the next, was generally different: b computed from the data concerning the first female is different from b computed from the data concerning the second female.

It is thus possible to draw the conclusion that the female plant genotype plays a part in determining the pollen fertilization ability: this is a characteristic of the male gametophyte, but it may be greater or less according to the stylar tissues where it grows.

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Transmission of nucleolus organizer region deficiencies

In animals, gametes deficient for most chromosomal segments are transmissible and the resultant hypoploid zygote either survives or dies. In plants, the gametophytic screen usually prevents the transmission of gametes deficient for most chromosomal segments. However, maize gametes deficient for the chromosomal segment distal to the nucleolus organizer region (NOR) of chromosome 6, the satellite, are readily transmissible at least through the egg (Phillips, et al., 1971, Crop Sci. 11:525-528; Phillips 1975, MGCNL 49:118-119; and Phillips, unpublished). The question is: How much of the NOR is essential for the normal development of the gametophyte and subsequent gametic transmission?

NOR-interchange heterozygotes provide excellent material to test for the dependency of various distal portions of the NOR. Pollen sterility of NOR-interchange heterozygotes would be an expected 25% if one of the duplication-deficiency (Dp-Df) combinations does not abort and adjacent-2 disjunction is rare. None of the NOR-interchange heterozygotes possesses 25% pollen abortion; most are not significantly different from the 50% expectation if both Dp-Df chromosome combinations abort (Table 1). However, a large amount of variability in pollen phenotype percentages appears to exist among plants heterozygous for a particular interchange. Variability also was reported for T6-9a by E. G. Anderson (Amer. Nat. 68:345-350, 1934). In addition, all of the NOR interchange heterozygotes possess some pollen that is smaller than normal and either well-filled or partially-filled with starch, suggesting that certain Dp-Df gametes may be transmissible at least through the egg. Competition effects usually eliminate the pollen transmission of Dp-Df gametes.

A genetic test for transmission of Dp-Df gametes from NOR-interchange heterozygotes was prompted by the observations of variability in pollen sterility and smaller but well-filled or partially-filled pollen phenotypes. The yellow-white endosperm marker (Y y) was used since it is the most convenient marker located near the NOR. Another chromosome 6 marker, sugary-2 (su2), also was employed in these tests. The Y locus is approximately 20 map units from the NOR while su2 is independent, being about 40 map units from Y. Backcross Y:y ratios should be 1:1 if the Dp-Df chromosome combination that is deficient for a portion of the NOR is not transmitted. If Dp-Df gametes deficient for a part of the NOR do function, the ratio should approach 2Y:1y. If the Dp-Df gamete deficient for a portion of the other chromosome involved in the interchange functions, then the ratio would be reversed, approaching 1Y:2y. The results in Table 2 indicate that none of the NOR-interchange heterozygotes regularly transmits a terminal NOR-deficiency through either pollen or ovules. A few heterozygous plants of certain interchanges, particularly T6-7(5181) and T6-9d, appear to transmit NOR-deficiencies but further tests are needed on these exceptions. The occurrence of these exceptions may be related to the variability observed in pollen phenotypes. Among the interchanges with certain plants producing abnormal Y:y ratios, there is no obvious relationship with the position of the break in the NOR.

Interchange T6-10(5519) consistently transmitted through the ovules Dp-Df gametes deficient for the distal portion of 10L and duplicate for the secondary

Table 1. Pollen phenotypes and frequencies of plants heterozygous for various NOR-interchanges.

Interchange	Chromosome 6	Other	No. plants	Pollen Phenotypes‡ Normal %	Devoid %	Well-filled %	Part-filled %	Percent abortion
1-6Li	S.C.* - prox.	1L.81						
1-6(4986)	"	1S.11	6+	68.3 ± 12.9	20.4 ± 2.3	11.0 ± 13.5	0.7 ± 0.8	31.9 ± 13.0
1-6(5495)	"							
1-6(6189)	Het* .10	1S.50	4	54.1 ± 6.1	23.9 ± 3.6	8.5 ± 5.6	13.4 ± 7.9	45.9 ± 6.1
2-6(027-4)	S.C. - prox.	2L.04	4	62.3 ± 6.7	18.6 ± 8.2	11.0 ± 5.1	8.0 ± 7.0	37.7 ± 6.7
2-6(8786)	Het .88	2S.97	4	55.8 ± 4.4	1.7 ± 1.7	26.2 ± 9.0	16.3 ± 7.4	44.2 ± 4.4
2-6(5419)	S.C. - .25	2L.82	6	58.7 ± 6.5	2.9 ± 2.4	16.9 ± 6.6	21.4 ± 3.9	41.2 ± 6.5
3-6(030-8)	S.C. - .25	3S.05	10	64.7 ± 12.1	16.2 ± 6.3	11.5 ± 7.3	7.6 ± 4.0	35.2 ± 12.1
3-6(032-3)	S.C. - midway	3S.34	8	63.5 ± 9.8	11.4 ± 3.9	14.0 ± 8.3	11.1 ± 3.6	35.9 ± 9.3
4-6(4341)	Het .50	4S.36	9	59.6 ± 4.1	21.6 ± 6.7	14.6 ± 4.1	4.2 ± 3.3	40.3 ± 4.2
5-6f	S.C. - midway	5S.23	8	63.8 ± 10.2	23.2 ± 3.2	10.1 ± 6.8	2.8 ± 5.7	36.0 ± 10.3
5-6(8696)	"	5L.79	5	56.8 ± 3.5	5.9 ± 8.5	16.7 ± 6.8	20.5 ± 4.9	43.2 ± 3.5
6-7(4964)	Het .32	7L.67	4	51.6 ± 3.9	13.8 ± 10.1	4.96± 3.7	29.7 ± 5.5	48.5 ± 4.0
6-7(035-3)	S.C. - .25	7L.59	9	62.4 ± 8.2	15.3 ± 7.3	5.9 ± 5.0	16.3 ± 8.4	37.3 ± 8.2
6-7(5181)	Het .71	7L.85	6	64.3 ± 7.3	6.2 ± 2.9	11.8 ± 8.3	17.7 ± 1.1	35.7 ± 7.3
6-9a	Het .67	9L.32	6	62.5 ± 5.0	18.6 ± 1.9	13.5 ± 6.8	5.4 ± 5.8	37.5 ± 5.0
6-9d	Het .46	9L.84	7	60.8 ± 6.7	16.1 ± 10.6	14.3 ± 11.6	8.7 ± 3.3	38.9 ± 6.9
6-10(5519)	S.C. - prox.	10L.10	7	64.4 ± 12.0	11.3 ± 5.6	11.0 ± 5.9	13.3 ± 6.5	35.4 ± 12.2

* S.C. = Secondary Constriction Het. = NOR-heterochromatin

+ A minimum of 500 pollen grains were classified per plant.

‡ Well-filled = pollen smaller than normal and well-filled with starch by IKI staining.
Part-filled = smaller but partially filled with starch.

Table 2. Transmission tests of NOR-deficiencies from NOR-interchange heterozygotes using a linked marker gene.

Interchange	F_1 used as ♀ Y:y	F_1 used as ♂ Y:y	Number paired reciprocal backcrosses
1-6Li	210:192(2)†	70:70(1)	0
1-6(4986)	267:252(1)	219:232(2)	1
1-6(5495)	150:157(1)	267:251(2)	1
1-6(6189)	101:114(1)	131:115(1)	1
2-6(027-4)‡	126:119(2)	174:187(2)	2
2-6(8786)	210:198(1)	166:179(1)	1
	185:214(1)	43:2?*(1)	1
2-6(5419)	114:85*(1)	64:66(1)	1
	119:100(1)	194:193(1)	1
	110:103(1)	71:118**(1)	1
3-6(030-8)	165:150(1)	272:225(2)	1
	87:59*(1)		0
	186:147*(1)		0
3-6(032-3)	231:220(2)	302:312(2)	1
4-6(4341)	213:202(2)	70:53(2)	1
5-6f	264:284(1)		0
5-6(8696)	105:86(1)	182:185(1)	1
	116:103(1)	244:194*(1)	1
		52:32*(1)	0
6-7(4964)	395:375(2)	197:233(2)	1
6-7(035-3)	318:118 F_2(1)	154:153(1)	0
6-7(5181)	1356:1331(11)	363:360(3)	2
	284:184**(1)	28:30(1)	1
	101:109(1)	228:173**(1)	1
	143:97**(1)		0
	131:180**(1)		0
	141:177*(1)		0
6-9a	245:217(3)	226:238(2)	2
6-9d	271:230(2)	176:134(2)	1
	112:119(1)	196:121**(1)	1
		118:85*(1)	0
6-10(5519)	257:420**(3)	534:504(5)	2

* Significant Chi-square test for goodness of fit (.05 level)

** (.01 level)

† Data mostly from backcrosses of F_1 (interchange x marker stock) to recessive marker stock. Ears giving homogeneous data are pooled, others are reported separately. Number of ears pooled are given in parentheses. Both reciprocal crosses are reported separately if one had a Y:y ratio deviating significantly from 1:1. If ears with a Y:y ratio differing significantly from 1:1 also have a significant deviation of Su2:su2, one would expect that the deviation for Y:y is not due to Dp-Df transmission; such ears are not included in the data presented above. Ears included in the table differing significantly from 1Y:1y have Su2:su2 ratios not significantly different from 1:1.

‡ Data for linked chromosome 2 marker virescent-4.

constriction and the satellite. Plants with this chromosome combination may be useful in future NOR studies. Duplicate-deficient plants have been recovered from this interchange by E. B. Patterson (Eucarpia, 1973) and utilized in studies on male sterility.

When crossing plants heterozygous for T2-6(5419) or T4-6(4341), two of the NOR-interchanges, with pollen from plants heterozygous for polymitotic (po), Patterson (MGCNL 33:131, 1959) obtained occasional small seed that gave rise to plants with the polymitotic phenotype. The po locus is assumed to be proximal to the NOR since it maps proximally to ragged (rgd), which is proximal to the midpoint of the NOR-heterochromatin, based on tests with TB-6a (R. G. Palmer and E. Dempsey, 1968, MGCNL 42:75-77). One could speculate that the unexpected po plants are not due to the simple transmission of Dp-Df gametes but are the result of a breakage event after the first postmeiotic division that would generate a chromosome deficient for a terminal portion of 6S including the entire NOR. The mechanism could be similar to that described for Neurospora (D. D. Perkins et al., 1972, Genetics 71:s46) and Aspergillus (Lieber 1973, Univ. of Sheffield, Ph.D. Thesis) where certain chromosomes of duplicate-deficient progeny undergo structural modifications. Data presented in Table 2 give no positive evidence for transmission of Dp-Df gametes from T4-6(4341) and mixed evidence for T2-6(5419). Occasional transmission of Dp-Df gametes could have occurred but not in sufficient frequency to result in an abnormal Y:y ratio. Additional evidence has been gained in cooperation with Dr. E. B. Patterson against the chromosome breakage hypothesis to explain po progeny in crosses of heterozygous interchanges with Po/po as pollen parent. Cytological examination of occasional po progeny in crosses involving T3-6(030-8) and T6-7(5181) revealed a heteromorphic chromosome 6 bivalent as expected in a duplication-deficiency heterozygote. No evidence of chromosome breakage was apparent. The po gene must be in the NOR-secondary constriction or the satellite. Since T3-6(030-8) has a break in the NOR-secondary constriction and T6-7(5181) has one in the NOR-heterochromatin, rare transmissions of NOR-deficiencies apparently occur at least for the distal 29% of the NOR-heterochromatin and the site giving rise to the secondary constriction. Study of progeny of these and other maize NOR-interchanges may provide valuable materials for future NOR investigations.

The conclusion we reach from these studies is that the NOR-heterochromatin and at least a large portion of the site giving rise to the secondary constriction are usually necessary for normal gametophytic development and transmission, although occasional transmissions occur of NOR-deficiencies.

R. L. Phillips

Progress in establishing a true-breeding line that will produce "all male-sterile" progeny when crossed on genetic male-sterile plants

I am now assuming that certain of the ms plants among the progeny of ms ms or Ms ms pollinated by X-rayed pollen from a normal stock may have received a treated chromosome with an inactivated Ms allele. When those male steriles are crossed with pollen of a normal inbred, the progeny which received that chromosome through the female would, when selfed, produce only fertile (non-male sterile) progeny. The progeny which received the normal, untreated chromosome carrying ms would segregate 3 fertile: 1 ms when selfed. There are eight lines that have behaved in this manner, indicating that the inactivated Ms allele was transmitted through the female. Plants in those cultures which did not segregate ms were selfed and test crossed on ms as a test to identify plants that might be homozygous for the inactivated allele and also to test transmissibility through the pollen. For three lines which had normal pollen and normal seed set, the progeny from the test crosses of certain plants included ms plants indicating pollen transmission. For one of the three lines, there were 85 ms in a total of 506 plants (17% male steriles), for another line 4 ms in 139 (3% male-steriles), and in the other line 9 ms in 15 (possibly 1:1). Since in these lines pollen and ovule transmission occurs, one would expect to obtain the homozygote for the inactivated Ms allele. Too few