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Interspecific hybridization between *Sesbania aculeata* Pers. (4n race) and *S. speciosa* Taub. ex Engler (2n race) and cause of failure of viable seed-formation

By R. M. DATTA and S. K. SEN

With 8 Figures

Introduction

Sesbania aculeata is a suffruticose annual shrub yielding a strong durable useful fibre (WATT 1908). It is recommended as a good green manuring crop (MUKHERJEE and AGARWAL 1950; F. A. O. Ag. St. 1953).

Sesbania speciosa is a large tree-like annual shrub, being a native of South Africa. It is an ideal green-manure crop as well as a cattle fodder (ANANTA KRISHNA RAO 1957, F. A. O. Ag. St. 1953).

Usefulness of both of them is detailed in a previous communication (DANA and DATTA, in press). Both these species are recommended as ideal green manuring crops (F. A. O. Ag. St. 1953). Each has got the capabilities to grow under adverse conditions and has got a certain number of desirable agronomic characters, which, when combined, are expected to yield better results in our agriculture. These authors further observed inter alia after studying the karyotypic differences:

„Thus *S. aculeata* and *S. speciosa* differ greatly from each other from the points of view of chromosome size and number. All these differences are sufficient to account for the differences in their specific behaviours. But the types of chromosomes are almost similar in the both species. This indicates a close phylogenitic relationship between them.

From these observations it can be concluded that the work of hybridization in these two species has got enough possibilities to be success."

The somatic chromosome number of *Sesbania aculeata* Pers. (4n race) is found to be 24 ($2L^s + + 2L + 6M + 14S$). This confirms the previous record of HAQUE (1946). KAWAKAMI (1930), however, recorded 16 as the haploid number in this species and later on RAO (1946) recorded the somatic chromosome number as 12. The somatic chromosome number of *S. speciosa* Taub. ex Engler is found to be 12 ($2L^s + 4M + 6S$). Due to their suggestive phylogenetic relationships the reciprocal crossings were undertaken in 1958 to see if they cross successfully.

Materials and Methods

The plants of *Sesbania aculeata* and *S. speciosa* were grown in rows in the fields of the Department of Agriculture, Calcutta University at 35, Ballygunge Circular Road, Calcutta — 19.

The flowers of *S. aculeata* (4n race) remain open from 2^{30} P. M. to 5^{00} P. M. I. S. T., while those of *S. speciosa* (2n race) do so from 1^{30} P. M. to 4^{00} P. M. I. S. T. (I. S. T. = Indian Standard Time).

Flowers of the respective species were carefully emasculated in the previous afternoon with a finely pointed loose sterile forceps and bagged with cellophane paper bags. In the next noon the bags are removed and after carefully pollinating the emasculated flowers with the pollen from the desired parents, they were immediately bagged and labelled.

One week after pollinations the bags were removed and record was taken as to which the flowers had set pods or fallen in the bag. Every set pod was checked individually, while they are continuing to grow or had fallen off. In these crosses, the number of flowers pollinated, number of pods set, and harvested were recorded. The cross pods were harvested after their full maturity. Seeds were extracted pod-wise. They were then classified as non-full and full seeds and their percentages were calculated. Full seeds, when obtained, were weighed and compared with the weight of the same number of seeds of their female parents taken randomly from the bulked selfed seeds.

Notes were taken from the date of pollination to maturity of the pods both in the self-and cross-pollinations; comparative measurements were taken of the mean length of the seed bearing regions of the pods and seed: husk ratios were taken.

For studying preliminary cytogenetical aspects 10 (ten) cross pods (from each group) were fixed in NAVASHIN's fixative at 1 and 3 days.

They were then dehydrated in ethyl alcohol series and the paraffin schedule was followed.

Sections were cut at 10—12 μ thick and stained in HEIDENHAIN's haematoxylin to see the details of the fertilization processes.

Observations

After crossing 56 flowers of *S. speciosa* (2n race) with *S. aculeata* (4n race) the pod set was observed to be 12.5 per cent and only 57.1 per cent of the set pods remained till maturity and were harvested. In the case of *S. aculeata* ♀ × *S. speciosa* ♂, out of 49 flowers pollinated, the pod set observed to be 8.2 per cent and only 75 per cent of the set pods remained till maturity and were harvested (Table 1). In the former case 4 pods matured in 50 days after crossing

Table 1. *Summary of the reciprocal crosses between S. speciosa and S. aculeata and also of the respective parents.*

Sl. No.	Cross: Parent ♀	Cross: Parent ♂	No. of flowers pollinated	No. of pods set	% of pods set	No. of pods harvested	% of pods harvested	Nature of seeds: Non-full	Nature of seeds: Full	Percentage of seeds: Non-full	Percentage of seeds: Full
1.	*S. speciosa* 2n (61.6 mg/m)	*S. aculeata* 4n	56	7	12.5	4	57.1	62	4 (38.2 mg/m)	93.9	6.1
2.	*S. aculeata* 4n	*S. speciosa* 2n	49	4	8.2	3	75.0	25	0	100.0	0.0
3.	*S. speciosa* 2n	*S. speciosa* 2n	24	23	95.8	23	100.0	6	1144	0.9	99.1
4.	*S. aculeata* 4n	*S. aculeata* 4n	25	25	100.0	25	100.0	1	811	0.1	99.9

Table 2.

Cross: Parent ♀	Cross: Parent ♂	Mean No. of days taken from pollination to maturity	Mean length of pod (cm)	Mean length of seed bearing portion (cm)	Seed : Husk
S. speciosa 2n	*S. aculeata* 4n	49.7	11.6	9.7	12 : 9
S. aculeata 4n	*S. speciosa* 2n	46.2	11.2	10.3	3.2 : 8
S. speciosa 2n	*S. speciosa* 2n	42.3	28.6	25.2	2 : 2.3
S. aculeata 4n	*S. aculeata* 4n	42.4	22.4	21.6	1.3 : 1

(Table 2). They were smaller in size when compared to the normal of the mother parent and contained 62 non-full and 4 normal looking full seeds (Table 1). These 4 normal-looking full seeds weighed 38.2 mgm., when compared to the same number of seeds (61.6 mgm.) of the mother parent taken at random. In the latter case 3 pods matured in 47 days after crossing. They were also smaller in size when compared to the normal pod of the mother parent and contained 25 non-full seeds only (Table 1). No full seeds were obtained from them (Table 1).

It is evident from the Table 1 that 42.9 per cent of the set pods failed to reach maturity and shed during different stages of growth in case of *S. speciosa* ♀ × *S. aculeata* ♂. In case of *S. aculeata* ♀ × *S. speciosa* ♂ 25 per cent of the set pods failed to mature and shed during different stages of development.

All the seeds were separately sown in pots next year (May 1959) but they did not germinate.

The average number of ovules per pod and number of seeds per gramme of these two species when selfed are given below (Table 3) for comparative studies:

Table 3.

Species	Average number of ovules in a pod	No. of seeds per gramme
S. speciosa (2n)	41	65
S. aculeata (4n)	32	58

As the seeds were found to be of varying qualities, cytological observations were made from the cross ovaries of *S. speciosa* ♀ × *S. aculeata* ♂ fixed at 1 and 3 days. In 1 day's materials no entry of the pollen tube through the micropyle was observed and the embryosac (normal type) was found intact.

In the 3 days' materials the entry of the pollen tube into the embryosac is complete and fertilization of the egg is sometimes complete (Figs. 1 and 2) and the process of triple fusion is also seen in some cases (Fig. 4). In many instances, discharge of two sperms from the pollen tube is not complete. In the Fig. 3 one sperm is found inside the burst pollen tube and another is still unfertilized. One polar nucleus is

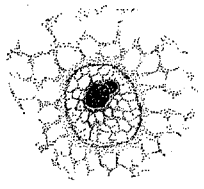

Fig. 1. An embryosac in 3 days' material of the cross *S. speciosa* ♀ × *S. aculeata* ♂ shows the fertilization is complete. (× 1650)

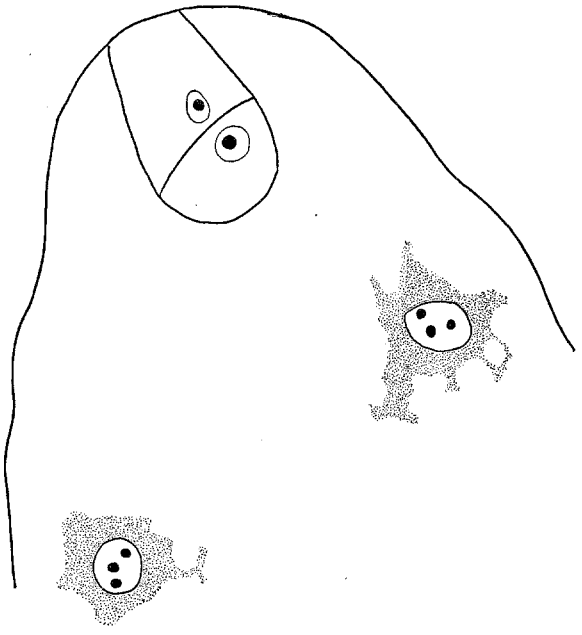

Fig. 2. An embryosac in 3 days' material of the cross *S. speciosa* ♀ × *S. aculeata* ♂ shows the two-celled proembryo and the initiation of the formation of cellular endosperm. (× 1000)

found near the egg and there is no polar fusion yet. In rare instances two-celled proembryo (Fig. 2) has been observed. Thus it appears that fertilization in this cross material is a bit slower. Formation of non-full seeds suggest that the embryo or/and endosperm has not developed properly, though nuclear endosperm nuclei, several in number, have been observed in rare cases (Fig. 5).

In the course of cytological studies of the cross ovaries of *S. aculeata* ♀ × *S. speciosa* ♂, it is observed that the pollen tube bursts by this time (3 days) and discharges the sperms inside the embryosac. In certain cases fertilization of the egg and triple fusion nucleus are observed (Figs. 6 and 7). Very rarely it has been noticed that the triple fusion nucleus divides once by this time (3 days) to form two nuclei with three nucleoli each. No further division takes place by this time as seen in the former case but two-celled proembryo was seen (Fig. 8).

It is thus evident from comparative studies that in the latter 2n sperm is much slower in fertilization and subsequent processes resulting in the formation of non-full seeds only.

Discussion

In *Galeopsis tetrahit* (x = 16) ♀ × *G. pubescens* or *speciosa* (x = 8 in both) ♂, fertilization occurs but in the reciprocal crosses it does not according to MÜNTZING (1930a). In the crosses *tetrahit* (x = 16) or *bifida* (x = 16) ♀ × *pubescens* (x = 8) or *speciosa* (x = 8) ♂, fertilization occurs but embryo and endosperm cease development at a comparatively early stage, but unfortunately no comparison can be made with the reciprocal cross which does not succeed. The seed obtained from the cross high number ♀ × low number ♂ is usually good, but it may not equal the normal and it cannot be said definitely whether the very reduced development in *Galeopsis* means that the unusual quantitative relation has a better result in the genus than in others or whether qualitative differences between the tetraploid and diploid species are responsible. Since *tetrahit* contains only P and S chromosomes, MÜNTZING (1930b) concludes that the seeds obtained by pollinating *tetrahit* with *pubescens* and *speciosa* are non-viable because the numerical relation between mother plant, endosperm, embryo, instead of being 2:3:2, is 4:5:3, which is, therefore, „eine quantitative letale Konstellation". It must, however, be realized and noted that this relation of 4:5:3 is one that produces viable seeds in many other genera and it is evident from various cases that in general it would be very difficult to predict from the quantitative relations between the three tissues concerned which would be viable and which non-viable.

THOMPSON (1930) gave data showing that a greater number of seeds was obtained from different crosses including *Brassica juncea* (x = 18) ♀ × *B. oleracea* (x = 9) ♂ than from the reciprocal. THOMPSON refers these differences to embryo and endosperm development. WATKINS (1932), in discussing this, is of opinion that since the number of seeds is involved, it seemed to him far more likely that pollen tube growth was the cause.

CHRISTOFF's (1928) and EAST's (1928) statements regarding the unbalanced development of embryo and endosperm was explained by THOMPSON (1930) as due to the pollen tube growth. This conclusion was confirmed by KOSTOFF (1930), who examined a few crosses in detail and found that while *Nicotiana rustica* (x = 24) ♀ × *N. paniculata* (x = 12) ♂ and *N. tabacum* (x = 24) ♀ × *N. glauca* (x = 12) ♂ were easily made, in the reciprocals the pollen tubes did not reach

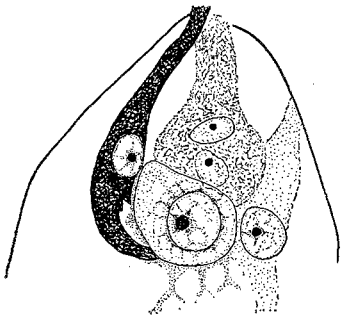

Fig. 3. An embryosac in 3 days' material of the cross *S. speciosa* ♀ × *S. aculeata* ♂ shows the burst pollen tube and the unfertilized egg and the unfused polar nuclei. (× 1650)

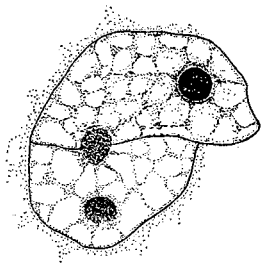

Fig. 4. An embryosac in 3 days' material of the cross *S. speciosa* ♀ × *S. aculeata* ♂ shows the process of triple fusion. (× 1650)

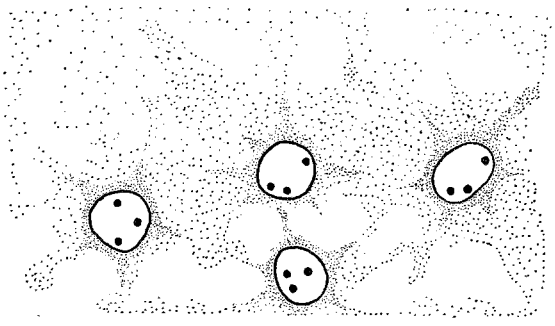

Fig. 5. Presence of nuclear endosperm in the embryosac of the 3 days' material of the cross *S. speciosa* ♀ × *S. aculeata* ♂. (× 1000)

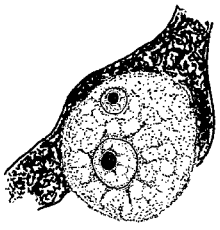

Fig. 6. An embryosac in 3 days' material of the cross *S. aculeata* ♀ × *S. speciosa* ♂ shows the process of fertilization. (× 1650)

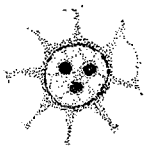

Fig. 7. An embryosac in 3 days' material of the cross *S. aculeata* ♀ × *S. speciosa* ♂ shows the process of triple fusion. (× 600)

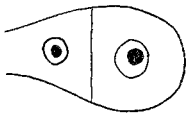

Fig. 8. An embryosac in 3 days' material of the cross *S. aculeata* ♀ × *S. speciosa* ♂ shows the two celled proembryo. (× 1000)

the ovary in the first case and only rarely did so in the second. BRIEGER (1928) observed that in the cross *N. tabacum* (x = 24) ♀ × *N. Rusbyi* (x = 12) ♂ many seeds were obtained but not so in case of its reciprocal. Further no capsules were produced in the following crosses:

(a) *N. tabacum* (x = 24) ♀ × *N. acuminata* (x = 12) ♂
(b) *N. tabacum* (x = 24) ♀ × *N. trigonophylla* (x = 12) ♂
(c) *N. tabacum* (x = 24) ♀ × *N. paniculata* (x = 12) ♂
(d) *N. bigelovii* (x = 24) ♀ × *N. trigonophylla* (x = 12) ♂
(e) *N. nudicaulis* (x = 24) ♀ × *N. paniculata* (x = 12) ♂.

The reciprocal crosses all gave capsules without viable seeds. So there is no certainty that fertilization had taken place. KOSTOFF (1930) definitely stated that in *N. paniculata* (x = 12) ♀ × *N. tabacum* (x = 24) ♂ the pollen tubes rarely reached the ovary so that growth appeared to have been retarded. It must be remembered, however, that exceptions are to be looked for, when allopolyploids were crossed.

Further irregularities can occur after the pollen tube enters the ovary, though the matter is uncertain and the evidence chiefly negative. One cannot, therefore, concentrate and proceed directly from the pollen tube growth to the problem of seed development as WATKINS (1932) suggested. Furthermore, the latter author (1932) discussed, „Besides general uncertainty there are two special difficulties:

(1) When a wide cross produces poorly developed, aborted seeds as it frequently does, we may not be able to decide, unless a cytological examination has been made, whether fertilization has failed or whether embryo, endosperm or both have aborted.

(2) We can learn most about the conditions necessary for normal seed development from exceptional case, but we have no guarantee that an exceptional seed was produced by a normal fertilization process so that its genetical constitution remains uncertain."

Both WATKINS (1932) and HOWARD (1939) had shown clearly the fundamental importance of the endosperm: zygote genome ratio in the development of viable seeds.

Later on, HOWARD (1947—48) observed that when 2n *Nasturtium officinale* ♀ × *N. uniseriatum* (4n, an allotetraploid) ♂ took place, 14 large empty seeds were obtained. In case of *N. uniseriatum* (4n) ♀ × *N. officinale* (2n) ♂, 9 small good seeds were found. In all these good development of a high percentage of ovules took place. This must have meant that pollen tube growth and fertilization plus some development of the embryo and endosperm occurred. As good seeds were produced in *N. uniseriatum* ♀ × 2n *N. officinale* ♂, the seed-results in the crossing experiments were explained by reference to endosperm: embryo relations. It is suggested that a single genome of *N. officinale* has a strength of 1.0 and a single genome of *N. uniseriatum* a strength of 1.41 for a single genome of *N. uniseriatum* is less than a strength of 2.0 which might be expected since *N. uniseriatum* is an allotetraploid, one of whose parent species is *N. officinale* (HOWARD and MANTON, 1946). This lower strength may be due to *N. uniseriatum* having evolved since its production part way to the diploid condition (cf. DARLINGTON, 1937, p 225 and also HOWARD, 1942, p 110). It might, however, be due to the strength of the other parent species of *N. uniseriatum* (this other parent is not known) having a low strength of genome for seed formation. According to him the first alternative seems more reasonable.

In case of *S. speciosa* (2n) ♀ × *S. aculeata* (4n) ♂, the numerical relation between mother plant, endosperm and embryo is 2n:4n:3n. Full seeds but less in weight when compared to normal occur and when grown they are non-viable. This ratio obviously falls outside the range as suggested by WATKINS (1932) and as such lethality can be explained.

In case of *S. aculeata* (4n) ♀ × *S. speciosa* (2n) ♂, the same relation stands as 4n:5n:3n. No full seeds are obtained. It has become lethal as MÜNTZING (1930a, b) and WATKINS (1932) suggest.

No doubt this disbalance in the quantitative ratio can explain lethality in these two cases. But, to the authors it appears that genomic differences of these two species cannot at all be ignored. Possibly, here lies the main cause of failure of seed development. Quantitative ratio may accelerate or hasten the process of lethality caused by qualitative disbalance. If these quantitative disbalance could not have been present, the qualitative difference might not have caused so drastic an effect.

Summary

In *Sesbania aculeata* Pers. ♀ × *Sesbania speciosa* Taub. ex Engler ♂, pod set was 8.2 per cent and the percentage of pod harvested (out of set pods) was 75. All seeds out of those harvested cross pods were non-viable.

In *Sesbania speciosa* Taub. ex Engler ♀ × *Sesbania aculeata* Pers. ♂, the pod set was 12.5 per cent and the percentage of pod harvested (out of set pods) was 57.1. All seeds out of those harvested pods were non-viable.

The genomic difference of the two species, *aculeata* (4n race) and *speciosa* (2n race) is the main cause of failure of seed development.

In the end we offer our sincere thanks to Dr. P. K. SEN, Khaira Professor of Agriculture and Head of the Department, Calcutta University for granting all facilites to carry out this investigation in this laboratory.

Zusammenfassung

Zwischen der tetraploiden *Sesbania aculeata* Pers. (2n = 24) und der diploiden *Sesbania speciosa* Taub. ex Engler (2n = 12) wurden experimentell Artkreuzungen durchgeführt.

49 Kreuzungen von *S. aculeata* × *S. speciosa* ergaben in 4 Fällen (8,2%) Hülsenansatz. 3 dieser Hülsen konnten geerntet werden. Sie enthielten 25 taube Samen.

Bei 56 reziproken Kreuzungen wurden 7 Hülsen angesetzt (12,5%) und 4 davon geerntet. Sie enthielten 62 taube und 4 entwickelte, aber nicht keimfähige Samen.

Es wird gefolgert, dass für den Ausfall der Samenentwicklung die Genom-Unterschiede der beiden *Sesbania*-Arten die Hauptursache darstellen.

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Aus dem Institut für Landw. Botanik der Universität Bonn

Vereinfachte Prüfung der Additivität bei Streuungszerlegungen (Varianzanalysen)

Von **F. WEILING**

Mit 1 Abbildung

Als das wohl bestbekannte stochastische Analyseverfahren darf die Streuungszerlegung gelten. Ursprünglich von R. A. FISHER für Belange des landwirtschaftlichen Ertragsversuchswesens entwickelt, ist ihre allgemeine Bedeutung schnell erkannt worden. Weniger gut sind dagegen vielfach die Voraussetzungen bekannt, unter denen die Streuungszerlegung erfolgversprechend angewendet werden kann. Die Nichtbeachtung dieser Voraussetzungen hat oft zur Folge, daß die Möglichkeiten, die die Streuungszerlegung bietet, nicht gänzlich ausgeschöpft oder gar das Verfahren als solches gelegentlich als unzulänglich betrachtet werden.

Unter den 4 Voraussetzungen für die Anwendbarkeit der Streuungszerlegung: Additivität der Einzeleffekte, Streuungsgleichheit in den verschiedenen Behandlungs- (Versuchs-)reihen, Normalität und stochastische Unabhängigkeit der Einzeldaten, nimmt die Additivität die erste und wichtigste Stelle ein, wie wohl EISENHART (1947) als erster herausgestellt hat. Die relativ späte Erkenntnis der Bedeutung der Additivität beruht darauf, daß diese die Bedingungen der Streuungsgleichheit und Normalität in gewissem Umfang umfaßt, so daß sie in vielen Fällen implicite gegeben ist. TUKEY hat 1949 für einfache und doppelte Streuungszerlegungen einen Test mitgeteilt, mit dessen Hilfe das Fehlen der Additivität geprüft werden kann. Auf eine Anregung SNEDECORS hin hat er 1955 eine allgemeine Form dieses Testes angegeben und sie an einem „lateinischen Quadrat" demonstriert. Dieser Test beruht im wesentlichen darauf, daß von dem bei der Streuungszerlegung sich ergebenden „Fehler" die durch die Abweichung vom additiven Modell sich ergebende Summe von Abweichungsquadraten (ΣAQ) mit einem Freiheitsgrad abgezogen und gegen den alsdann verbleibenden Rest getestet wird. Leider ist die Durchführung dieses Testes selbst in seiner einfachen Form recht umständlich und bei größerem Umfang der Versuchsdaten erheblich aufwendiger als die eigentliche Streuungszerlegung. Dies mag, abgesehen davon, daß dieser Test bisher wenig bekannt ist (eine eingehende Darstellung siehe bei SNEDECOR, 5. Aufl. 1956), die Ursache dafür sein, daß er bisher wenig angewendet wird. Bei der Bedeutung, die der Streuungszerlegung im landwirtschaftlichen und nicht zuletzt im züchterischen Versuchswesen zukommt, seien daher für den Fall einer einfachen und doppelten Streuungszerlegung eine Vereinfachung des Testverfahrens dargestellt, sowie für den Fall einer mehrfachen Streuungs. zerlegung gewisse Gesichtspunkte mitgeteilt, die di Beurteilung der Additivität zu erleichtern vermögene

1. Das Testverfahren im Falle einer einfachen und doppelten Streuungszerlegung

Dieses Testverfahren sei zunächst in der von TUKEY angegebenen und von SNEDECOR übernommenen Form an einem kurzen Beispiel soweit dargestellt, wie es zum Verständnis der Vereinfachung erforderlich ist.

Beispiel: Beurteilung der Zahl der Univalente in den Pollenmutterzellen (PMZ) dreier F_1-Artbastarde *Cucurbita moschata* × *C. foetidissima* (vgl. WEILING 1960) (siehe Tab. 1).

Tabelle 1.

Zahl der PMZ	Pflanze 1	Pflanze 2	Pflanze 3	Summe X_j	Durchschnitt $\bar{x}_j$	Abweichung $d_j = \bar{x}_j - \bar{x}$	Produktsumme $p_j = \Sigma x_{ij} d_i$
1	8	10	26	44	14,67	— 0,53	+ 234,4
2	2	6	28	36	12,00	— 3,20	+ 334,8
3	8	22	30	60	20,00	+ 4,80	+ 247,2
4	2	10	30	42	14,00	— 1,20	+ 348,0
5	6	11	29	46	15,33	+ 0,13	+ 291,2
Summe X_i	26	59	143	228			1455,6
Durchschnitt $\bar{x}_i$	5,2	11,8	28,6		15,2		
Abweichung $d_i = \bar{x}_i - \bar{x}$	— 10,0	— 3,4	+ 13,4				

Anmerkung: Σd_i und Σd_j müssen gleich o sein.