Chromosomes 2 and 6 are involved in the Twt-translocation

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A new translocation closely associated with the dominant mutation *Twt* (twisted tendrils) has recently been described (2). Gene *Twt* was mapped 8 cM from *a* (anthocyanin inhibition) in the direction of *lf* (lower flowering node). Trisomic analysis confirmed that the interchange chromosome includes the segment *His(2-6) — a — Twt* of linkage group IA (2). This linkage group is believed to belong to chromosome 6 (4, 5), making chromosome 6 a component of the Twt-translocation. Below we present cytogenetic data that identify chromosome 2 as the other chromosome involved in this translocation.

The Twt-line was crossed with known translocation lines from Lamm's tester set (5). Results of cytological analysis of the F_1 hybrids are given in Table 1.

Table 1. Chromosome pairing in F_1 hybrids between the Twt line and tester interchange lines.

Cross No.	Parental Lines	Chromosomes of tester line involved in translocation*	Chromosome configuration at metaphase I of meiosis		
			No. of bivalents	No. of rings of 4	No. of rings of 6
1	Twt x L84	3, 6	4	0	1
2	Twt x L83	3, 5	3	2	0
3	Twt x L21	3, 4	3	2	0
4	Twt x LI 14	1, 2	4	0	1
5	Twt x L108	2, 7	4	0	1

*Structural types of the tester interchange lines are given according to Lamm (5) and linkage groups are denoted in agreement with the version of the pea genetic map published in Vol. 25 of Pisum Genetics (8).

Results from the first three crosses confirm the involvement of chromosome 6 in the Twt-translocation (cross 1; Fig. 1 left) and exclude chromosomes 3, 4 and 5 as candidates for the other member of the interchange (crosses 2 and 3). The presence of one ring of six and four bivalents in both crosses 4 and 5 (Fig. 1 centre and right) suggests that chromosome 2 is the other chromosome involved in the Twt-translocation. The structural type of the Twt-translocation is thus postulated to be T(2,6).

In an attempt to confirm this conclusion we crossed the Twt-line with lines carrying markers of linkage group VI, the linkage group currently assigned to chromosome 2. However, joint segregation analysis (Table 2) gave no significant linkage between *Twt* and group VI markers *Pl, Prx-3* and *Acp-4,* and only a weak linkage between *Twt* and *wlo* . The lack of linkage with these standard markers suggests that either the markers chosen do not cover the entire chromosome or that the wrong linkage group has been assigned to chromosome 2.

Table 2. Joint segregation data for *Twt* and markers of the linkage groups IA, IB and VI and the breakpoint of the translocation Twt.

Gene pair	Number of progeny with designated phenotype.[1]									$\chi 2$	Recomb. frac. ± S. E.
	A/B	A/h	A/b	h/B	h/h	h/b	a/B	a/h	a/b		
a) JI 73 (*A, twt, His7^F, d, Idh^F*) x Twt (*a, Tw, His7^S, D^{co}, Idh^S*)											
a-Twt	2	45	22	-	-	-	21	5	0	63.1****	7 ± 3
d-Twt	6	42	6	-	-	-	0	3	16	35.8****	11 ± 4
His7 - Twt	18	3	0	2	35	6	0	4	11	80.1****	10 ± 3
Idh - Twt	18	5	1	5	41	6	0	6	15	77.9****	13 ± 3
a - His7	15	36	5	-	-	-	0	6	14	30.5****	14 ± 4
a - Idh	20	42	8	-	-	-	0	9	16	29.3****	18 ± 4
d - His7	7	30	6	-	-	-	0	6	9	13.2**	21 ± 6
d - Idh	9	41	4	-	-	-	0	3	16	41.9****	9 ± 3
His7 - Idh	9	6	2	4	32	4	0	6	15	47 3****	17 ± 3
b) Twt (*and, Twt. Acp-4^S. Prx-3^F*) x Fast (*And, twt, Acp-4^F, Prx-3^S*)											
And - Twt	5	66	27	-	-	-	20	5	1	66.0****	10 ± 3
Acp-4 - Twt	5	17	3	29	26	16	3	12	13	18.0**	42 ± 4
Prx-3 - Twt	4	12	9	20	31	20	9	15	4	4.4	58 ± 4
And - Acp-4	30	38	30	-	-	-	2	17	7	7.5*	45 ± 5
Prx-3 - Acp-4	6	18	12	22	29	12	10	16	9	4.7	55 ±4
c) Twt (*Twt, D^{co}, Wlo*) x NGB1514 (*twt, d, wlo)*											
Twt - d	296	-	35	-	-	-	38	-	88	163****	17 ± 4
Twt - wlo	214	-	35	-	-	-	72	-	26	7.6**	41 ± 4
d - wlo	218	-	30	-	-	-	68	-	31	18.0****	36 ± 5
d) Twt (*Twt, pl*) x K-3953 (*twt, Pl*)											
Twt - Pl	105	-	31	-	-	-	13	-	5	0.2	45 ± 6

[1]A,a=first gene; B,b=second gene; h=heterozygous. Where both genes are dominant, the capital letter stands for the dominant allele. Where the second gene is codominant, a capital A stands for the dominant allele of the first gene and capital B for an allele of the second gene which is in coupling with A. Where both genes are codominant, a capital letter stands for an allele of the first parent. *, **, **** P<0.05, 0.01 and 0.0001, respectively. Data were analysed using the CROS program developed by S.M. Rozov.

In contrast to the lack of linkage with group VI markers, *Twt* displayed clear linkage with genes on linkage group IB *(d, and, Idh)* (Table 2). Although *a* and *d* were placed on the same linkage group on the classical pea map, recent evidence (3, 6) indicates that the two genes are not on the same chromosome. Paruvangada et al. (6) found linkage of gene *Enod1* with both *a* on group IA and *Fum* on group II and they suggest groups IA and II should be joined. They found no evidence of linkage between *Enod2* and group IB markers. Likewise, in an earlier report, Kosterin (3) failed to show linkage not only between *d* and *lf* but also between *d* and the more distally situated group IA loci *His7* and *blb. Twt* maps in the vicinity of *lf* and would not be expected to show linkage with *d.* However, our data indicate a recombination value of 10 to

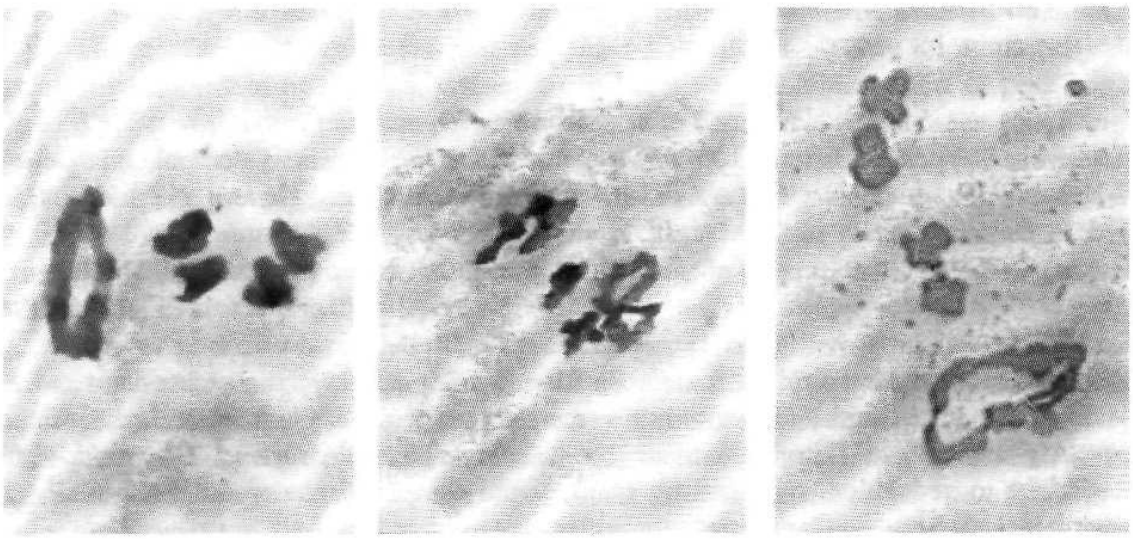

Fig. 1. Chromosomal configurations at the first metaphase of meiosis in pollen mother cells of F_1 hybrids: Left) Twt x L-84; Centre) Twt x L-l14; Right) Twt x L-108. Acetocarmine staining.

15% for *d* and *Twt.* This apparent contradiction may be explained if 1) the translocation strongly reduces the recombination in the lower part of linkage group I or 2) *d* belongs to the other linkage group involved in the translocation. The former hypothesis is weakened by our finding that the map distance between *His7* and *Twt* is comparable to the distance between these loci in the absence of the translocation (1). Moreover, based on the data from cross JI 73 x Twt, *Twt* maps equally well between *a* and *His7* and between *His7* and *d,* indicating pseudo-linkage of the two regions and supporting the latter hypothesis. We also find a weak linkage observed between *d* and *wlo* (Table 2), suggesting that *d* may be part of linkage group VI, the linkage group conventionally assigned to chromosome 2 (7).

However, we do not have compelling evidence for combining linkage group IB with any of the other linkage groups in pea. Our results only demonstrate that translocation Twt involves chromosomes 2 and 6, that linkage group IA represents one of the chromosomes (presumably chromosome 6), and that linkage group IB displays linkage with *Twt* and what appears to be pseudo-linkage with linkage group IA in crosses involving the Twt translocation.

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