Theor Appl Genet (1984) 67: 123–129

Modification of the properties of a translocation in the German cockroach by selection

D. G. Cochran and M. H. Ross

Department of Entomology, Virginia Polytechnic Institute and State University,
Blacksburg, VA 24061, USA

Received June 2, 1983; Accepted August 11, 1983
Communicated by A. Robertson

Summary. A stock of *Blattella germanica* bearing the interchange T(3;12)/3;12 was subjected to close inbreeding with selection for random disjunction at metaphase I. After 3–4 generations of selection, interchange quadrivalent chiasma frequency decreased, variability in free bivalent chiasma frequency increased sharply, and individuals with either random or directed disjunction were present in the stock. Random disjunction was modified from a ratio of 2 : 1 : 1 : 2 (adj.-1; alt.-1; adj.-2; alt.-2) to a ratio of 1 : 1 : 1 : 1. After 7–8 generations of selection, chiasma frequency appeared to stabilize at lower than normal levels and variability decreased for both quadrivalents and free bivalents. Directed disjunction was modified from a ratio of 2 : 1 : 1 : 4 to 1 : 1 : 1 : 2, and no individuals with the original high level of directed disjunction were detected. Chains-of-four tended to orient randomly, especially in individuals where the ring quadrivalents showed directed disjunction. Relaxation of inbreeding, but not selection, produced an increase in chiasma frequency and variability in both free bivalents and quadrivalents, but the modified ratios for both random and directed disjunction were retained. These results are discussed with respect to inbreeding effects and genetic control of chiasma frequency and metaphase I disjunction in interchange quadrivalents.

Key words: Interchange quadrivalents – Disjunction – Chiasma frequency – *Blattella* – Cockroach

Introduction

Classic cytogenetic studies on rye provide a major portion of the evidence on genotypic control of disjunction in interchange heterozygotes (Lawrence 1958, 1963; Sun and Rees 1967; Rees and Sun 1965; Thompson 1956). Recent work on interchanges has focused more on analyses of metaphase I orientations. Sybenga (1975) reviewed and, in several instances, clarified results from these studies, especially with respect to complex inter-relationships between disjunction and chiasma frequency (C.F.) and/or position. A new aspect of orientation was introduced by investigators that reported data on alternate-2 as well as the generally recognized alternate, adjacent-1, and adjacent-2 metaphase I orientations (Cochran 1976, 1977; Endrizzi 1974; Lacadena and Candela 1977; Naranjo and Lacadena 1979; Vosselman 1981). What this means, of course, is that for each adjacent-disjunction type there is a corresponding alternate type, both of which result in viable gametes. The existence of alternate-2 was questioned by Boussy (1982), but the material from *Blattella germanica* (L.), and other species as well, presents strong evidence against Boussy's argument (Cochran 1983; Rickards 1983).

The discovery on two occasions of altered disjunction-orientation patterns in an interchange heterozygote, T(3;12)/3;12, in *B. germanica* offered a promising opportunity to combine studies on orientation with those on control mechanisms (Ross and Cochran 1977, 1979). Normally the stock shows 70–72% alternate disjunction (Ross and Cochran 1975) with an underlying orientation pattern in ring quadrivalents that fits a 2 : 1 : 1 : 4 ratio of adjacent-1, alternate-1, adjacent-2, and alternate-2, respectively (Cochran 1976). The alteration was a change to random disjunction with an orientation pattern fitting a 2 : 1 : 1 : 2 ratio (Cochran 1977). An attempt was made to maintain and possibly develop a true-breeding random disjunction trait by selection (Ross and Cochran 1982). A preliminary assessment from embryonic lethality data showed that two main groups were still present; one with approximately 50% lethality in matings of T/+ males (presumed random disjunction) and the other with lethality centered around 38–46% (presumably a low degree of directed alternate disjunction). The major change from the group used as a source of the selections was an apparent narrowing of the difference between the two groups due to a lowered frequency of alternate disjunction.

This paper presents cytological data gathered in the course of the above selection experiments on T(3;12)/3;12. In many instances, it has been possible to obtain data on chaining and C.F. at diplotene-diakinesis and on the disjunction situation at metaphase I in the same individual. The results document changes which have occurred over about 16 generations of selection.

Materials and methods

Physical properties of T(3;12)/3;12 quadrivalents were described earlier (Ross and Cochran 1975). In brief, the interchange involves a small chromosome (No. 3) and the longest chromosome of the karyotype (No. 12). The breakpoint on chromosome 3 is near the center of the chromosome and apparently very close to the centromere; that on chromosome 12 is centrally located but is separated by a short interstitial segment from the submetacentric centromere. Chiasmata occur in terminal or near-terminal positions and, in most quadrivalents, there is one chiasma in each arm (7% rupture into chains-of-four). These characteristics apply to the original stock, i.e., a backcross system utilizing the chromosome 3 marker hooded-prontotum (*hd*) for identification of T/+ individuals.

The selected lines which furnished the main material for this study were described elsewhere (Ross and Cochran 1982). They originated from intercross progeny of T(3;12)/3;12 ♀ × T(7;12)/7;12 ♂ in which each genotype was identifiable by a morphological mutant (Ross and Cochran 1979). Males with random disjunction (47–51% alternate) and those with directed alternate disjunction (62–64% alternate) occurred in about equal frequencies. The latter differed from the original stock in having a lower frequency of alternate-2 orientations. Five lines were initiated from matings of T(3;12)/3;12 ♂ to non-translocation carrying ♀ (*hd/hd*) in which embryonic lethality fell within the range typical of random disjunction (47–53%). Selection by sib matings was continued for ca. 12 generations, following which the lines were combined and selections made from mass matings.

Males for cytological study were drawn randomly from the selected lines at about the 3rd–4th generation of selection and again at about the 7–8th generation. A smaller group was studied 3–4 generations after instituting mass-matings. Lethality data had shown similar types of response in the 5 lines, with patterns in each like that of the pooled data presented earlier (Ross and Cochran 1982, Fig. 2E). Testes from 3rd–4th instar nymphs were prepared for examination as previously described (Cochran and Ross 1969). All were progeny from first egg cases.

Results

The pertinent characteristics of the original T(3;12)/3;12 stock are presented in Table 1. It is evident that the stock was reasonably homogeneous with respect to autosomal C.F. and the amount of quadrivalent chaining. The latter is, of course, inversely related to the C.F. occurring in the quadrivalent. Changes that occurred in the course of selection are described below according to 1) chiasma frequency 2) disjunction and 3) relationships between chiasma frequency and disjunction.

Table 1. Translocation characteristics of the original T(3;12)/3;12 males

C.F.A.[a]	C.F.Q.[b]	% Chaining[c]	% Alt. disj.[d]	Reference
1.33±0.02[e]	3.93	7.0	72.2	Ross and Cochran 1975
–	–	–	66.0	Cochran 1976
1.34±0.06	3.94	6.5±1.8	68.0	Cochran unpublished

[a] C.F.A. = mean chiasma frequency/autosomal bivalent; [b] C.F.Q. = mean chiasma frequency in the 4 arms of the quadrivalent. [c] at diplotene-diakinesis; [d] at metaphase I (rings only); [e] assumed autosome value on wild type individuals (Keil and Ross 1983) Mean ± SE

Chiasma frequency

Figure 1 shows chiasma frequencies of free bivalents and quadrivalents of T(3;12)/3;12 males for each period of study, i.e., following 3–4 and 7–8 generations of selecting closely related pairs for 50% embryonic lethality and, finally, at 3–4 generations after instituting mass-matings. The first set of data (Fig. 1, I) differed from those typical of the original T(3;12)/3;12 stock and, presumably, the group used to initiate selection. C.F. among free bivalents was slightly, but significantly, higher (1.36 ± 0.32 vs 1.34 ± 0.06, $P < 0.01$). However, the greatest difference was the extensive variability (Fig. 1, range 1.19–1.62). Variability among the quadrivalents was also high but, in addition, mean C.F. was low (3.85 vs. 3.94 in the original stock). These characteristics were due to the break-up of the quadrivalent ring into chains-of-four, as shown in Table 2, column 3 (mean of 15.1 ± 2.8 compared to 6.5 ± 1.8 from Table 1). No unusual chaining was noted among the source group of the selection lines (intercross progeny). T(3;12)/3;12 quadrivalents ordinarily show little chaining (Table 1).

Figure 1, I and II, document changes that occurred in C.F. between the 3rd–4th and 7th–8th generations of selection. C.F. in the free bivalents apparently became stabilized at a lower than normal level (Ave. = 1.27 ± 0.19). This is a substantial decrease in the mean C.F., as well as in the variability, from that found at the 3rd–4th generation (1.36 ± 0.32). A somewhat different pattern was seen in the quadrivalents. Variability decreased but C.F. seemed to have stabilized at two levels rather than one. If considered from the point-of-

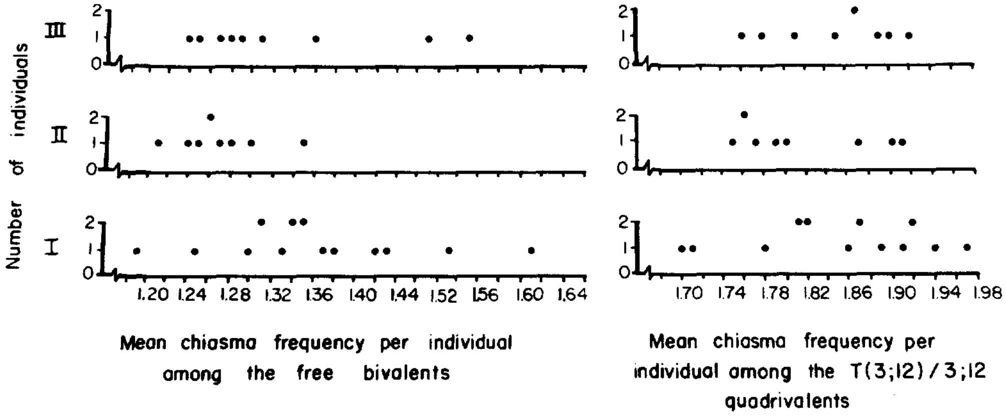

Fig. 1. Chiasma frequency among free bivalents and quadrivalents of T(3;12)/3;12 males sampled in the course of selection for 50% embryonic lethality. *I* sampled at 3–4 generations; *II* sampled at 7–8 generations; *III* sampled at 3–4 generations after a shift to selection by mass-matings (see text)

view of chaining, the majority of individuals studied had diplotene-diakinesis chaining in the range of 20–25% of the cells, but three had values approaching that of the original stock, i.e., 8.8–12.8% (Table 2, column 6).

Following mass-mating a shift occurred in C.F. from the lower means and reduced variability among both free bivalents and quadrivalents, seen at 7–8 generations, towards the higher means and greater variability found at 3–4 generations (Fig. 1, III vs. II and I, respectively). Among the free bivalents, the mean C.F. was intermediate (1.34 ± 0.33) between the two earlier sets of data, but the variability equaled that at 3–4 generations (1.36 ± 0.32). In contrast, variability among the quadrivalents was greater than that at 7–8 generations (Fig. 1, III vs. II) but an increase in the mean C.F. resulted in equality to that found at 3–4 generations (3.85 ± 0.19 vs. 3.85 ± 0.25, respectively).

Disjunction

As far as we are aware no individuals in the original stock of T(3;12)/3;12 exhibited less than about 65% directed disjunction (Table 1, column 4). Heterogeneity apparently entered from crosses involving T(7;12)/7;12

Table 2. Disjunction and chaining in T(3;12)/3;12 males following selection for 50% embryonic lethality

I. At 3–4 generations			II. At 7–8 generations			III. After mass-mating		
Individual no.[a]	% Alt. disj. (rings only)	% Chaining[b]	Individual no.[a]	% Alt. disj. (rings only)	% Chaining[b]	Individual no.[a]	% Alt. disj. (rings only)	% Chaining[b]
1	71.6	17.8	1	59.8	20.8	1	57.0	10.0
2	67.4	3.2	2	59.8	20.3	2	56.2	11.0
3	65.4	11.0	3	57.4	24.3	3	53.6	22.0
4	65.4	13.4	4	57.3	–	4	52.6	15.0
5	62.4	9.3	5	57.0	9.9	5	52.2	7.7
6	58.3	29.1	6	55.4	8.8	6	48.5	12.5
7	52.9	6.2	7	54.3	–	7	–	12.6
8	52.7	21.8	8	53.2	–	8	–	18.8
9	51.2	18.8	9	53.1	–	9	–	23.9
10	50.9	17.9	10	51.9	12.8			
11	50.5	7.7	11	51.6	24.1			
12	50.5	14.3	12	50.8	–			
13	50.4	19.1	13	50.4	22.6			
14	49.2	8.1	14	47.3	25.3			
15	40.1	30.1						
16	–	13.0						

[a] The individual data are arranged on the basis of decreasing % alternate disjunction at metaphase I, except for those where observations were limited to the % chaining

[b] Chains-of-four

(Ross and Cochran 1982). Judging from the lethality data, a few males among these intercross progeny retained disjunction frequencies similar to the original stock, but most of those with directed disjunction showed a reduced frequency of alternate types (ca. 58–62%). Roughly one-third of the males almost certainly showed random disjunction. Following 3–4 generations of selection for the latter trait, about half of the males exhibited random disjunction among metaphase I ring quadrivalents (Table 2, column 2). Four still showed disjunction like that of the original stock (65–72%) and 2 had an intermediate level like that prevalent among the source group (58–62%). These data confirm the existence of considerable variability in this characteristic. Nevertheless, the underlying orientation patterns suggest two main cell type ratios (Table 3). Using a X^2 statistic the ratios of adjacent-1 : alternate-1 : adjacent-2 : alternate-2 adequately fit a 1 : 1 : 1 : 1 and 2 : 1 : 1 : 4 for individuals with random and directed disjunction, respectively.

Table 3. Comparison of metaphase I cell types from T(3;12)/3;12 males of the original and the selected stocks

Source	Adj.-1	Alt.-1	Adj.-2	Alt.-2	% alt. disj
Original[a] stock	167	76	72	388	66.0
Inbred[b] (directed disj.)	51	34	27	118	66.1
Inbred[c] (random disj.)	57	57	61	63	50.4

[a] From Cochran 1976

[b] After 3–4 generations of selection for random disjunction in males. Pooled data from individuals with 62–67% alternate disjunction

[c] After 3–4 generations of selection for random disjunction in males. Polled data from individuals with 47–53% alternate disjunction

Continued selection through 7–8 generations produced further changes (Table 2, II). The highest level of directed disjunction was only about 60%. The entire upper range of this characteristic appears to have been eliminated from the population by selection. Although the frequency of males with random disjunction apparently did not change very much, the distinction between directed and random disjunction is less clearcut.

The underlying orientation patterns could be analyzed for chains as well as intact quadrivalents (rings) (Table 4) because most individuals showed an unusually high percent chaining (Table 2, column 6). Orientation patterns from individuals showing directed disjunction (55–60% alternate) are presented in Table 4. Those from intact rings fit a ratio of 1 : 1 : 1 : 2 ($X^2_3=3.19$, $P>0.30$). This is a marked shift from the ratio of 2 : 1 : 1 : 4 underlying the somewhat higher level of directed disjunction seen at 3–4 generations. Chain orientations in these same individuals showed complete randomness. The data fit a 1 : 1 : 1 : 1 ratio ($X^2_3=1.93$, $P>0.50$).

Corresponding data from those individuals classified as showing random disjunction at metaphase I (47–53% alternate disjunction) are given in Table 5. In this case the data fit a 1 : 1 : 1 : 1 ratio for both rings ($X^2_3=1.64$; $P>0.80$) and chains ($X^2_3=6.78$; $P>0.05$). On the basis of these data (Tables 4 and 5) it appears that the chain configurations at metaphase I orient independently of the orientation exhibited by intact quadrivalent rings. However, in some individuals,

Table 4. Counts of metaphase I cell types from T(3;12)/3;12 males showing directed disjunction after 7–8 generations of selection for random disjunction

Adj.-1	Alt.-1	Adj.-2	Alt.-2	% Alt. disj. (rings only)	% chaining
34 (0)[a]	20 (1)	34 (0)	70 (0)	57.0[b]	9.9[c]
29 (4)	29 (4)	26 (6)	53 (7)	59.8	20.3
44 (9)	46 (11)	50 (8)	94 (8)	59.8	20.8
25 (5)	22 (1)	24 (5)	44 (0)	57.4	24.3
16 (2)	16 (0)	19 (4)	31 (0)	57.3	–
44 (7)	37 (3)	45 (4)	73 (6)	55.3	–
39 (6)	36 (5)	39 (3)	61 (3)	55.4	–
231 (33)	206 (25)	237 (30)	426 (24)	57.4 ± 1.3	18.8 ± 2.5

[a] Cell counts as intact quadrivalents (rings) and as chains-of-four (in parenthesis) at metaphase I. Chains identified following Cochran (1976)

[b] Fits a 1 : 1 : 1 : 2 ratio at $P>0.05$; all others fit this ratio at $P>0.50$

[c] Percent chaining at diplotene-diakinesis in the same individuals. Based on metaphase I cells, the percent chaining is 9.2%

Table 5. Counts of metaphase I cell types from T(3;12)/3;12 males showing random disjunction after 7–8 generations of selection for random disjunction

Adj.-1	Alt.-1	Adj.-2	Alt.-2	% Alt. disj. (rings only)	% chaining
33 (18)[a]	35 (11)	46 (13)	36 (7)	47.3	25.3[b]
29 (7)	30 (2)	27 (9)	27 (3)	50.4	22.6
25 (9)	23 (2)	20 (4)	25 (2)	51.6	24.1
27 (2)	24 (1)	23 (2)	30 (1)	51.9	12.8
26 (4)	22 (12)	26 (6)	37 (6)	53.2[c]	–
13 (2)	11 (4)	15 (0)	14 (2)	47.2	–
23 (4)	26 (4)	26 (2)	25 (3)	51.0	–
176 (46)	171 (36)	183 (36)	194 (24)	50.4 ± 1.5	21.2 ± 2.4

[a] Cell counts as intact quadrivalents (rings) and as chains-of-four (in parenthesis) at metaphase I

[b] Percent chaining at diplotene-diakineses in the same individuals. Based on metaphase I cells, the percent chaining is 16.4%

[c] This value is in the range of overlap between random and directed disjunction and fits both the 1:1:1:2 ($P > 0.30$) and the 1:1:1:1 ($P > 0.20$) ratios. All others fit the 1:1:1:1 ($P > 0.30$)

Table 6. Counts of metaphase I cell types from T(3;12)/3;12 males after 3–4 generations of a change from inbreeding to mass mating with selection for random disjunction

Adj.-1	Alt.-1	Adj.-2	Alt.-2	% Alt. disj. (rings only)	% chaining
Directed disjunction					
25 (0)[a]	25 (0)	27 (0)	44 (0)	57.0	10.0[b]
31 (0)	28 (1)	22 (0)	40 (0)	56.2	11.0
56 (0)	53 (1)	49 (0)	84 (0)	56.6 ± 0.8	10.5 ± 0.8
Random disjunction					
16 (2)	14 (0)	19 (1)	19 (0)	48.5	12.5
19 (4)	19 (1)	20 (1)	26 (4)	53.6	22.0
18 (0)	18 (0)	18 (0)	22 (0)	52.6	15.0
6 (0)	7 (0)	5 (0)	5 (0)	52.2	7.7
59 (6)	58 (1)	62 (2)	72 (4)	51.7 ± 1.5	14.3 ± 2.4

[a] Cell counts as intact quadrivalents (rings) and as chains-of-four (in parenthesis) at metaphase I

[b] Percent chaining at diplotene-diakinesis in the same individuals. Based on metaphase I cells, the percent chaining is 0.4% for directed disjunction cells and 4.9% for random disjunction cells

where counts of chains were highest, random disjunction in rings seems to correlate with a tendency towards higher numbers of cells with adjacent disjunction in chains. The only disconcerting feature of these data is that in both cases (Tables 4 and 5) the percent chaining is somewhat lower at metaphase I than it is at diplotene-diakinesis. If anything, one would expect the opposite to occur. No ready explanation for this finding is apparent.

Only limited data were obtained on metaphase I disjunction for the inbred, mass-mated stock (Table 2, III and Table 6). It appears that the higher levels of directed disjunction are still rare or absent (Table 6). The apparent decline in the percent chaining has also impacted upon the number of metaphase I cells with ruptured quadrivalents (Table 2, last column). Indeed, the numbers are so small that their value is questionable. What is apparent, however, is that the orientation patterns underlying both directed (1 : 1 : 1 : 2; $X^2_2 = 3.61$; $P > 0.30$) and random ($X^2_3 = 1.96$; $P > 0.50$) disjunction remain as they were at 7–8 generations of selection (Tables 6 and 4–5, respectively).

Relationship between chiasma frequency and disjunction

Table 2 shows that both high and low frequencies of chaining occurred in individuals with either random or directed disjunction as expressed in intact rings. Independence of C.F. from the factor controlling disjunction in rings is also apparent in that mass-matings caused a reversal of changes in C.F. (Fig. 1), but disjunction and orientation patterns were similar to those at 7–8 generations (Tables 4–5 and 6, respectively).

However, C.F. did have an indirect influence on disjunction. The absence of directed disjunction (alternate) in chains, noted above, reduced the overall frequency of alternate disjunction in individuals showing directed disjunction in rings, at least in those recorded at 7–8 generations (Table 4). The average alternate disjunction based on all orientations recorded is 56.2 compared to 57.4% for intact rings (9% recorded as chains). If the comparison was based on 18.8% chaining, alternate disjunction would be estimated at 55.7%.

Discussion

Interchange heterozygotes in *B. germanica* are of interest because of the precise ratios which occur among the four orientation types at metaphase I (Cochran 1976, 1977). Structural features that may facilitate the expression of similar ratios among quadrivalents of different interchanges were noted earlier (Ross and Keil 1982). On the other hand, changes in such ratios within specific interchanges appear to be genetically controlled (Ross and Cochran 1977, 1979). The present experiments provide new evidence for genetic control and, concomitantly, add to our understanding of C.F. and disjunction – chiasma frequency relationships in this species.

A certain amount of inbreeding was an unavoidable part of the selection procedure. Characteristics that reverted towards the original values in the selected stock following mass-mating are almost certainly attributable to inbreeding per se. They include the mean chiasma frequency of the total group and inter-individual variation, as would be predicted from studies on inbreeding and chiasmata in other organisms (Karp and Jones 1982, 1983; Rees 1955; Rees and Thompson 1956; Sybenga 1958, 1975). However, the changes observed in *B. germanica* departed from expected patterns in that (1) an initial decrease in mean frequency was restricted to the quadrivalents, (2) interindividual variation increased prior to a decrease in mean frequency among free bivalents, and (3) in the most severely inbred group the mean frequency was stabilized at a lower-than-normal level in the free bivalents and approached this situation in the quadrivalents.

Mather (1938) and Diez and Puertos (1981) postulated control of chiasmata at the cellular level. Our data support this hypothesis because the initial decreases in C.F. occurred among bivalents that could best afford the loss, i.e., those within the quadrivalent where frequency approached 2 chiasmata per bivalent. Also, the changes in C.F. followed a similar pattern in the quadrivalents and free bivalents. The difference in timing may be attributed, at least in part, to the higher frequency that characterizes quadrivalents in *B. germanica* (Keil and Ross 1983; Ross and Cochran 1981; Ross and Keil 1982). Arana et al. (1980) suggested that this property might result from a breakdown in chiasma interference due to the physical arrangement of the interchange heterozygotes.

Low inter-individual variation in C.F. showed stabilization both among wild-type (Keil and Ross 1983) and at the new lower level among free bivalents following inbreeding of T(3;12)/3;12. C.F. among quadrivalents was not completely stabilized at a level lower than that typical of quadrivalents, but further selection could have had this result. The apparent lower effective level of C.F. could have adaptive significance as it would protect against univalency.

The changes in disjunction frequency and underlying orientation patterns were less variable and, presumably, had a simpler genetic basis than those associated with C.F. Males with random and directed disjunction were present throughout the selections and apparently remained in roughly equal frequencies. This suggests maintenance of heterozygosity by some type of genetically balanced system. Orientation patterns where ring quadrivalents showed either directed or random disjunction underwent single, discrete changes. The former shifted from one fitting a 2 : 1 : 1 : 4 ratio (ca. 65% alternate) to a 1 : 1 : 1 : 2 (57–60% alternate) of adjacent-1, alternate-1, adjacent-2, alternate-2, respectively; the latter, from a 2 : 1 : 1 : 2 ratio (Cochran 1977) to one with complete randomness, i.e., a 1 : 1 : 1 : 1. Each change represented about a 50% reduction in the frequency of adjacent-1 and alternate-2 orientations. If selection established homozygosity for a monofactorial modifier, this could explain why expression of the directed disjunction trait was held to a lower-than usual proportion of alternate orientations. The similarity of the changes suggests that a single modifier may have been responsible for those individuals with directed and random disjunction, but it then becomes difficult to account for the time element. The new random pattern occurred first at the 3rd–4th generation of selection; that underlying directed disjunction was not seen until the 7–8th generation.

Sybenga (1975) called attention to the role of genotypic differences in the control of disjunction and C.F. Variations reported here are also attributable to genetic factors. However, the alterations in disjunction in ring quadrivalents were apparently independent of C.F. C.F. had an indirect effect that resulted from a lack of expression of directed disjunction (alternate) in chains. A decrease in C.F. caused increased chaining and this, in turn, decreased the overall frequency of alternate orientations in individuals where alternate disjunction was favored in cells with intact rings. The possibility that orientations also differed in rings and chains where individuals showed random disjunction in rings cannot be ruled out since chains showed a tendency towards more adjacent than alternate configurations. If the latter reflects a real difference, then the genetic factors responsible for directed vs. random disjunction in rings are expressed in chains, but in a different manner than in rings. Otherwise, it appears that the factor controlling directed disjunction is expressed only in rings. Sybenga (1968) also found higher frequencies of adjacent orientations among chains than among rings.

Rickards (1964) noted a possible effect on orientation from genetically-controlled changes in chiasma position. We did not study this trait specifically, but did not note any unusual non-distal chiasmata. If a change(s) of position was responsible for altered orientation patterns, it would have to occur in such a manner as to affect adjacent-1 and alternate-2 in a similar manner. A non-distal chiasma in a different selected strain was associated with both variability and unbalance of the normally discrete ratios (Diez, personal communication), in contrast to the regular ratios maintained here in the course of selection. Precise ratios reported in earlier work on *B. germanica*, including that on T(3;12)/3;12, were associated with distal chiasmata localization (Cochran and Ross 1974; Cochran 1976, 1977; Keil and Ross 1983). This argues gainst altered chiasma position as a basis for the changes in disjunction and underlying orientation patterns. It also casts doubt on whether increased variability in C.F. at the 3rd–4th generations of selection reflected changes in chiasma position, as might be expected (Jones 1974; Karp and Jones 1982; Rees 1955). The variability suggests a breakdown in control (Sybenga 1975), but possibly it involved the number of distally-localized chiasmata. We suspect that the seeming "all-or-none" event in the altered orientation patterns seen here may be evidence of genetic differences that affect spindle fiber structure and/or formation (Nicklas 1974; Rickards 1965).

Acknowledgements. We wish to thank Mrs. Nancy Boles and Mrs. Elizabeth Watson for technical assistance. This study was supported, in part, by research grant PCM-8001620 from the National Science Foundation.

References

Arana P, Santos JL, Giraldez R (1980) Chiasma interference and centromere co-orientation in a spontaneous translocation heterozygote of *Euchorthippus pulvinatus gallicus* (Acrididae; Orthoptera). Chromosoma 78:327–340

Boussy IA (1982) Alternate-2 disjunction does not exist. Genetics 100:505–509

Cochran DG (1976) Disjunction types and their frequencies in two heterozygous reciprocal translocations of *Blattella germanica* (L.). Chromosoma 59:129–135

Cochran DG (1977) Patterns of disjunction frequencies in heterozygous reciprocal translocations from the German cockroach. Chromosoma 62:191–198

Cochran DG (1983) Alternate-2 disjunction in the German cockroach. Genetics 104:215–217

Cochran DG, Ross MH (1969) Chromosome identification in the German cockroach. J Hered 60:87–92

Cochran DG, Ross MH (1974) Cytology and genetics of T(9;11) in the German cockroach and its relationship to other chromosome 9 traits. Can J Genet Cytol 16:639–649

Diez M, Puertas MJ (1981) Chiasma distribution in asynaptic *Locusta migratoria.* Chromosoma 84:431–437

Endrizzi JE (1974) Alternate-1 and alternate-2 disjunctions in heterozygous reciprocal translocations. Genetics 77:55–60

Jones GH (1974) Correlated components of chiasma variation and the control of chiasma distribution in rye. Heredity 32:375–387

Karp A, Jones RN (1982) Cytogenetics of *Lolium perenne.* 1. Chiasma frequency variation in inbred lines. Theor Appl Genet 62:177–183

Karp A, Jones RN (1983) Cytogenetics of *Lolium perenne.* 2. Chiasma distribution in inbred lines. Theor Appl Genet 64:137–145

Keil CB, Ross MH (1983) Chiasma frequency in male *Blattella germanica* (Dictyoptera; Blattellidae). Can J Genet Cytol 25:65–71

Lacadena JR, Candela M (1977) Centromere co-orientation at metaphase I in interchange heterozygotes of rye, *Secale cereale* L. Chomosoma 64:175–189

Lawrence CW (1958) Genotype control of chromosome behavior in rye. 6. Selection for disjunction frequency. Heredity 12:127–131

Lawrence CW (1963) The orientation of multiple associations resulting from interchange heterozygosity. Genetics 48: 347–350

Mather K (1938) Competition for chiasmata in diploid and trisomic maize. Chromosoma 1:119–128

Naranjo T, Lacadena JR (1979) Analysis of centromere co-orientation in a rye-wheat derivative by means of C-banding. Chromosoma 73:227–235

Nicklas RB (1974) Chromosome segregation mechanisms. Genetics 78:205–213

Rees H (1955) Genotypic control of chromosome behavior in rye. 1. Inbred lines. Heredity 9:93–116

Rees H, Sun S (1965) Chiasma frequency and the disjunction of interchange associations in rye. Chromosoma 16: 500–510

Rees H, Thompson JB (1956) Genotypic control of chromosome behavior in rye. 3. Chiasma frequency in homozygotes and heterozygotes. Heredity 3:409–424

Rickards GK (1964) Some theoretical aspects of selective segregation in interchange complexes. Chromosoma 15: 140–155

Rickards GK (1965) An analysis of co-orientation in mitosis and meiosis. J Theor Biol 9:332–349

Rickards GK (1983) Alternate-1 and alternate-2 orientations in interchange (reciprocal translocation) quadrivalents. Genetics 104:211–213

Ross MH, Cochran DG (1975) The German cockroach, *Blattella germanica.* In: King RC (ed) Handbook of genetics, vol 3. Plenum Press, New York, pp 35–62

Ross MH, Cochran DG (1977) Analysis of a double reciprocal chromosome translocation in the German cockroach. J Hered 68:231–237

Ross MH, Cochran DG (1979) Properties of a three chromosome double translocation heterozygote in the German cockroach. J Hered 70:259–266

Ross MH, Cochran DG (1981) Synthesis and properties of a double translocation heterozygote involving a stable ring-of-six interchange in the German cockroach. J Hered 72:39–44

Ross MH, Cochran DG (1982) Genetics and cytogenetics of the German cockroach. In: Pal R, Kitzmiller JB (eds) Cytogenetics and genetics of vectors. Kodansha, Tokyo, pp 181–195

Ross MH, Keil CB (1982) C-band morphology of T(8;9)/8;9 in *Blattella germanica.* Theor Appl Genet 63:289–293

Sun S, Rees H (1967) Genotypic control of chromosome behavior in rye. 9. The effect of selection on the disjunction frequency of interchange associations. Heredity 22:249–254

Sybenga J (1958) Inbreeding effects in rye. Z Vererbungsl 89:338–354

Sybenga J (1968) Orientation of interchange multiples in *Secale cereale.* Heredity 23:73–79

Sybenga J (1975) Meiotic configurations. In: Frankel R, Grossman M, Linskens HF, de Zeeuw D (eds) Monographs on theoretical and applied genetics, vol I. Springer, Berlin Heidelberg New York, pp 1–251

Thompson JB (1956) Genotypic control of chromosome behavior in rye. 2. Disjunction at meiosis in interchange heterozygotes. Heredity 10:99–108

Vosselman L (1981) Meiotic segregation of five different reciprocal translocations in the onion fly, *Hylemya antiqua* (Meigen). Chromosoma 81:727–738