

## Y-Chromosome Hyperploidy in *Rumex*

JERZY ŻUK

Department of Genetics, Polish Academy of Sciences, Warsaw (Poland)

**Summary.** 1. Male and female Y-chromosome hyperploid plants were obtained and morphologically and cytologically investigated.

2. Conjugation of sex chromosomes was investigated in ♂ plants with 1, 2 and 3 additional Y chromosomes. Conjugation between sex chromosomes was end-to-end. Association between Y-chromosomes was partly based on conjugation between homologous segments and partly due to heterochromatin fusion.

3. Transmission of the additional Y chromosome to the progeny was studied. In all cases transmission of the extra Y chromosome was very low. The reasons for this phenomenon are probably nonrandom fertilization, nonrandom degeneration of megaspore, and reduced seed setting and seed fertility in plants with additional Y chromosomes.

4. The phenotypic effect of Y chromosome hyperploidy was investigated. Plants with extra Y chromosomes are shorter and die earlier. The fertility of such plants is low. Thus, although Y chromosomes are heterochromatic and nonactive (except in the premeiotic interphase of microsporogenesis) they have a marked influence on the appearance of Y-chromosome hyperploid plants.

### Introduction

Y chromosomes in *Rumex thyrsoiflorus* are heterochromatic and late-replicating, and they have no effect on sex determination (Żuk, 1963, 1969a, 1969b). However, they are not genetically inert as data were obtained indicating that they are responsible for the fertility of male plants and for the sex ratio (Żuk, 1970).

The data here presented concern the effect of extra Y chromosomes on sex chromosome conjugation and on the fertility and morphology of male and female plants. The pattern of transmission of supernumerary Y chromosomes to the progeny is also discussed.

### Material and Methods

In the course of studies on polyploidy and sex determination in *R. thyrsoiflorus* one particular female plant with karyotype  $XXYY + 12A = 16$  instead of  $XX + 12A = 14$  was obtained (Fig. 1). The cross of this

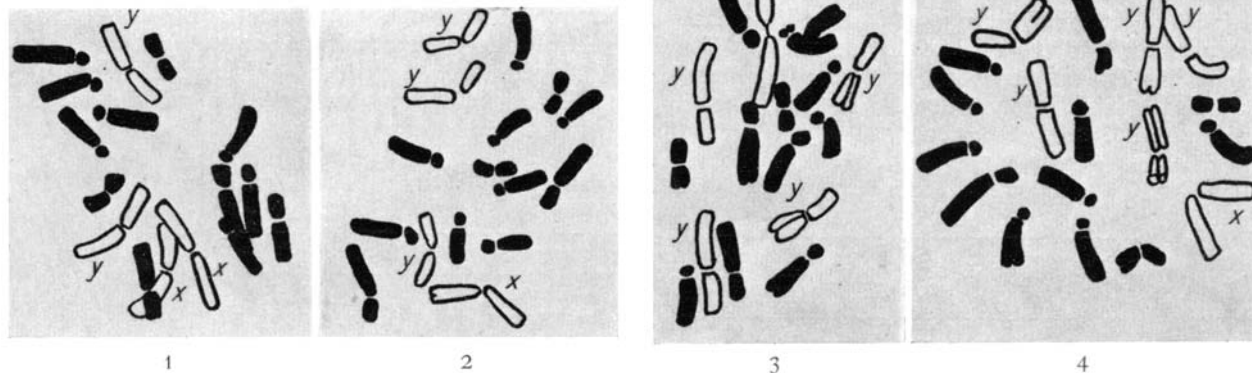
female plant with a normal male plant  $XY + 12A = 15$  gave many male and female plants with additional Y chromosomes. Male plants  $XYYY + 12A = 17$  and female plants  $XXYY + 12A = 16$  were chosen as parental forms for further crosses, giving more Y-chromosome hyperploid plants with 1, 2 and 3 additional Y chromosomes (Figs. 2, 3, 4).

The methods of cytological analysis were the same as described previously (Żuk, 1963, 1969c).

### Results

#### 1. Sex chromosome conjugation in male plants with additional Y chromosomes

In normal male plants  $XY_1Y_2 + 12A = 15$  sex chromosomes form a trivalent  $Y_1-X-Y_2$ . The homologous segments of X and Y chromosomes are very short, and at diakinesis sex chromosomes associate end to end giving a long characteristic trivalent



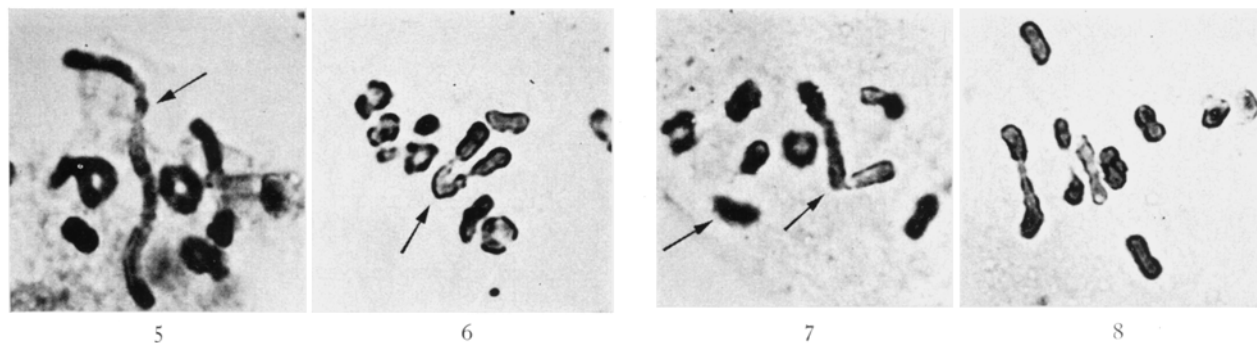
Figs. 1–4. Metaphasal plates from root tips.  $\times 1700$

Fig. 1. Female plant with karyotype  $16 = XXYY + 12A$

Fig. 2. Male plant with karyotype  $16 = XYYY + 12A$

Fig. 3. Male plant with karyotype  $17 = XYYYY + 12A$

Fig. 4. Male plant with karyotype  $18 = XYYYYY + 12A$



Figs. 5–8. Chromosome association at meiosis in normal male plants and in those with additional Y chromosomes.  $\times 1700$

Fig. 5. Diakinesis in normal plant with karyotype  $15 = XY + 12 A$ . Arrow indicates YXY trivalent

Fig. 6. MI in plant with karyotype  $16 = XYYY + 12 A$ . Arrow indicates YXYY tetraivalent

Fig. 7. Diakinesis in plant with karyotype  $16 = XYYY + 12 A$ . Arrows indicate YXY trivalent and univalent formed by Y chromosome

Fig. 8. Late metaphase in PMC of plant with karyotype  $16 = XYYY + 12 A$ . Note prereducational YY bivalent

with the X chromosome occupying the central position (Fig. 5). In plants with additional Y chromosomes various modifications of sex chromosome conjugation were observed.

**Conjugation in plants with an additional Y chromosome.** Male plants with chromosome constitution  $XYYY + 12 A = 16$  (Fig. 2) may possess either one  $Y_1$  chromosome and two homologous  $Y_2$  chromosomes or one  $Y_2$  chromosome and two homologous  $Y_1$  chromosomes. Unfortunately  $Y_1$  and  $Y_2$  chromosomes are usually not morphologically distinguishable. In such plants four different patterns of sex chromosome conjugation were observed: YXYY (Fig. 6), YXY + Y (Fig. 7), XY + YY and XY + Y + Y. Association between sex chromosomes was as a rule end-to-end. Two different configurations of the tetraivalent XYYY were observed. In the chain configuration YXYY, presented in Fig. 6, two Y chromosomes conjugate with two homologous ends of the X chromosome as in a normal trivalent. The third Y chromosome is attached to the end of the Y chromosome not involved in conjugation with the X chromosome. It is known that in *Rumex* Y chromosomes are heterochromatic and unable to take part in conjugation with X chromosomes except for the small terminal fragment. Thus, in the tetraivalent in question the additional Y chromosome is obviously attached to the fully heterochromatic and nonhomologous end of the other Y

chromosome, and this association should be considered as a heterochromatic fusion rather than a real conjugation. In another tetraivalent configuration all homologous ends of Y chromosomes are involved in conjugation in such a way that two Y chromosomes (obviously two  $Y_1$  or two  $Y_2$ ) conjugate with one end of an X chromosome, schematically  $Y_1 - X \begin{matrix} \leftarrow Y_2 \\ \leftarrow Y_2 \end{matrix}$  or  $Y_2 - X \begin{matrix} \leftarrow Y_1 \\ \leftarrow Y_1 \end{matrix}$ . The third Y chromosome conjugates with the second arm of the X chromosome in the normal way. As seen in Table 1, the most frequent associations were YXY + Y (trivalent and Y chromosome as a univalent) and XY + YY (two bivalents). In the first case the additional Y chromosome does not affect normal sex chromosome conjugation because a normal YXY trivalent is formed. However, quite frequently the extra Y chromosome tends to conjugate with its homologue forming a bivalent ( $Y_1 Y_1$  or  $Y_2 Y_2$ ) and preventing formation of the normal sex chromosome trivalent. In such a case two sex chromosome bivalents were observed. The formation of one sex chromosome bivalent XY and two Y chromosome univalents was also observed but this phenomenon cannot be reasonably explained. It is, however, possible that the association between Y homologues is less persistent than the Y–X association, and the two Y chromosomes observed as univalents are the result of some kind of desynapsis. Prereducational

Table 1. Sex chromosome conjugation in male plants of *R. thyrsiflorus* with one additional Y chromosome

No. of plant	Karyotype	Pattern of sex chromosome association in diakinesis				Total
		YXYY	YXY + Y	XY + YY	XY + Y + Y	
22	$16 = XYYY + 12 A$	3	42	40	6	91
26	$16 = XYYY + 12 A$	6	22	18	11	57
61	$16 = XYYY + 12 A$	8	18	11	14	51
65	$16 = XYYY + 12 A$	12	12	28	8	60
	Total	29	94	97	39	259

Table 2. Sex chromosome segregation in Anaphase I in male plants of *R. thyrsoiflorus* with one additional Y chromosome

No. of plant	Karyotype	Pattern of sex chromosome segregation	
		XY - YY	X - YYY
22	16 = XYYY + 12 A	17	2
26	16 = XYYY + 12 A	20	6
61	16 = XYYY + 12 A	6	6
65	16 = XYYY + 12 A	2	3
Total		45	17

the sex chromosome, observed sometimes in M I (Fig. 8), suggests such a possibility.

Sex chromosome segregation in A I was also analyzed. As may be seen from Table 2, the most frequent was segregation  $XY \leftrightarrow YY$ . Another possible pattern of segregation,  $X \leftrightarrow YYY$ , was much less frequent. This fits well with the data concerning chromosome conjugation as it was to be expected that segregation of the most frequent associations  $YXY + Y$  and  $XY + YY$  should be of the  $XY \leftrightarrow YY$  type. Apart from the two mentioned above, no other types of sex chromosome segregation were found.

*Conjugation in plants with 2 additional Y chromosomes.* Four male plants with chromosome constitution XYYYY were obtained. In one plant two Y chromosomes were short and metacentric, two others were longer and submetacentric (Fig. 3). It is very

likely that this plant had two homologous  $Y_1$  chromosomes and two  $Y_2$  chromosomes.

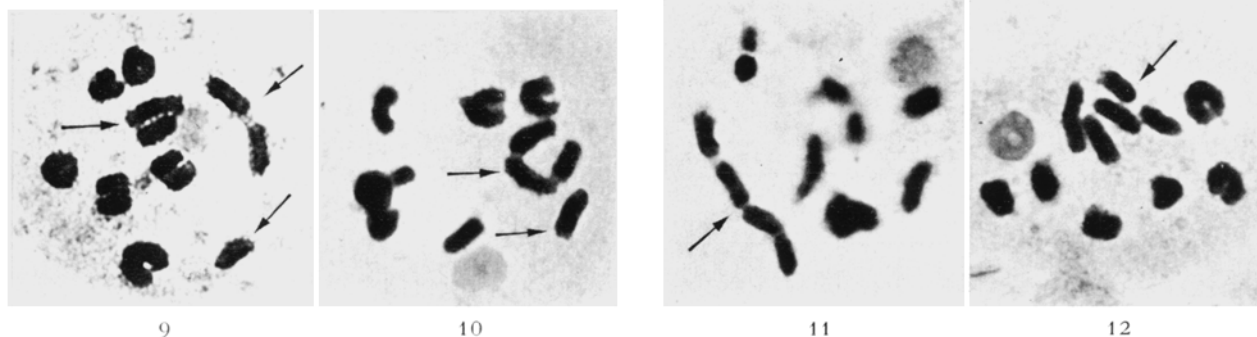
In this plant various combinations of sex chromosome association were observed, as shown in Table 3. Most frequent was the association  $XY + YY + Y$  (Fig. 9). This configuration is similar to the association  $X + Y + YY$  observed frequently in the XYYY plant (Table 2). Surprisingly, configurations with an YXY trivalent were less frequent than in plants with one additional Y chromosome. When a sex trivalent was formed, the two additional Y chromosomes were seen as a bivalent or as two univalents (Fig. 10). The relatively low frequency of such configurations may be explained as the result of the presence of two homologous pairs of Y chromosomes ( $Y_1 Y_1$  and  $Y_2 Y_2$ ). It seems that in such a case homologous Y chromosomes tend to conjugate with one another preventing formation of the sex chromosome trivalent. A few pentavalents and tetravalents with one univalent (Fig. 11) were also observed. In such configurations associations between Y chromosomes seem to be the result of heterochromatic fusion, as homologous parts of one  $Y_1$  and one  $Y_2$  chromosome are already involved in association with the X chromosome. In one cell, only univalents were observed (Fig. 12), but it might have been merely a technical artefact.

Segregation of sex chromosomes in this plant was not analyzed, but probably segregations  $XY - YYY$  and  $XY - YY$  were most frequent.

*Conjugation in plants with 3 additional Y chromosomes.* In the male plant with karyotype XYYYYY

Table 3. Sex chromosome conjugation in male plant of *R. thyrsoiflorus* with two additional Y chromosomes

Karyotype	Pattern of sex chromosome association in diakinesis							Total
	YYXY or YXY	YXY + Y	YXY + YY or XY + YYY	YXY + Y	XY + YY + Y	XY + Y + Y + Y	X + Y + Y + Y	
17 = XYYYYY + 12 A	4	5	10	11	53	9	1	



Figs. 9-12. Chromosome association at meiosis in male plants with additional Y chromosomes.  $\times 1700$

Fig. 9. Diakinesis in plant with karyotype 17 = XYYYYY + 12 A. Arrows indicate two bivalents XY, YY and a Y univalent

Fig. 10. Diakinesis in plant with karyotype 17 = XYYYYY + 12 A. Arrows indicate YXY trivalent and two Y univalents

Fig. 11. Diakinesis in plant with karyotype 17 = XYYYYY + 12 A. Arrow indicates tetravalent formed by sex chromosomes

Fig. 12. Diakinesis in plant with karyotype 17 = XYYYYY + 12 A. Arrow indicates X and Y univalents

Table 4. Sex chromosome conjugation in male plant of *R. thyriflorus* with three additional Y chromosomes

Karyotype	Pattern of sex chromosome association in diakinesis							Total
	YYXYY + Y	YXY + YYY	YXY + YY + Y	XY + YY + YY	XY + YY + Y + Y	XY + Y + Y + Y + Y	YXY + Y + Y + Y	
18 = X + YYYYYY + + 12 A	1	1	17	21	34	4	3	81

+ 12 A = 18 (Fig. 4)  $Y_1$  and  $Y_2$  chromosomes were indistinguishable. Only one such plant was obtained. Analysis of diakinesis revealed the combinations of sex chromosome associations shown in Table 4. Again, as in plants XYYY and XYYYYY, combinations with the XY bivalent were more frequent than combinations with the sex chromosome trivalent YXY. It was observed that three additional Y chromosomes may form a trivalent YYY, or a bivalent and a univalent YY + Y, or only univalents Y + Y + Y. The Y chromosome trivalent was observed in one cell only. Pentavalents YYXYY were also very rare and should be considered as being due to heterochromatic fusion between Y chromosomes.

Segregation of sex chromosomes was not analyzed.

In all plants with additional Y chromosomes there was no indication of loss of additional Y chromosomes in ontogenesis or during meiotic division.

### 2. Transmission of additional Y chromosomes to progeny

Transmission of additional Y chromosomes was investigated in the progeny of two crosses:

$$\begin{aligned} \text{♀ } XXYY + 12 A &= 16 \times \text{♂ } XYY + 12 A = 15 \\ \text{♀ } XXYY + 12 A &= 16 \times \text{♂ } XYYYYY + 12 A = 17 \end{aligned}$$

Table 6. Pollen fertility of plants with additional Y chromosomes

No.	Karyotype	Pollen fertility
1	XYY + 12 A	= 15 85%
2	XYY + 12 A	= 15 86%
3	XYY + 12 A	= 15 89%
4	XYYYY + 12 A	= 16 78%
5	XYYYY + 12 A	= 16 25%
6	XYYYY + 12 A	= 16 89%
7	XYYYY + 12 A	= 16 52%
8	XYYYYY + 12 A	= 17 90%
9	XYYYYYY + 12 A	= 18 47%

In both crosses female plants had two additional Y chromosomes. It seems probable that in such plants two X chromosomes conjugate side to side as in a normal female plant. Two Y chromosomes may be attached (by their homologous ends) to the X-chromosome bivalent or may form two univalents. The most likely segregation of sex chromosomes is XY and XY, so the gametes XY + 6 A should be the most frequent. In the first cross the male parent produced two types of gametes, X + 6 A = 7 and XY + 6 A = 8, in equal proportion; therefore in the progeny the karyotypes ♀ XXY + 12 A = 15 and ♂ XYYY + 12 A = 16 should be the most frequent. In the second cross, the male parent XYYYYY should produce mainly four types of gametes, XY, XYY, YYY, YY, roughly in equal proportions. Thus in the progeny of this cross plants with karyotypes ♀ XXYYY + 12 A = 17, ♂ XYYY + 12 A = 16 and ♂ XYYYYY + 12 A = 17 should be the most frequent.

As shown in table 5, in both crosses plants with additional Y chromosomes were less frequent than could have been expected from the presumed pattern of sex chromosome segregation. Most plants had normal karyotypes or only one additional Y chromosome, which suggests that transmission of extra Y chromosomes to the progeny is very restricted. It seems that gametes with additional Y chromosomes may be eliminated in fertilization as a result of competition with normal gametes.

### 3. Fertility of plants with additional Y chromosomes

Pollen fertility was estimated in 6 plants with 1, 2 and 3 extra Y chromosomes and compared with that of normal male plants (Table 7). All Y hyperploid and normal plants (Nos. 1–7 in Table 6) were the progeny of the cross ♀ XXYY + 12 A = 16 × ♂ XYY + 12 A = 15 described in the previous section. Plant No. 8 with 3 extra Y chromosomes was

Table 7. The seed fertility in crosses involving plants with extra Y chromosomes

Cross	The number of seeds collected	The number of seeds sown	The percent of seed germinated
♀ XX + 12 A = 14 × ♂ XYYY + 12 A = 16	240	240	14
♀ XX + 12 A = 14 × ♂ XYYYYY + 12 A = 17	130	130	23
♀ XX + 12 A = 14 × ♂ XYYYYY + 12 A = 17	100	100	79
♀ XXYY + 12 A = 15 × ♂ XYY + 12 A = 15	330	150	24
♀ XXYY + 12 A = 16 × ♂ XYY + 12 A = 15	—	100	79
♀ XXYY + 12 A = 16 × ♂ XYYYY + 12 A = 16	130	130	42
♀ XXYY + 12 A = 16 × ♂ XYYYYY + 12 A = 17	164	164	42

Table 5. Karyotypes in progeny of crosses between plants with additional Y chromosomes

Karyotype of the progeny	$XX + 12A = 14$	$XXY + 12A = 15$	$XXYY + 12A = 16$	$XXYY + 12A = 16$	$XXYY + 12A = 16$	$XXYY + 12A = 17$	$XXYY + 12A = 15$	$XXYY + 12A = 16$	$XXYY + 12A = 17$	$XXYY + 12A = 17$	$XXYY + 12A = 17$	$XXYY + 12A = 18$
Sex	♀	♀	♀	♀	♀	♂	♂	♂	♂	♂	♂	♂
Frequency of karyotypes in cross	24	25	2	—	—	10	8	2	—	—	—	—
Frequency of karyotypes in cross	6	14	12	1	20	9	2	1	—	—	—	—

Table 8. The height of ♀ and ♂ plants with additional Y chromosomes

Cross	Karyotypes	$XX + 12A = 14$ ♀	$XXY + 12A = 15$ ♀	$XXYY + 12A = 16$ ♀	$XXYY + 12A = 16$ ♀	$XXYY + 12A = 17$ ♀	$XXYY + 12A = 15$ ♂	$XXYY + 12A = 16$ ♂	$XXYY + 12A = 17$ ♂	$XXYY + 12A = 18$ ♂
♀ $XXYY + 12A = 16$	mean height of plants in cm	125	109	73	—	87	65	53	—	—
♂ $XXYY + 12A = 15$	number of measured plants	24	25	2	—	13	8	2	—	—
♀ $XXYY + 12A = 16$	mean height of plants in cm	94	81	70	45	79	62	55	30	—
♂ $XXYY + 12A = 17$	number of measured plants	6	10	10	1	18	10	1	1	1

obtained from the cross ♀  $XXYY + 12A = 16 \times$  ♂  $XYYY + 12A = 17$ . Normal plants produced from 85 to 90% of morphologically good pollen. The pollen fertility of  $Y$ -hyperploid plants varied between 25 and 90%. It was interesting that among plants with one additional  $Y$  chromosome, one exhibited markedly reduced pollen fertility (up to 25%), while in the other two pollen fertility was more or less normal (78 and 89%). The fertility of the plant with two extra  $Y$  chromosomes was quite normal (90%), and in the plant with 3 additional  $Y$  chromosomes it was reduced to 47%. These data indicate that in most cases additional  $Y$  chromosomes do not reduce pollen fertility in any drastic way.

Fertility of plants with additional  $Y$  chromosomes was also estimated by comparison of seed setting and seed germination in crosses involving plants with additional  $Y$  chromosomes, and in crosses between normal plants. The results are given in Table 7. Seed setting in crosses between normal plants was about 1000 seeds per cross. Seed setting in all crosses involving  $Y$  hyperploid plants was drastically reduced even to as little as 100 seeds. Seed germination varied from cross to cross but usually was much lower (14–79%) than germination of seeds from the cross between normal plants (80%). It was surprising that in two crosses between plants with identical chromosome constitution but of different origin (crosses No. 2 and No. 3) seed germination was 23% and 79% respectively. It resembles the variation in pollen fertility observed for male plants not differing in their karyotypes. The cause of this phenomenon remains obscure, but genetic rather than chromosomal factors should be responsible for the differences observed.

#### 4. The phenotypic effect of $Y$ chromosome hyperploidy

Male and female plants with one additional  $Y$  chromosome are indistinguishable in their morphology from normal plants. The presence of two or more additional  $Y$  chromosomes usually influences strongly the morphological features of plants. Leaves of such individuals, especially when young, are curled, pale green and their shape different than that typically observed in normal seedlings. Moreover, the number of leaves and flower stems is markedly reduced and such plants are shorter than normal individuals. Table 8 presents the results of measurements of the progeny obtained from two crosses between plants with additional  $Y$  chromosomes. It is seen that the height of the plant is inversely proportional to the number of additional  $Y$  chromosomes. Even plants with one additional  $Y$  chromosome, whose leaf morphology is not changed, are shorter than normal plants. Also, the viability of  $Y$  chromosome hyperploid plants is lower than that of normal plants. *R. thyrsoflorus* is a perennial species and normal diploid individuals remain vigorous for several years;

the longevity of  $Y$  hyperploid plants was markedly reduced in comparison to that of normal plants.

### Discussion

In mammals including man (Hayward, 1962; Utakoji, 1966; Mittwoch, 1967; Solari, 1969), and in dioecious plants (Jacobsen, 1957; Westergaard, 1958; Smith, 1964), the most common association between  $X$  and  $Y$  chromosomes during meiosis is the end-to-end configuration. It has been demonstrated in various organisms that the end-to-end association of the  $X - Y$  pair is the result of chiasma formation between minute homologous regions (Ohno, Kaplan and Kinoshita, 1959; Utakoji, 1966; Solari, 1969). Data presented in this paper show that in *Rumex thyrsoflorus*, both in normal and  $Y$ -chromosome hyperploid plants, associations between sex chromosomes are usually end to end. Autoradiographical data and cytological observation (Žuk, 1969a) showed that both  $Y$  chromosomes are entirely late-replicating (heterochromatic) and the  $X$  chromosome is entirely euchromatic. Thus if the association between sex chromosomes  $YXY$  in *Rumex* is based on synapsis between homologous segments of  $X$  and  $Y$  chromosomes, these homologous segments in  $Y$  chromosomes are very short, below the resolving power of autoradiography. Thus it is possible that  $Y$  chromosomes in *R. thyrsoflorus* are composed of large differential heterochromatic segments, and very small euchromatic ones homologous to the  $X$  chromosome.

In *Rumex*, as well as forming chiasmata between the distal homologous ends of  $X$  and  $Y$  chromosomes,  $Y_1$  and  $Y_2$  chromosomes can produce associations by heterochromatic fusion. If a sex trivalent is formed in an  $XYYY + 12A = 16$  plant, association between the chromosomes  $Y_1$ ,  $X$  and  $Y_2$  is based on the homology between  $Y_1$ ,  $Y_2$  and  $X$  chromosomes. Association of an additional  $Y_1$  or  $Y_2$  chromosome with the trivalent is based on heterochromatic fusion because homologous segments of  $Y$  and  $X$  chromosomes are already involved in association. It seems that association by heterochromatic fusion can take place mainly between partly homologous  $Y_1 + Y_1$  or  $Y_2 + Y_2$  chromosomes, because in normal  $YXY + 12A = 15$  plants it has never been observed. This is not surprising, because in the opposite case the regular behaviour of the sex chromosome mechanism would be highly disturbed. Association between the nonhomologous  $Y$  and the heterochromatic  $S$  chromosome has already been reported in *Rumex* (Žuk, 1969b) and in other organisms (Riley and Law, 1965). Recently Maguire (1969) has shown that distribution of large heterochromatic knobs in premeiotic interphase nuclei of maize is not random. Two large heterochromatic  $K 10$  regions were found to be localized very significantly nearer to each other than random expectations predicted. Thus it seems that the tendency of heterochromatin to clump during inter-

phase, especially during premeiotic interphase, may be the reason for nonhomologous heterochromatic association in meiosis.

Analysis of anaphase cells in plants with one additional Y chromosome revealed that segregation of sex chromosomes was nonrandom. Segregation  $XY - YY$  was about 3 times more frequent than segregation  $X - YYY$ , and not one case of segregation  $Y - XYY$  was observed. Nonrandom segregation of sex chromosomes in  $XYYY + 12 A = 16$  plants is partly the result of the pattern of sex chromosome association in meiosis. Associations  $YXY + Y$  and  $XY + YY$  were very frequent. The most frequent segregation resulting from such association should be  $XY - YY$ . Non-random segregation of sex chromosomes has also been shown in  $XYY$  males of *Drosophila* by Grell (1969).

In *Rumex*, transmission of extra Y chromosomes to the progeny was greatly reduced. This was true for both female and male gametes. Low transmission of extra chromosomes of the trisomics have been reported in many plants (Burnham, 1962). This is also true for heterochromatic Y sex chromosomes in *R. thyrsoflorus*.

What mechanism may be responsible for low transmission of additional Y chromosomes to the progeny. In male plants with extra Y chromosomes no case of loss of the extra Y chromosome during ontogenetic development or during meiotic division was observed. All Y chromosomes were transmitted to the gametes. Pollen fertility of male plants with additional Y chromosomes is usually quite good, so that selective degeneration of pollen grains with additional Y chromosomes is almost excluded. Therefore the most probable explanation is nonrandom fertilization. The more Y chromosomes are present in pollen grains the poorer their chance to fertilize. This may be connected with the deleterious effect of extra Y chromosomes on germination and growth of pollen tubes.

Meiosis in female plants was not investigated but it is probable, that if the basal megaspore contains the extra Y chromosome it fails to produce the embryo sac. Consequently the embryo sac may be produced by another megaspore with the normal haploid complement. A similar possibility was postulated by McClintock and Hill (1931) to explain the failure of the extra chromosome to be transmitted to 50% of the progeny in trisomics of maize. In *Rumex*, even in normal plants, transmission of  $YY + 6 A$  gametes is much lower than of  $X + 6 A$ , and the resulting female plants are much more numerous in the population (Žuk, 1963). It may be speculated that in both cases the mechanism of low transmission of Y chromosomes is the same.

Y-chromosome hyperploidy individuals have been obtained in *Drosophila* (Dronamraju, 1965; Mittwoch, 1967; Lewis and John, 1968; Grell, 1959, 1969),

in humans (Chu, 1964; Jacobs, Brunton and Melville, 1965), in mouse (Cattanach, 1961; Russell and Chu, 1961; Mittwoch, 1967) and in *Melandrium* (Westergaard, 1958). In man, mouse and *Melandrium*, individuals with an extra Y chromosome were male, because in these organisms the Y chromosome is strongly male-determining. In *Drosophila* the Y chromosomes carry no male-determining genes but the addition of an extra Y chromosome affects fertility. The fertility of  $XYY$  males is only about 0.5–3.0%. Similarly, by comparing females with 0, 1, 2 Y chromosomes Grell (1969) has found that the fertility varied inversely to the hyperploidy. In man,  $XYY$  males are mentally subnormal and behave aggressively, and  $XXY$  and  $XXYY$  have Klinefelter's syndrome.  $XXY$  mice are morphologically indistinguishable from normal males, but they are sterile. It is possible, as postulated by Mittwoch (1967), that the apparent lack of phenotypic abnormalities in mice with an abnormal sex chromosome is connected with the fact that the chromosomes in mouse contain a large proportion of heterochromatin, so that modifications of the karyotype may be less damaging than those in man. The same is also true for *Rumex*: both the Y chromosomes are heterochromatic. Male and female plants with one extra Y chromosome are almost normal in appearance. They are only about 20 cm lower. Morphological pollen fertility of male plants with one extra Y chromosome ranges between 50–90%. Seed setting and germination of female plants with one additional Y chromosome is 30%.

Two or three extra Y chromosomes have a much more pronounced effect. Female plants are about 30 cm and male plants about 30 cm lower than normal ones. The leaves are often curled and pale. Seed setting and seed germination are much lower than in normal plants. The female plant with three extra Y chromosomes is completely sterile.

Thus additional Y chromosomes in *Rumex* have some effect on the phenotype and fertility of plants. This effect is much less pronounced than in other organisms because Y chromosomes are heterochromatic and have no male-determining genes, and probably because in plants the shift in chromosomal balance has less drastic effects than in organisms with a much higher level of organization like mammals including man.

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### Zusammenfassung

Die Arbeit berichtet von Untersuchungen über die Wirkung überzähliger Y-Chromosomen auf die Paarung der Geschlechtschromosomen und die Fertilität und Morphologie männlicher und weiblicher Pflanzen von *Rumex thyrsoflorus*.

Die Geschlechtschromosomen bei den untersuchten ♂ Pflanzen mit 1, 2 und 3 überzähligen Y-Chromosomen zeigen end to end-Paarung. Die Assoziation der Y-Chromosomen basiert teils auf einer Paarung homologer Segmente, teils auf einer Heterochromatinfusion. In allen untersuchten Fällen war eine Übertragung des überzähligen Y-Chromosoms auf die Nachkommenschaft sehr gering. Die Gründe hierfür sind möglicherweise präferentielle Befruchtung, präferentielle Degeneration der Megaspore sowie geringer Samenansatz und geringe Fertilität der Pflanzen mit überzähligen Y-Chromosomen. Auch der phänotypische Effekt einer Hyperploidie von Y-Chromosomen wurde untersucht. Pflanzen mit überzähligen Y-Chromosomen sind kürzer und sterben früher ab. Ihre Fertilität ist gering. Obwohl die Y-Chromosomen heterochromatisch und inaktiv sind (außer in der prämeiotischen Interphase der Mikrosporogenese), haben sie doch einen deutlichen Einfluß auf den Habitus von Pflanzen mit überzähligen Y-Chromosomen.

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Dr. Jerzy Żuk  
Department of Genetics  
Polish Academy of Sciences  
Rakowiecka 36  
Warsaw (Poland)