Theor. Appl. Genet. 56, 85-89 (1980)

Genetics of Desynaptic Mutants in Pearl Millet

M.V. Subba Rao
Department of Botany, Andhra University, Waltair (India)

Summary. Two desynaptic mutants, one of spontaneous origin and the other induced through colchicine treatment, were obtained in pearl millet. The desynpatic character was a monogenically controlled recessive one. Tests for allelism have indicated that the desynaptic genes of the two sources were allelic. Both complete and medium-strong desynaptic plants followed a monogenic pattern of inheritance and were found to be allelic. Medium-strong desynpatic plants on selfing produced both complete and medium-strong desynaptics in approximately equal numbers. It is suggested that the differential expression of the desynaptic character might be due to the presence of modifying genes.

Key words: Pearl millet – Desynapsis – Modifying genes

Introduction

Desynapsis in pearl millet, *Pennisetum typhoides*. S. & H., was first reported by Krishnaswamy, Raman and Madhavamenon (1949). Since then several workers (Patil and Vohra 1962; Jauhar 1969; Manga 1972; Dhesi et al. 1973; Minocha et al. 1975) have studied the asynaptic or desynaptic mutants in detail. Working with asynaptic plants obtained in the progeny of inbred lines of pearl millet, Manga (1972) suggested that the expression of the character might be the consequence of certain gene combinations and not a single gene controlled one. Minocha et al. (1975) studied the inheritance of desynapsis in this crop plant and reported that the desynaptic character was controlled by a single recessive gene: the gene symbol '*ds*' was proposed.

The present study deals with the genetic analysis of two desynaptic mutants, their variable expression and allelic relationship.

Materials and Methods

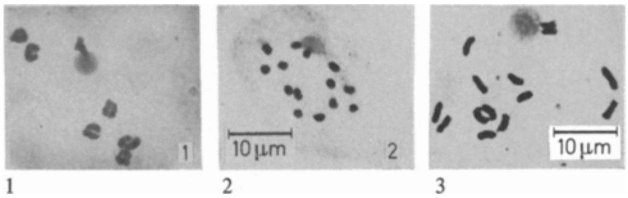
The desynaptic mutants of *P. typhoides* S. & H., (2n = 14) used in the present study were isolated from two sources, one of spontaneous origin located in an inbred line (VG 212) and the other (I.P. 1475) induced through colchicine treatment (plumules treated with a 0.4% solution for two hours). For cytological study young spikes were fixed in 3:1 methanol: glacial acetic acid for 24 hours and then preserved in 70% methanol in a refrigerator. All the fixations were made on the same day and nearly at the same time. Customary acetocarmine squash preparations were used for the study of pollen-mother cell (PMC) meiosis. To study the inheritance pattern of the desynaptic character, reciprocal crosses were made between desynaptic plants and normal (synaptic) plants of standard diploid stock (Fig. 1).

Following the classification of Prakken (1943) the various desynaptic mutants used in the present study were grouped into two categories viz., (a) complete desynaptics with an average of 10 or more univalents per PMC at diakinesis (Fig. 2) and (b) medium-strong with an average of 4 to 9 univalents per PMC at diakinesis (Fig. 3).

Results

1 Inheritance of a Desynaptic Mutant of Spontaneous Origin

The inbred line from which this desynaptic mutant was isolated was selfed for three generations. In the progeny



Figs. 1-3. Chromosome pairing in normal and desynaptic plants. 1 Diakinesis in a normal plant showing 6 ring bivalents and one rod bivalent, 2 Diakinesis in a completely desynaptic plant showing 14 univalents, 3 Diakinesis in a medium-strong desynaptic plant showing 2 ring bivalents, one rod bivalent and 8 univalents

Table 1. Segregation of the desynaptic plants in F_2 and F_3 generations

	Crosses/Parents	Generation	Frequency distribution of the desynaptic plants as to the different mean numbers of univalents[a, b]											Total no. of desynaptic plants	Normal plants	Total no. of plants	x^2 -value (3 normal: 1 desynaptic)
			4	5	6	7	8	9	10	11	12	13	14				
			Inbred source														
1	Complete desynaptic ♀ X normal ♂	F_2	2	5	10	9	3	1	2	4	14	11	10	71	163	234	3.2820
2	Normal plants of F_2 generation[a]	F_3[c]	1	4	8	6	3	1	1	2	5	7	4	42	107	149	0.6465
3	a) Medium-strong desynaptic ♀ X normal ♂	F_2	3	6	5	7	1	1	2	3	2	4	2	36	100	136	0.0883
	b) Reciprocal of cross 3-a	F_2	2	6	15	10	3	2	2	3	4	10	8	65	150	215	2.8667
4	F_1 (complete desynaptic X normal) ♀ X F_1 (medium-strong desynaptic X normal) ♂		1	8	10	12	5	1	1	4	12	8	17	79	195	274	1.9464
			Colchicine Source														
1	Complete desynaptic ♀ X normal ♂	F_2	3	4	10	9	5	1	3	7	10	13	6	71	203	274	0.0779
2	Normal plants of F_2 generation[a]	F_3[c]	1	5	7	8	6	4	1	3	9	10	3	57	160	217	0.1536
3	a) Medium-strong desynaptic ♀ X normal ♂	F_2	2	3	6	7	5	1	1	1	12	4	8	50	130	180	0.6
	b) Reciprocal of cross 3-a	F_2	3	1	5	8	6	1	3	2	4	4	6	43	103	146	1.3151
4	F_1 (Complete desynaptic X normal) ♀ X F_1 (Medium-strong desynaptic X normal) ♂		1	3	15	9	6	7	2	4	15	13	4	79	186	265	3.0201

[a] Desynaptic plants with mean univalent frequencies between 4 to 9 are categorized as medium-strong and those between 10 to 14 as complete

[b] While calculating the mean univalent number per plant, values ⩽ 0.5 are included in the lower class and values ⩾ 0.5 are included in the following higher class

[c] Data taken from the segregating progenies

raised after third generation selfing only one desynaptic plant was observed in a population of 97 plants. Hence it is assumed that the desynaptic condition might be the result of gene mutation rather than the result of inbreeding. This mutant was completely desynaptic and was completely self-sterile since no seed could be obtained on selfing.

1.1 Crosses of Complete Desynaptic x Normal Plants

The complete desynaptic plant was crossed reciprocally to normal plants of the standard stock. No seed was obtained from the cross where the desynaptic plant was used as male parent while a few seeds were obtained when it was used as the female parent. Plants raised from these F_1 seeds were all normal with respect to the synaptic behaviour of the chromosomes at meiosis. The F_1 plants were selfed and in the F_2 generation a 3:1 ratio of normal to desynaptic character was observed. Among these desynaptic plants of the F_2 generation two categories viz., complete and medium-strong, could be distinguished (Table 1).

Complete desynaptic plants of the F_2 generation were almost completely self-sterile and only 1 or 2 seeds were obtained on selfing. These seeds gave rise to complete desynaptic plants. The data on the results of the test crosses between F_1 plants and complete desynaptic plants gave no extra information since the number of plants available from such crosses was too small.

The medium-strong desynaptic plants obtained in the F_2 generation were also self-sterile but not to the same extent as the completely desynaptic ones. On selfing, these medium-strong desynaptic plants gave rise to both complete and medium-strong types in approximately equal numbers (Table 2).

Among the F_2 progeny some normal plants were selected at random and were selfed. In the F_3 generation some of them bred true for the normal character while some segregated in the 3 normal to 1 desynaptic condition (Table 1).

1.2 Crosses of Medium-Strong Desynaptics x Normal Plants

The medium-strong desynaptic plants obtained in the F_2 generation of the earlier cross were again crossed reciprocally to normal plants of the standard stock. The percentage of seedset when these desynaptics were used as male parents was low compared to the corresponding reciprocal cross. All the F_1 plants were normal and upon selfing, in the F_2 generation, gave rise to 3 normal and 1 desynaptic (complete and medium-strong put together) plants (Table 1). No differences were observed among the reciprocal crosses.

In the progeny of the test crosses involving F_1 plants and medium-strong desynaptic plants, both normals and desynaptics appeared in approximately equal numbers and here also complete and medium-strong desynaptics were realised (Table 3).

1.3 Crosses Between Complete and Medium-Strong Desynaptics

Complete and medium-strong desynaptic plants were reciprocally crossed with one another but no seed was ob-

Table 2. Frequencies of desynaptic plants in the selfeld progeny of medium-strong desynaptic plants

	No. of plants					
	Inbred source			Colchine source		
Segregating line	Complete desynaptic	Medium-strong desynaptic	Total	Complete desynaptic	Medium-strong desynaptic	Total
1	6	11	17	4	7	11
2	4	9	13	9	6	15
3	5	1	6	8	11	19
4	2	1	3	7	6	13
5	1	4	5	4	2	6
6	1	–	1	2	5	7
7	2	3	5	3	6	9
8	–	–	–	8	11	19
9	–	–	–	1	6	7
Total	21	29	50	46	60	106

Table 3. Segregation of the desynaptic plants in the test cross, medium-strong desynaptic × (medium-strong desynaptic × normal) F_1

	No. of plants				
Progeny	Complete desynaptic	Medium-strong desynaptic	Total desynaptic	Normal	Total
Inbred source					
1	2	–	2	5	7
2	2	1	3	6	9
3	–	1	1	4	5
4	1	1	2	7	9
5	1	2	3	3	6
6	–	1	1	5	6
7	2	3	5	8	13
8	2	4	6	11	17
Total	10	13	23	49	72
Colchicine source					
1	2	2	4	9	13
2	3	1	4	4	8
3	3	6	9	7	16
4	4	7	11	8	19
5	4	1	5	7	12
6	–	–	–	3	3
7	–	1	1	–	1
8	1	2	3	6	9
9	–	3	3	5	8
10	3	4	7	11	18
Total	20	27	47	60	107

tained. Hence crosses between complete and medium-strong desynaptic plants were made employing a third parent i.e., these two types were first crossed separately to a normal plant of the standard stock and the resulting F_1 plants which were normal were then intercrossed. Interestingly, the progeny of these intercrosses segregated for complete as well as medium-strong desynaptics and normal plants: the ratio of normal to desynaptic was a good fit to the 3:1 ratio (Table 1). Here also complete and medium-strong desynaptics appeared in approximately equal numbers.

In all these segregating generations of the desynaptics (Table 1), the same range of the mean numbers of univalents per plant was realised i.e., among both the complete and medium-strong types, the various mean univalent categories were observed in each generation.

2 Inheritance of Colchicine Induced Desynaptic Mutants

Of the 100 plumules that received treatment with 0.4 percent colchicine for 2 hours, 88 seedlings survived and one of them showed the desynaptic condition at meiosis. This single desynaptic plant was also completely desynaptic and was similar in its cytological behaviour to that of spontaneous origin. Studies on the inheritance of this desynaptic mutant which were carried out on similar lines as for those of the desynaptic mutant of spontaneous origin, revealed the following features (Table 1):

(a) The complete desynaptic mutant showed a monogenic type of inheritance.

(b) The medium-strong desynaptic mutant also showed a monogenic pattern of inheritance.

(c) As in the case of the spontaneous desynaptic mutant, the progeny from crosses between complete desynaptic × normal (F_1) and medium-strong desynaptic × normal (F_1) segregated for the 3 normal and 1 desynaptic condition.

3 Tests for Allelism Between Desynaptic Mutants of the Two Sources

The complete desynaptic mutants obtained spontaneously as well as from colchicine treatment were crossed to normal plants of the standard stock. The F_1 plants thus obtained from these two sources were intercrossed reciprocally. The progeny of these crosses again segregated for 3 normal and 1 desynaptic plants (Table 4). Similar results were obtained in the progeny of intercrosses which were carried out using the medium-strong desynaptic plants (Table 4). In all the above cases no differences were observed among the reciprocal crosses.

Discussion

The present study indicates that in both sources (spontaneous and induced), the desynaptic (*ds*) character is inherited as a monogenic recessive and the '*ds*' genes of the two sources are allelic. No differences among the reciprocal crosses were ever observed thereby excluding the possible role of cytoplasmic factors in the inheritance of this character. Both complete and medium-strong desynaptic mutants showed the same pattern of inheritance. Sjodin (1970) reported a more or less similar situation in *Vicia faba* where both medium-strong and weak asynaptics showed a monofactorial type of inheritance. Likewise, in *Triticum monococcum* Smith (1936) showed that both complete and medium-strong asynaptics followed a 15:1 type of inheritance.

Several workers have reported the variable expression of the asynaptic or desynaptic genes as evidenced from the number of univalents per PMC. Koller (1938) in *Pisum sativum* and Li, Pao and Li (1945) in wheat, suggested the presence of modifying genes which were perhaps respon-

Table 4. Results of the allelism test between the desynaptic genes of the two sources

Cross	No. of plants					x^2 -value (3 normal: 1 desynaptic)
	Complete desynaptics	Medium-strong desynaptics	Total desynaptics	Normal	Total	
F_1 (Complete desynaptic of inbred source X normal) ♀ X F_1 (Complete desynaptic of colchicine source X normal) ♂	35	33	68	168	236	1.6328
Reciprocal of the above cross	26	18	44	106	150	1.2800
F_1 (medium-strong desynaptic of inbred source X normal) ♀ X F_1 (medium-strong desynaptic of colchicine source X normal) ♂	15	21	36	111	147	0.0023
Reciprocal of the above cross	23	26	49	126	175	0.6876

sible for the differential expression of the desynaptic gene. In *Nicotiana rustica* x *N. tabacum* derivatives Swaminathan and Murty (1959) observed a gradation in pairing frequency from regular bivalent formation to complete asynapsis. They attributed this to the existence of gene dosage effect and argued that since partially asynaptic plants gave rise to complete asynaptic ones, it is not likely that altogether different genes control the types of asynapsis.

Prakken (1943) who classified the asynaptic condition into three categories, however, states that a classification according to the number of univalents and bivalents at metaphase is rather arbitrary, for in many cases the metaphase pairing is highly influenced by external and internal conditions (modifying genes or chromosomal abnormalities).

In none of the desynaptic mutants used in the present study were chromosomal abnormalities observed. As the desynaptic condition was found to be single gene controlled and the two genes responsible for complete and medium-strong desynaptic conditions were allelic, it appears that for the differential expression of the same gene either environmental factors or modifying genes should be responsible. Since the various univalent classes (either complete or medium-strong) are being recovered in each of the segregating generations it appears that the variable expressivity of the desynaptic character too has a definite genetic basis rather than environmental. Further, since all the plants under study were grown under more or less similar field conditions and also that the medium-strong desynaptics on selfing, gave rise to complete desynaptics, it seems more likely that some modifying genes must be responsible for the differential expression of the '*ds*' gene.

Acknowledgement

The author wishes to thank Prof. J.V. Pantulu for his helpful discussions during the course of the study.

Literature

Dhesi, J.S.; Jagtar, S.; Gill, B.S.; Sharma, H.L.: Cytological studies of Desynaptic stock in pearl millet, (*Pennisetum typhoides*). Cytologia **38**, 311-316 (1973)

Jauhar, P.P.: Partial desynapsis in pearl millet, *Pennisetum typhoides*. Naturwissenschaften **56**, 571-572 (1969)

Koller, P.C.: Asynapsis in *Pisum sativum*. J. Genet. **36**, 275-306 (1938)

Krishnaswamy, N.; Raman, V.S.; Madhavamenon, P.: Abnormal meiosis in *Pennisetum typhoides* I. Desynapsis. Proc. Ind. Acad. Sci. **30**, 195-206 (1949)

Li, H.W.; Pao, W.I.; Li, C.H.: Desynapsis in the common wheat. Amer. J. Bot. **32**, 92-101 (1945)

Manga, V.: Cytogenetic studies of pearl millet (*Pennisetum typhoides*). Ph.D. thesis. Andhra University, Waltair, India (1972)

Minocha, J.L.; Dhesi, J.S.; Sidhu, J.S.: Inheritance of desynapsis in pearl millet. Ind. J. Genet. Plant Breed. **35**(3), 470-471 (1975)

Patil, B.P.; Vohra, S.K.: Desynapsis in *Pennisetum typhoides*. Curr. Sci. **32**, 345-346 (1962)

Prakken, R.: Studies of asynapsis in rye. Hereditas **29**, 475-495 (1943)

Sjodin, T.: Induced asynaptic mutants in *Vicia faba*. Hereditas **66**, 215-232 (1970)

Smith, L.: Cytogenetic studies in *Triticum monococcum* L. and *Triticum aegilopoides* Bal. Univ. Missouri Agri. Exp. Sta. Res. Bull. **248**, 1-38 (1936)

Swaminathan, M.S.; Murty, B.R.: Aspects of asynapsis in plants. I. Random and non-random chromosome associations. Genetics **44**, 1271-1280 (1959)

Received February 5, 1979
Accepted April 7, 1979
Communicated by Tsunewaki

Dr. M.V. Subba Rao
Department of Botany
Andhra University
Waltair 530 003
A.P. (India)