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Generative transmission of the extra chromosome in a rye tertiary trisomic and its relation with inbreeding depression and pollen quality

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Summary. Transmission of the extra (translocated) chromosome of tertiary trisomic T282W of rye (*Secale cereale* L.) upon selfing, through the male and/or the female, ranged from 0% to 36% in different inbred lines. Tetrasomics arising from simultaneous male and female transmission were not recovered and thus apparently not viable. Low seed weight, poor seed germination and a low transmission rate were correlated with low seed weight and reduced plant vigour. Inbreeding depression was concluded to affect transmission rate through its effect on the relative viability of trisomic seeds or seedlings.

Male transmission in testcrosses with disomics averaged 7%, but varied between lines. Genetic factors were involved, but their expression remains uncertain. Pollen quality, as determined by a fluorescence reaction, was somewhat lower in trisomics than in disomics of the same genetic background and was not correlated with male transmission rate, which appears to be determined mainly by relative pollen-tube growth of euploid and aneuploid gametophytes. The results are discussed in relation to the use of tertiary trisomics in balanced chromosomal systems for hybrid breeding.

Key words: Rye – Tertiary trisomic – Transmission – Inbreeding – Pollen quality

Introduction

Tertiary trisomics carry a translocated extra chromosome. In rye, *Secale cereale*, the most important source of the extra chromosome is the reciprocal translocation (interchange) heterozygote, in which the extra chromosome is usually the shorter of the two translocation chromosomes (De Vries 1983). An interesting application of tertiary trisomics is the breeding of hybrids with nuclear gene-conditioned male sterility. The system was first described in barley by Ramage (1965) (see also Wiebe and Ramage, 1971). When the dominant allele *Ms* of the male sterility gene is located on the translocated chromosome and the recessive allele *ms* on both of the two corresponding normal chromosomes, the trisomic is male fertile. If the extra chromosome is not transmitted through the pollen and no recombination between *ms* and the translocation breakpoint occurs, all male gametes participating in fertilization will carry the *ms* allele. Thus, when the tertiary trisomic is used to pollinate male-sterile disomics, the progeny will exclusively consist of male-sterile disomics. This progeny is used as the all-male-sterile seed parent in a hybridization programme. The tertiary trisomics can be maintained by selfing, which results in fertile tertiary trisomics and male-sterile disomics: balanced tertiary trisomy (BTT).

Aspects of the construction and application of BTT in rye were studied by De Vries (1984), who also isolated several different tertiary and other types of trisomics. For the successful application of the BTT system in hybrid breeding, male transmission of the translocated chromosome should be excluded, but pollen production and pollen quality should be high. In addition, for the efficient maintenance of the BTT after selfing, transmission of the extra chromosome through the female should be high, even in inbred lines.

In earlier experiments aneuploid microspores were shown to have a slower development than euploids, but no correlation between rate of development and male transmission was observed (Janse 1985, 1987a). Re-

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stricted pollination showed that certation between euploid and aneuploid pollen grains plays a predominant role in determining male transmission. Therefore, a large proportion of the aneuploid microspores, although retarded, must have reached maturity before anthesis (Janse 1987b). These three studies were carried out on different genotypes of a single tertiary trisomic. As a result it was not possible to conclude, whether the results are typical for this trisomic only, or whether they are representative of the general behaviour of tertiary trisomics in rye. In the study presented here the role of genetic factors, the effect of inbreeding depression on transmission rates and the possible correlation of male transmission with pollen quality in different inbred lines and hybrids of a second tertiary trisomic of rye were investigated.

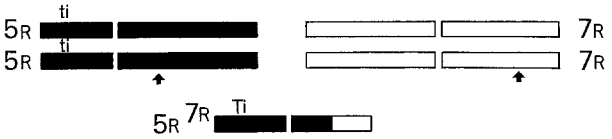

Fig. 1. The chromosomes involved in tertiary trisomic T282W. Translocation breakpoints (*arrows*) and arm length ratios are according to Sybenga and Wolters (1972). Alleles of the tigrina locus are indicated (*ti*) (De Vries and Sybenga 1984)

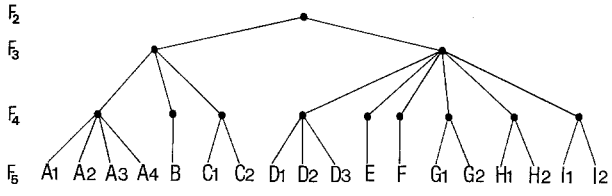

Fig. 2. Origin of the F_5 lines of tertiary trisomic T282W

Material and methods

Tertiary trisomic

The extra chromosome in this tertiary trisomic is the short translocation chromosome of the reciprocal translocation T282W, one of the translocations of the tester set developed by Sybenga and Wolters (1972). The extra chromosome consists of the short arm, the centromere, and a proximal segment of chromosome 5R, and a (translocated) segment of the short arm of 7R (Fig. 1). The nomenclature is according to Sybenga et al. (1985). The recessive, conditionally lethal gene *Ti*/*ti* located on the short arm of 5R (De Vries and Sybenga 1984) is used as a selective marker. In the tertiary trisomic studied, the dominant allele (*Ti*) is carried by the translocation chromosome and the recessive alleles (*ti*) by the unchanged 5R chromosomes (Fig. 1). Homozygous recessive *titi* plants show coiling of the leaves with yellow transverse striping ("tigrina"). They are usually viable when grown in the greenhouse at about 20 °C, but do not survive in the field. Janse (1985, 1987a, b) used the same gene in her studies on a single tertiary trisomic. In her trisomic the translocation chromosome had the same short arm of 5R and a part of the long arm, but the exchanged segment was from 3R.

Segregation, recombination and transmission in inbred lines

A total of 18 F_5 lines resulting from self-fertilization of F_4 tertiary trisomics were used in this study. Some of these were grown in the spring of 1985 and 1986, but most were grown in the spring of 1987. Their origin and relation to each other is shown in Fig. 2.

For each line mean seed weight, germination percentage and seedling mortality were recorded. The plants were scored for *ti* about 12 days after sowing. While the dominant allele could be used as a marker for the presence of the translocation chromosome, all of the plants were karyotyped in order to study recombination between *ti* and the translocation breakpoint. Root tips were pretreated with a saturated solution of α-bromonaphtalene (2 h, 26 °C), macerated in 1 *N* HCl for 12 min at 59°–60 °C and stained with Schiff's reagent (Feulgen reaction). Squash preparations were made in 45% acetic acid. The translocated chromosome could be recognized in the trisomics because it is significantly smaller than any of the normal chromosomes.

If m and f represent male and female transmission rates, respectively, and r is the recombination fraction, the frequencies of disomic and trisomic wild types and tigrinas can be expressed as (de Vries 1984):

	Wild type	Tigrina	Total
2n+1:	$[m(1-f)+f(1-m)]\times(1-r+r^2)$	$[m(1-f)+f(1-m)]\times(r-r^2)$	$m(1-f)+f(1-m)$
2n:	$(1-m)(1-f)\times(2r-r^2)$	$(1-m)(1-f)(1-r)^2$	$(1-m)(1-f)$

When tetrasomics have a low viability, transmission rates are greatly underestimated (Janse 1987a), and then these formulae are not suitable for estimating male and female transmission separately. However, the total fraction of trisomics is a good indication of the transmission through either the male or the female. The recombination fraction can then be estimated from the segregation of wild types and tigrinas among the trisomics and the disomics with the use of these formulae in an adjusted form. When different values for r are obtained, maximum likelihood estimates are used to derive a representative estimate.

Segregation, transmission and recombination in testcrosses

Female parents with a normal karyotype (2n=14) and homozygous recessive for *ti* were used in testcrosses set up for determining male transmission rates. As male parents, two or three tertiary trisomics having relatively good transmission upon selfing and sufficient vigour to produce several ears and enough pollen to make the testcrosses were selected from F_5 lines. The plants in the testcross progenies were scored for *ti*. Wild types were expected to be trisomic unless recombination had occurred. To avoid excessive labour we only karyotyped wild-type plants. The frequency of wild-type trisomics in the testcross progeny can be expressed as m(1-r) and that of wild-type disomics as r(1-m) (Janse 1987a). m and r can then be estimated. In addition, testcrosses with tertiary trisomics from some of the testcross progenies ("F_1") were made and analysed in the same way. These were heterotic, which may have affected male transmission. As all tigrina plants used in the testcrosses had the same genetic background, genetic differences may be expressed in the F_1 (testcross-derived) tertiary trisomics. Some F_5 plants were selfed to obtain F_6 lines, and testcrosses were made with a few of these F_6 tertiary trisomics.

Pollen quality

Pollen quality was assessed using a fluorochromatic reaction (FCR), which tests (1) the presence of an active esterase and (2)

Table 1. Segregation for *ti* and chromosome number (14 or 15) in 18 F_5 lines. Mean seed weight, germination and seedling mortality in each line are given, as are estimates for total transmission (t) and recombination fraction (r)

F_5 line	Number of seeds	Mean weight (mg)	Germination (%)	Seedling mortality (%)[a]	*Ti*		*titi*		Total	t	r
					15	14	14	15			
A1	81	12.3	19 (23)	1 (5)	0	2	15	0	17[b]	0.0	0.06
A2	66	16.8	45 (68)	5 (11)	1	4	35	0	40	0.03	0.05
A3	29	10.0	1 (3)	1 (100)	–	–	–	–	–	–	–
A4	40	14.0	11 (28)	1 (9)	0	4	6	0	10	0.0	–[c]
B	122	13.8	39 (32)	8 (21)	1	3	27	0	31	0.03	0.05
C1	70	19.3	47 (67)	14 (30)	3	1	29	0	33	0.09	0.02
C2	49	18.4	11 (22)	2 (18)	0	0	9	0	9	0.0	0.0[d]
D1	95	19.3	86 (91)	8 (9)	28	2	48	0	78	0.36	0.02
D2	87	18.7	67 (77)	20 (30)	6	4	37	0	47	0.13	0.05
D3	77	17.4	58 (75)	10 (17)	10	2	36	0	48	0.21	0.02
E	64	11.3	18 (28)	4 (22)	0	3	11	0	14	0.0	0.11
F	39	17.2	16 (41)	4 (25)	3	2	7	0	12	0.25	0.12
G1	64	18.3	46 (72)	9 (20)	8	3	24	2	37	0.27	0.11
G2	41	17.8	30 (73)	5 (17)	5	2	18	0	25	0.20	0.05
H1	76	16.3	51 (67)	9 (18)	11	2	29	0	42	0.26	0.03
H2	33	17.6	7 (21)	3 (43)	0	0	4	0	4	0.0	0.0[d]
I1	98	19.7	47 (48)	12 (26)	2	2	30	0	34	0.06	0.03
I2	46	19.8	10 (22)	5 (50)	0	0	5	0	5	0.0	0.0[d]

[a] Seedling mortality as percentage of plants germinated
[b] Plus one tetraploid (2n=28) tigrina plant
[c] This parent was probably a recombinant itself
[d] Recombination estimate not reliable due to low numbers of plants

the integrity of the plasmalemma of the vegetative cell (Heslop-Harrison and Heslop-Harrison 1970). A high correlation with germinability is usually obtained (Heslop-Harrison et al. 1984). In partly dehydrated pollen the membranes are largely dissociated and need rehydration, a process that normally takes place on the stigma (Shivanna and Heslop-Harrison 1981). Freshly dehisced pollen was collected from the first emerging ears of trisomic and disomic plants and placed in a watchglass in a petri dish with moistened filterpaper for 1 h to allow rehydration. Fluorescein diacetate (FDA) was made up as a stock solution in acetone at a concentration of 2 mg/ml. Immediately before the test was to be carried out drops of the FDA stock solution were added to 1 ml of a 20% sucrose solution supplemented with 10^{-2} M $CaCl_2$ until persistent clouds indicated saturation. Pollen was added to this medium and incubated at room temperature in the dark for about 45 min. By then fluorescein, which is produced upon hydrolysis of FDA by esterase, had accumulated in the viable pollen grains. On a slide 500 pollen grains were studied under a Zeiss UV microscope with a mercury light source and BP365 excitation and LP397 barrier filters. The test was carried out twice for each plant during its flowering period.

Results

Transmission and recombination in inbred lines

Segregation of chromosome number and marker gene and estimates of the total transmission rate and recombination fraction for the F_5 lines are given in Table 1. The percentage of trisomics, which is an expression of transmission through either the male or the female gametophytes, ranged from 0% to 36%. Tetrasomics did not appear in any of the progenies. On an average only 48% of the seeds germinated, and 26% of the seedlings died at an early stage.

A significant positive correlation ($r=0.78$; $P<0.01$) was found between seed germination and transmission rate, but not between germination and seed weight ($r=0.45$; $0.05<P<0.10$, Table 1). Seedling mortality showed a significant negative correlation with germination ($r=-0.50$; $P<0.05$), but was sometimes based on very few plants.

Between lines, mean seed weight and germination are expected to be affected by the degree of inbreeding depression. Lines A1, A2, A3, A4, B, C1 and C2, all descending from the same F_3 line (Fig. 2), without exception showed a very low transmission rate and a strong inbreeding depression; germination averaged 29%. The other lines, descending from another F_3 line (Fig. 2) were generally more vigorous and showed higher transmission rates. Large differences occurred within this group. Most F_5 lines descending from the same F_4 line showed a similar behaviour, except for H1 and H2.

Table 2. Segregation for *ti* and chromosome number among the wild types in progenies of testcrosses $2n \times (2n+1)$, with tertiary trisomics from six different F_5 lines used as a male parent

F_5 line	Plant	Number of seeds	Germination (%)	*Ti*		*titi*	Total	m	r
				15	14				
D1	1	83	72 (87)	10	0	59	69	0.15	0.0
	2	38	27 (71)	1	0	23	24	0.04	0.0
	Total	121	99 (82)	11	0	82	93	0.12	0.0
D2	1	91	72 (79)	2	2	61	65	0.03	0.03
	2	138	134 (97)	10	8	115	133	0.09	0.07
	3	31	31 (100)	2	1	28	31	0.07	0.03
	Total	260	237 (91)	14	11	204	229	0.06	0.05
D3	1	79	78 (99)	7	1	66	74	0.10	0.02
	2	20	18 (90)	1	0	17	18	0.06	0.0
	3	18	18 (100)	1	0	15	16	0.07	0.0
	Total	117	114 (97)	9	1	98	108	0.08	0.01
F	1	21	21 (100)	1	1	19	21	0.05	0.05
	2	67	61 (91)	4	2	53	59	0.07	0.04
	Total	88	82 (93)	5	3	72	80	0.07	0.04
G1	1	76	66 (87)	1	2	63	66	0.02	0.03
	2	103	93 (90)	12	3	78	93	0.13	0.04
G2	1	114	107 (94)	4	8	94	106	0.04	0.08
	2	89	89 (100)	3[a]	5	80	88	0.04	0.06
	Total	203	196 (97)	7	13	174	194	0.04	0.07

m, estimates of male transmission; r, recombination factor
[a] Including one unidentified primary trisomic

Recombination in the F_5 lines ranged from 0% to 12% (Table 1). The progenies with the smallest recombination fractions contained few plants, which makes these figures less reliable. Some of the F_5 lines belonging to the same F_4 group seemed to show a slightly higher or lower recombination rate than others, but these differences were not distinct.

Transmission and recombination upon testcrossing

Table 2 shows segregation for *ti* and chromosome number among the wild-type class of testcross progenies from some of the F_5 lines. Male transmission rates (m) and recombination fraction (r) were estimated. Germination was good in all testcross progenies. Male transmission of the extra chromosome was observed in all lines. In one progeny a primary trisomic was found. Homogeneity in segregation among the progenies of the same F_5 line was tested. In some cases the euploid *Ti* class was too small and had to be combined with the *ti* class. No significant differences at $P = 0.05$ were found except for line G1, where one plant (G1/1) showed a lower and the other (G1/2) a higher male transmission rate (Table 2). For the other lines the different progenies were pooled; m and r were estimated again (Table 2). Line D1 differed significantly ($P<0.05$) from D2 and G2: it had a relatively high male transmission rate and a relatively low recombination frequency. Segregation in testcross progenies from D3 trisomics differed from that of trisomics from line G2, but this was probably largely due to differences in recombination. G1/1 differed significantly ($P<0.05$) from D1 and G1/2 from G2. Other differences were not found to be significant at the $P=0.05$ level, but G1/1 showed the lowest and G1/2 the highest transmission rate of all progenies. As in the tertiary trisomic T240W, where one line showed a consistently high male transmission rate (Janse 1987a), genetic factors may have segregated in F_5 line G1 and may also have caused the higher male transmission rate in D1 when compared with some other lines.

To further study these possible genetic factors, we selfed G1/1 and G1/2 and also made testcrosses with some of the F_6 tertiary trisomics (Table 3). Additional testcrosses were made with three tertiary trisomics derived from the testcross progenies of G1/1, G1/2 and a D1 trisomic (F_1 s in Table 3). In the progeny of one of the two F_6 tertiary trisomics originating from G1/1 the number of disomic *Ti* plants was too high to solve m and r, and the two trisomic *Ti* plants recovered were both primary trisomics. The parental F_6 trisomic was most likely a recombinant itself and carried a *Ti* allele on one of the normal chromosomes. New formulae had to be deduced for this situation. Estimates for m would then refer to the male transmission rate of an extra normal

Table 3. Segregation for *ti* and chromosome number in progenies of testcrosses 2n × (2n + 1). Tertiary trisomics from F_6 lines and from testcross progenies with F_5 plants (see Table 2) were used as the pollinator

Origin	Plant	Number of seeds	Germination (%)	*Ti*		*titi*	Total	m	r
				15	14				
F_6 (G1/1)	1	71	64 (90)	1	3	60	64	0.02	0.05
	2	77	59 (77)	2[a]	25	29	56	–[b]	–[b]
F_6 (G1/2)	1	69	53 (77)	5	0	49	54	0.09	0.0
	2	122	87 (71)	4	5	76	85	0.05	0.07
	Total	191	140 (73)	9	5	125	139	0.07	0.04
F_1 (*titi* × G1/1)	1	81	69 (85)	4	2	62	66	0.06	0.03
F_1 (*titi* × G1/2)	1	112	105 (94)	6	2	93	101	0.06	0.02
F_1 (*titi* × D1)	1	70	58 (83)	0	0	56	56	0.0	0.0

[a] Both trisomics were probably primaries, as the translocated chromosome could not be detected
[b] The number of *Ti* plants (14) was too high to solve m and r. The parental trisomic was probably a recombinant itself, carrying a *Ti* allele on one of the normal chromosomes (see text)
m, estimates of male transmission; r, recombination fraction

Table 4. Quality of pollen from tertiary trisomics T282W and disomics in F_5 and F_6 lines and in a heterotic background (FCR method). The percentage of fluorescent pollen grains ($n = 500$) is given at three sampling dates (I, II, III) during the flowering season

Line	Plant	Type	Fluorescent			Mean
			I	II	III	
F (F_5)	1	(15) *Ti*	73	69	65	69
	2	(15) *Ti*	84	87	72	81
	3	(15) *Ti*	73	72	–	73
	4	(14) *Ti*	87	83	73	81
G2 (F_5)	1	(15) *Ti*	90	93	87	90
	2	(15) *Ti*	86	94	86	89
	3	(15) *Ti*	89	90	–	90
	4	(14) *Ti*	88	85	90	88
G1/1 (F_6)	1	(15) *Ti*	91	90	–	91
	2	(15) *Ti*	85	78	79	81
	3	(15) *Ti*	70	72	69	70
G1/2 (F_6)	1	(15) *Ti*	76	85	87	83
	2	(15) *Ti*	68	72	–	70
	3	(14) *Ti*	85	86	77	83
titi × G1/1 (F_1)	1	(15) *Ti*	73	75	–	74
titi × G1/2 (F_1)	1	(15) *Ti*	94	95	97	95
titi × D1 (F_1)	1	(15) *Ti*	92	94	96	94

chromosome instead of a translocated chromosome. The other F_6 tertiary trisomic descending from F_5 trisomic G1/1 again showed a relatively low male transmission rate (0.02). However, in two F_6 tertiary trisomics from G1/2 m was not as high as expected from the high rate in F_5, but was only moderate. The difference between the F_6 trisomic from G1/1 and the two F_6 trisomics from G1/2 was not significant at the $P = 0.05$ level. This may mean either that the difference in the F_5 did not have a genetic basis or that the genetic effect was not expressed in the F_6.

Pollen quality

Two F_5 and two F_6 lines and the F_1 were tested (Table 4). The plant numbers correspond with those used in Table 3. All plants had been grown in the same season. F_5 lines G1 and D1 were not tested because the plants had been grown in an earlier season than the F_6 and F_1. Pollen quality was generally high, ranging from 69% to 95% viable pollen. In the inbred lines, the pollen quality of the trisomics varied between plants and sampling dates; on average, it was a little lower than in comparable disomics. An exception was line G2, where all of the plants investigated produced pollen of high quality (Table 4).

Discussion

Transmission upon selfing

In general, total transmission rates upon selfing seem to be lower in this tertiary trisomic than in T240W, where transmission varied between 19% and 42% in the F_5 (Janse 1987 a). Since transmission through the pollen was shown to be considerable in testcrosses with the trisomic as male parent, it must be concluded that inviability of the zygotes or embryos was the main reason for the absence of tetrasomics in the progeny of selfed trisomics. In many species, seed weight, germinating ability and seedling viability of trisomics is poor compared with disomics (Khush 1973) which, however, can not explain the strong positive correlation that we observed between ger-

mination and transmission rate (Table 1). This correlation is expected to be negative, as seed populations with a high percentage of trisomics (and possibly tetrasomics) would exhibit a poorer germination but would still express a higher transmission rate. The same applies to average seed weight.

Apparently, relative germinability and seedling viability of trisomics vary between lines. In rye, strong inbreeding effects can occur in the F_5 (Sybenga 1958). It is to be expected that lines suffering from severe inbreeding depression will produce seeds with a poor germinating ability and that in these lines the germination of trisomics will be affected more severely than in lines more tolerant to inbreeding. The latter can, therefore, exhibit a higher transmission rate, even if the percentages of trisomics among the seeds were initially the same. In seed samples with a high trisomic frequency mean seed weight is lower because trisomic seeds are usually lighter than disomic seeds (Khush 1973). The combination of these two effects is probably the reason why the correlation between seed weight and transmission rate was not significant ($r=0.37$; $P>0.10$). Inbreeding depression also affects earlier processes: fertilization and embryonic development. In lines with poor seed germination and low transmission rates, the (few) trisomic plants remained small, flowered late and had narrow leaves and short ears that produced little pollen. Trisomics from lines D1, D2, D3, F, G1 and G2, with their higher germination percentages and transmission rates, were more vigorous even though they were always weaker than the wild-type disomics appearing in the same lines. It may be concluded, therefore, that genetic background affects transmission rate in part at least through its effect on inbreeding depression.

Male transmission upon testcrossing

Any genetically conditioned difference in male transmission rates between F_1 trisomics (Table 3) must have its origin in the corresponding F_5 lines, as the *ti* female testers had closely related genotypes. Both G1/1 and G1/2 F_1s showed a moderate male transmission rate and thus, like in the F_6, did not express the difference found between their parental trisomics, possibly because genetic factors determining male transmission were recessive. The F_1 derived by testcrossing the F_5 line D1 did not show any male transmission of the extra chromosome (Table 3), while the parental line showed a relatively high rate (Table 2). Although the total number of plants was small the difference was large enough to be highly significant ($P<0.02$). An interesting point is that recombinants were absent in testcrosses with both this F_1 tertiary trisomic and the corresponding F_5 trisomics.

Thus, from the results of the testcrosses no confirmation could be obtained of genetic factors determining male transmission rate and recombination in tertiary trisomics of T282W. In the tertiary trisomic T240W the male transmission rate reached about the same level as was obtained in the present study, but genetic factors where shown to be present that caused a consistent high male transmission rate in one line (Janse 1987a).

Pollen quality

Sybenga (1958) showed that pollen fertility in rye is usually strongly affected by inbreeding: after five generations of selfing it averaged 55%. In the present study pollen quality was much higher, even in the trisomics. However, some selection against inbreeding effects was carried out when lines with good transmission rates (Table 1) were selected and vigorous trisomics with acceptable pollen production were used for testcrosses and quality tests. Pollen of two of the three F_1 trisomics tested showed a consistently very high quality. However, the third produced pollen of a relatively low quality.

Pollen fertility has been shown to be high in the primary trisomics of many species. In *Nicotiana sylvestris* it ranged from 92% to 98%, whereas male transmission varied from 0% to 34% (Goodspeed and Avery 1939). In various barley primary trisomics, pollen fertility ranged from 72% to 97% (Tsuchiya 1960) and in rye it varied from 63% for the primary trisomic *stout* to 93% for *pseudonormal* (Kamanoi and Jenkins 1975). Among tertiary trisomics of pearl millet pollen fertility ranged from 3% to 95%, but from meiotic analyses it appeared that the tertiary trisomics exhibiting low pollen fertility carried a long translocation chromosome (Singh et al. 1982).

In the present material there does not seem to be a correlation between pollen quality and male transmission rate. This is most clearly seen in the F_1s. The trisomic derived from G1/2 showed a very high pollen quality and a moderate transmission rate, while that from G1/1 had the same transmission rate but a poorer quality. The F_1 trisomic from D1 produced high quality pollen that was not capable of transmitting the extra chromosome. Reduced viability of aneuploid pollen grains lowers the quality of the total sample. The quality is also affected by the physiological condition of the trisomic plant.

Inbreeding and selection in BTT systems

Inbreeding depression plays an important role in the transmission of the translocated chromosome in tertiary trisomic T282W upon selfing. In the tertiary trisomic T240W (Janse 1987a), the average transmission rate upon selfing was higher, but the tolerance to inbreeding was also greater. This was confirmed by the appearance of tetrasomics, although at a low frequency. It seems likely that the difference in mean transmission rate between the two trisomics was mainly caused by differences

in inbreeding tolerance rather than by a specific effect of the translocated chromosome.

No lines of either T240W or T282W were without male transmission: both euploid and aneuploid pollen grains were functional. In one line of T240W the male transmission rate (m) could be raised from 0.05 to 0.20 by pollination with very few pollen grains (Janse 1987b). In one tertiary trisomic T282W tested (F_5 plant G1/2) m could similarly be raised from 0.13 (Table 2) to 0.27; showing that in this plant at least 27% of the functional pollen was aneuploid. The total pollen produced probably contained even more. Apparently, certation between euploid and aneuploid pollen tubes plays an important role in both tertiary trisomic T282W and T240W.

When BTT lines with a fair tolerance to inbreeding and aneuploidy are selected for in rye, female transmission of the translocated chromosome upon selfing will probably be sufficient for the efficient maintenance of BTTs. Simple selection for high transmission rate upon selfing, however, carries the risk of selection genotypes with a higher maler transmission rate. Male transmission rate is not correlated with apparent pollen quality but is mainly determined by the relative pollen-tube growth of aneuploid pollen grains. This is the stage at which selection for low male transmission should be carried out.

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