅔ of the non-fasciated F_2-plants should be heterozygous for the *fasciata* alleles and the ratio of F_3-families segregating fasciated lines to the rest should be 2 : 1.

Even when we admit that the situation is sometimes more complicated (Lamprecht 1952, 1974; Marx and Hagedorn 1962; Gottschalk 1981a; Hartmann 1981, p. 136 ff.) as yet none of these complications detracts from the conclusion that the above results contradict the hypothesis of overdominant heterozygous fasciata alleles. Moreover all the families segregating in tall and normal height plants show a 3 : 1 segregation, already proving that the tall lines are dominant over the IL.

Nevertheless, to be as sure as possible in this case and as further segregation of other genes was to be expected, we raised 20 F_4-families of R 875 × 1001 and 28 F_4-families of 489 C × IL. The result was that only one of these families (of R 875 × 1001) continued to segregate fasciated plants. All the other 1600 plants were tall. There was, however, in several families recombination in internode number, so that we got differences of about 40 cm between tall and taller lines. Moreover, recombination of genes for flowering and ripening time (at least four different genes for the first fertile node), seed size (obviously polygenic), and branching occurred. In the backcrosses with the IL the superior number and length of the internodes proved to be dominant with a clear segregation of 3 long to 1 short in the following generation. Besides, selection of the smallest non-fasciated F_2/F_3 plants should have eliminated further segregation of fasciated lines. This was not the case.

(g) The Different Kinds of Fasciation in Relation to Heterosis

As long as the *fasciata* alleles themselves were thought to induce heterosis, different effects of the different alleles and/or polymeric genes was a reasonable hypothesis. Now the results have shown that the hybrid vigour depends mainly on the hypostatic dominant genes of the different *fasciata* lines. Additional proof for this was that the differences between the different F_1-hybrids have largely been fixed in homozygous recombinant lines. Conversely, given the same dominant genes for height, the fasciated lines may be affected very differently by the different types of fasciation, but the F_1 and the recombinants show all about the same height. Sometimes, however, there are special gene-interactions in the hybrids which are eliminated in certain recombinants derived from them. But they have nothing to do with fasciation. For example F_1 R 710 × IL was smaller than F_1 489 C × IL, but certain F_3-recombinants of the former reached the height of the latter. As pointed out above F_1 R 710 × IL was about 15 days earlier than F_1 489 C × IL, earliness affecting height to a certain degree. Recombinants as late as the IL proved to be longer than the hybrid F_1 R 710 × IL so that in this case, too, certain features of the F_1-hybrids were surpassed by recombination as it was with the number of fertile nodes in recombinants derived from the cross 489 C × IL and others. Again it must be stressed that certain features of the hybrids and their recombinants may be affected differently by environmental factors as different soils, water supplies and temperature.

(h) Comparison Between DGV, the Long Recombinants and Pisum arvense

Compared with 'Dippes Gelbe Viktoria' some of the mutant dominant genes hypostatic in many fasciated lines may be classified as positive from a selectionist

point of view: F_1-plants and recombinants are taller and more fruitful than the mother variety, on the whole appearing more vigorous than the latter. All the wild forms of the pea are genetically tall (Lamprecht 1974) and on the breeder's program for many generations there has been selection for short lines in order to do away with fences or other expensive devices. The result: dwarf plants with short internodes in zigzag-fashion. "Tall (*Le*/-) and dwarf (*Le*/*le*) (White, 1917) peas are distinguished mainly by alternate alleles at the *Le* locus on chromosome 4" (Marx 1977). Several features as height, lateness and seed number per plant strongly remind one of *Pisum arvense* (Figs. 3, 4) from which many of our cultured lines are derived. There are, however, also striking differences as colour of flowers and seeds and seed size which latter is very small in most wild forms. Nevertheless, back- and/or supressor-mutations of *le*/*le* and/or other loci are evidently involved in the revertant features.

(i) Heterosis in Combination with Non-fasciated Genotypes

In the examples discussed, heterosis occurred after having used fasciated mutants as one of the partners of the crosses. Similar results were obtained by using the neutron-induced *cochleata* mutant of Wellensiek's collection. The *cochleata* gene reduces the stipules to spoon-like organs. The plants are also thinner and a bit shorter than their IL. Furthermore the marked flower anomaly associated with this mutant sharply decreases the number of seeds per plant. In the F_1 of *coch* × 'Dippes Gelbe Viktoria', the negative influence of the recessive cochleata gene is eliminated by the normal allele of 'Dippes Gelbe Viktoria' and the dominant alleles for extraordinary plant height and seed production present in the genome of the cochleata mutant in a hypostatic state result in heterosis in F_1 (Figs. 3, 4). The cross was repeated once and corroborated the earlier results. Further evidence: (1) the IL of this *cochleata* mutant, Wellensiek's "Dominant" (unknown to the author when he began studying the first hybrids described above) as well as the F_1 Dominant × DGV compare in height and seed production with the hybrid *cochleata* × DGV. (2) Some non-segregating F_3-families of *cochleata* × DGV show height and seed production comparable with Dominant, including recombination abilities as shown above for 489 C × DGV. (3) In relation to DGV flowering and ripening was delayed in the hybrids. (4) After selecting of the best F_2-plants, F_3 ratio of families segregating *cochleata* plants to the rest was exactly 2 : 1 and thus in complete agreement with the conclusion that the *cochleata* alleles do not take part in the heterosis observed.

The difference between heterosis in this case and that induced by fasciated mutants seems to be simple: One IL, Wellensiek's Dominant, already possesses the dominant genes whose action is partly suppressed by the *coch* gene of the mutant. In our fasciated mutants the respective genes have mutated to the dominant state. But in both cases the full expression of the dominant genes is hindered by deleterious recessives and up to now no heterozygosity per se could be proved to be involved.

Moreover, a completely analogous case to the *cochleata* mutant was found in the mutant I/74 of Vasileva's collection. Its parental line 'Ramonski' is taller and better yielding than DGV, which characters are partly suppressed in the fasciated form. When the latter was crossed with DGV, the F_1 was superior to both parents (Figs. 3, 4) and through recombination the superior characters could be regained. According to all experience so far, the same holds true for further cases in which originally tall lines of different collections received one or more of the mutant *fasciata* genes.

Discussion

The above examples of heterosis caused by fasciated mutants and the revision of its original interpretation by further research may show how difficult it often is to decide the question whether dominance or overdominance is the basis of a case in question.

Beginning with Mendel (1866) up to Marx and Hagedorn (1962, there extensive literature) all the authors with the exception of Lamprecht (1952) came to the conclusion that "fasciation in *Pisum* is conditioned by a monofactorial recessive" (Marx and Hagedorn 1962, p. 42), although the latter authors already discussed the possibility of a system of modifiers "affecting the phenotypic expression in the presence of the major gene" (p. 40). Segregation studied by Milutinović (1972) and Gottschalk and Milutinović (1973 b) set forth certain cases in which about half of the F_2-individuals corresponded with the F_1 in length and seeds per plant. The hypothesis of monogenic heterosis, therefore, did not seem to be unjustified. Although several mutant genes of the fasciated lines were already known at the beginning of the 1970s, during the last 10 years it has become gradually evident how complicated many of the fasciated mutants really are (Gottschalk 1981 a). A system of epi- and hypostatic genes is involved and now the fact has been established that some hypostatic genes are dominant in relation to the initial line. Negative gene interactions between different mutant genes in the same line hinder the full expression of the positive dominant factors.

The above results agree with the theoretical suppositions and the examples given by Mather and Jinks (1971), Sinha and Khanna (1975), Simmonds (1979) and others, and may shed further light on the controversy about which of the different possible causes of heterosis is generally the most efficient (details Shull 1948; Fischer 1978; Lönnig 1980).

If dominance and epistasis are the main causes of heterosis in general, this would have tremendous im-

plications for plant breeding and population genetics. As for plant breeding nearly all the programs for maintaining heterozygous stocks would be only an expediency as long as it is not possible to combine the positive dominant genes in a homozygous line,' which would be the final aim. Concerning population genetics Muller (1950), Muller and Falk (1961), Falk (1961), Kimura (1968, 1979), Ohta (1976), and Latter (1981), to mention but a few authors, would be correct with their critique of the importance of overdominance as viewed by Wallace (1958), Ford (1965), Ayala (1978) and others – with far reaching consequences for the mutation concept, including its applicability to human populations.

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Note Added in Proof

During the vegetation period of 1982 it was possible to reinvestigate some of the recombinants on the first experimental field (see materials and methods). Extrapolation for length and yield was found to be correct for the following recombinants (Figs. 3 and 4):

Recombinant	Length		Seeds per plant	
	Expected	Found	Expected	Found
F_5 489 C × DGV	205.21%	214.30%	197.17%	194.72%
F_4 Mut VI/10 × DGV	215.36%	226.19%	243.80%	240.50%
F_5 R 875 × 1001	205.93%	207.23%	213.29%	212.63%

It was not found to be correct for the one recombinant derived from 251 A × DGV. Special gene-ecological reactions may be involved here. Length is, nevertheless, still better than in F_1 251 A × DGV (F_1: 169.49%; recombinant: 179.55%). All the recombinants thus show that superior hybrid length has nothing to do with heterozygosity per se. Although the situation for seed production per plant as a highly polygenic trait is more complicated than for plant height, the data obtained corroborate the same conclusion for yield.