PARAMUTATION (SOMATIC CONVERSION) AT THE *SULFUREA* LOCUS OF *LYCOPERSICON ESCULENTUM*

V. THE LOCALISATION OF *SULF*

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1. INTRODUCTION

THE *sulfurea* (*sulf*) locus of tomato, *Lycopersicon esculentum* Mill., is characterised by the occurrence of a particular type of genetic change, paramutation (= somatic conversion). The wild type allele *sulf*⁺ is stable in the homozygous condition. In vegetative cells of *sulf*⁺*sulf* heterozygotes, however, the *sulf*⁺ allele is heritably altered under the influence of the mutant *sulf* allele which is already present in the same nucleus; *sulf*⁺ is altered with a definite frequency to a *sulf* mutant allele, either of the *sulf*^{*pura*} or the *sulf*^{*vag*} group. The *sulf* series influences the colour of cotyledons and foliage leaves of tomato plants: *sulf*⁺ determines green leaves, *sulf*^{*pura*} pure yellow leaves, and *sulf*^{*vag*} yellow-green speckled leaves. The dominance relations are: *sulf*⁺ > *sulf*^{*vag*} > *sulf*^{*pura*} (Hagemann, 1958, 1966, 1969; summaries in English, 1965, 1969*a*). An important presupposition of studies about the genetic mechanism underlying the processes of paramutation (somatic conversion) is the knowledge of the exact position of the *sulf* locus within the tomato genome.

Studies with trisomics have proved that the *sulf* gene is on chromosome 2, the nucleolar chromosome of the tomato (Hagemann, 1969*a*). Knowing this, it was necessary to find out as exactly as possible the position of *sulf* within chromosome 2. Therefore experiments have been performed to determine the linkage relationship between the *sulf* locus and several genetic and cytological markers in chromosome 2.

The tomato is one of the relatively few plants that have been used extensively in genetics whose chromosomes can be analysed at the pachytene stage of meiosis (Brown, 1949; Barton, 1950). At this stage each of the 12 pairs of chromosomes is clearly differentiated into distinct regions of euchromatin and heterochromatin; the term euchromatin being used to describe those regions of the chromosomes which, in contrast to heterochromatin, do not retain a compact structure during interphase and prophase (Heitz, 1928).

During a series of experiments aimed at comparing the genetic activities of heterochromatin and euchromatin in tomato a number of chromosomal interchanges were synthesised (Snoad, 1961, 1962). Some of these interchanges involved chromosome 2, and they were derived from breakage and reunion in the large blocks of heterochromatin surrounding the centromere region.

The existence of the interchanges led to the suggestion that some of them should be used to locate *sulf* more precisely on chromosome 2.

In a series of experiments the linkage relations between *sulf* and several marker genes (*d*, *aw*, *o* and *s*) as well as the break points of two interchanges have been determined.

2. MATERIALS AND METHODS

(i) *The translocation lines*

X-irradiated pollen (4000 r) from the cultivar "Sutton's Best of All" was used to pollinate a line homozygous for the genes *d*, *o* and *s*. Out of the 289 resulting plants, nine proved to be heterozygous for an interchange involving chromosome 2. Two interchanges, D 48 (= T2-11) and D 58 (= T1-2), were used in the experiments to locate *sulf*. In both, the point of interchange in chromosome 2 was in the heterochromatic region between the centromere and the nucleolar organiser. These interchanges are illustrated in plate I together with pachytene in a normal plant in which each of the 12 pairs of chromosomes can be distinguished.

(ii) *The staining technique for pachytene*

The technique is based on that originally proposed by Dr M. S. Walters, the details of which were published by Brown (1949).

(a) *Fixation*. The anthers are left overnight in a mixture of propionic acid and alcohol (1 : 2). This gives a good fixation of the chromosomes as regards detail but, most important of all, it leaves the cytoplasm less granular and less likely to remain overstained than does acetic acid.

(b) *Mordanting*. The anthers are taken down to distilled water through an alcohol series. (If material has to be stored, it seems best done in 70 per cent. alcohol in a refrigerator at 3-5° C.) After 20 minutes in water, they are placed in 4 per cent. iron alum for 20 minutes. The iron alum is then removed by a series of washings with distilled water over a period of half an hour.

(c) *Staining*. An anther is crushed carefully in a drop of iron aceto-carmine (Belling, 1926) and any debris is removed. A coverslip is applied and immediately more aceto-carmine is added until it gently floats on the drop of stain. The slide is supported in this condition over a steam bath for 1-2 minutes (Barton, 1950) and heating is continued until the chromosomes and cytoplasm are both heavily overstained. As the aceto-carmine evaporates in the heat so it is replaced at the edge of the coverslip.

(d) *Differentiation*. After staining, drops of 45 per cent. acetic acid are placed at one side of the coverslip and the aceto-carmine is drawn out on the other side by means of small strips of filter paper. This process is continued until all the stain has been replaced by 45 per cent. acetic acid. The slide is replaced over the steam until the differentiation between the chromosomes and the cytoplasm can be seen, under the microscope, to be satisfactory. Spreading is accomplished by pressing the preparation quickly and evenly with the fingers, using several thicknesses of filter paper.

(e) *Permanent preparations*. The only satisfactory method involves the use of solid CO₂. After removing the coverslip the slide is immediately placed in absolute alcohol for only 10-15 seconds. After another brief period in fresh absolute alcohol the slide can be made permanent with

Euparal. As albumen is not needed for making these preparations there is obviously better spreading of the cells.

(iii) *The linkage experiments*

Figure 1 is a diagram of chromosome 2 of the tomato which illustrates the position of the markers *s*, *o*, *aw* and *d* as well as the break points of the interchanges D 58 (T1-2) and D 48 (T2-11) used in our experiments. The genic symbols are: *s* compound inflorescence, *o* oblate fruits, *aw* without anthocyanin, *d* dwarf plants (Barton, *et al.*, 1955; Rick and Butler, 1956).

In the first experiment the recombination values between *sulf* and the markers *d* and *aw* have been determined. In the second experiment linkage has been tested after crossing translocation heterozygotes of T1-2 and T2-11 (homozygous for *s*, *o* and *d*) with *sulf* homozygotes (*sulf^{pura}* or *sulf^{vag}*; homozygous for the wild type alleles *s⁺*, *o⁺* and *d⁺*).

The genotype of the plants with regard to *s*, *o* and *d* in the BC generation and its progeny was determined in the experimental field. Heterozygosity for the interchanges and homozygosity were found by determining the presence of normal and sterile pollen grains (heterozygosity) or of normal pollen only (homozygosity) in the anthers.

The synthesis of the translocation lines and the cytological studies have been done by B. Snoad at the John Innes Institute. The programme for the use of the translocation lines in the localisation of *sulf* has been discussed and made by both authors in co-operation between 1963 and 1966. The linkage experiments have been performed by R. Hagemann at Gatersleben and Halle.

3. RESULTS

(i) *Recombination between sulf and d or aw*

Grafted *sulf* homozygotes (*sulf^{pura}*) have been crossed with *aw* homozygotes and with homozygotes of different *dwarf* alleles; *d*, *d^{cr}* and *d^x* (Barton *et al.*, 1955; Clayberg *et al.*, 1960). Both *aw* and *d* are on chromosome 2 (fig. 1). The segregation in F₂ (table 1) shows free recombination between *sulf* and *aw* and also between *sulf* and *d*, *d^{cr}* and *d^x*. The markers *d* and *aw* are located in the distal part of the long arm of chromosome 2. The occurrence of free recombination between *sulf* and these markers indicates the position of *sulf* in the neighbourhood of the centromere, either in the very proximal part of the long arm or in the heterochromatic short arm of chromosome 2.

(ii) *Recombination between sulf and the break points of two interchanges as well as the markers s, o and d*

In order to determine the position of *sulf* more exactly, cytological markers were used which lie in the neighbourhood of the centromere of chromosome 2. These are the break points of the interchanges D 58 (T1-2) and D 48 (T2-11). After crosses between the heterozygotes of the translocations T 1-2 and T2-11 (*s*, *o*, *d*) and *sulf* homozygotes (*s⁺*, *o⁺*, *d⁺*) the linkage was determined between *sulf* and the break points as well as *s*, *o* and *d*. This experiment was done in the following steps:

(a) Plants, heterozygous for the translocation (T1-2 or T2-11) and homozygous for *s*, *o* and *d*, were crossed with *sulf* homozygotes (*sulf^{pura}* or *sulf^{vag}*) which were homozygous for *s⁺*, *o⁺* and *d⁺*.

(b) From the F_1 , heterozygotes of the type $T/+ \text{ sulf}^+ \text{ sulf}, s^+s, o^+o, d^+d$ were selected and back-crossed with *sulf* (*sulf^{vag}*) homozygotes. (In this step *sulf^{vag}* was used in order to get viable *sulf^{vag}* plants (*sulf^{vag}sulf^{vag}* or *sulf^{vag}sulf^{pura}*) in the next generation; *sulf^{pura}* homozygotes being lethal in the seedling stage.)

FIG. 1.—Diagram of chromosome 2 of the tomato illustrating the position of the markers *d*, *aw*, *o*, *s*, the *sulf* locus, the centromere (C), the break points of the interchanges D 58 (T1-2) and D 48 (T2-11) and the nucleolar organiser (NO).

(c) The back-cross generation segregated into green (*sulf*⁺) and yellow-green speckled (*sulf^{vag}sulf^{vag}* or *sulf^{vag}sulf^{pura}*) plants. It was determined for all BC plants whether or not they were heterozygous for the translocation.

TABLE 1
Tests for linkage between sulf and the markers (m) d, der, d^x and aw

Crosses		<i>sulf</i> ⁺ <i>m</i> ⁺	<i>sulf sulf</i> <i>m</i> ⁺	<i>sulf</i> ⁺ <i>m m</i>	<i>sulf sulf</i> <i>m m</i>	χ^2	P for 9 : 3 : 3 : 1
<i>d sulf</i> ⁺ × <i>d</i> ⁺ <i>sulf^{pura}</i>	observed:	1664.0	556.0	537.0	171.0	1.314	0.72
	expected:	1647.0	549.0	549.0	183.0	—	—
<i>der sulf</i> ⁺ × <i>d</i> ⁺ <i>sulf^{pura}</i>	observed:	573.0	216.0	175.0	59.0	4.916	0.18
	expected:	575.4	191.8	191.8	63.9	—	—
<i>d^x sulf</i> ⁺ × <i>d</i> ⁺ <i>sulf^{pura}</i>	observed:	733.0	223.0	213.0	66.0	5.534	0.15
	expected:	694.7	231.6	231.6	77.2	—	—
<i>aw sulf</i> ⁺ × <i>aw</i> ⁺ <i>sulf^{pura}</i>	observed:	1087.0	356.0	386.0	106.0	3.457	0.32
	expected:	1088.4	362.8	362.8	121.0	—	—

All green plants of the BC $T1-2 \times \text{sulf} \times \text{sulf}$ and of the BC $T2-11 \times \text{sulf} \times \text{sulf}$ were heterozygous for the particular translocation (table 2). This result leads to the conclusion that no crossing-over takes place between the break point of the translocations and *sulf*, i.e. there is absolute linkage between the break points and *sulf* (fig. 2, right column: no crossing-over in region 4).

TABLE 2
The presence or absence of translocation heterozygotes among the back-cross generation

		Number of plants heterozygous for the translocation	Number of plants without a translocation	Total
Green (<i>sulf</i> ⁺) plants	T 1-2	393	0	393
	T 2-11	392	0	392
Yellow-green speckled (<i>sulf^{vag}</i>) plants	T 1-2	14*	226	240
	T 2-11	22*	223	245

* Presumably due to paramutation, cf. text.

Among the yellow-green speckled *sulf^{vag}* plants the great majority (449 out of 485) did not contain a translocation—which is in accordance with the result obtained from the green plants.

However, 36 yellow-green speckled plants were heterozygous for the translocations (14 for T1-2, 22 for T2-11). This result distinctly deviates

FIG. 2.—Diagram of the genetic constitution of the F_1 and the back-cross plants after crossing translocation heterozygotes and *sulf* homozygotes.

from the results observed in the green plants. Taking into account the occurrence of genetic changes (paramutation) at the *sulf* locus, it seems probable that these exceptional plants did not occur as the result of crossing-over between the break point and *sulf*, but that they are the result of paramutation. (The frequency of paramutation in the *sulf*⁺*sulf* heterozygotes is at this level; cf. Hagemann, 1966, 1969*b*). The translocation chromosome of these plants carried *sulf*⁺; but by the paramutation which takes place with low frequency in *sulf*⁺*sulf* heterozygotes, this *sulf*⁺ allele has been changed to *sulf*. Therefore these plants cannot necessarily be considered to have arisen after crossing-over. Paramutation at the *sulf* locus of the tomato is unidirectional; there is only the change *sulf*⁺*sulf*→*sulf sulf*. This explains the entire lack of exceptional plants among the green BC plants.

Testing the BC plants for the presence or absence of the translocation chromosomes has therefore led to the result that the break points of the translocations and the *sulf* locus are absolutely linked.

TABLE 3

Determination of the genotype of back-cross plants (BC) by testing the progenies of selfed BC plants

Parents		Progenies of selfed BC plants			T1-2	T2-11	Sum of progenies tested	
		Segregation for:						
BC plants green (<i>sulf</i> ⁺)	{	No crossing-over	<i>s</i>	<i>o</i>	<i>d</i>	10	12	22
			<i>s</i>	<i>o</i>	—	8	5	13
		1 cross-over	<i>s</i>	—	—	6	6	12
			—	—	—	8	9	17
	{	More than 1 cross-over	<i>s</i>	—	<i>d</i>	1	3	4
			—	—	<i>d</i>	1	1	2
			—	<i>o</i>	<i>d</i>	1	2	3
			—	<i>o</i>	—	2	0	2
						<u>75</u>		
	BC plants yellow-green speckled (<i>sulf</i> ^{<i>vag</i>})	{	No crossing-over	—	—	—	12	14
—				—	<i>d</i>	6	8	14
1 cross-over			—	<i>o</i>	<i>d</i>	6	5	11
			<i>s</i>	<i>o</i>	<i>d</i>	8	2	10
{		More than 1 cross-over	—	<i>o</i>	—	0	1	1
			<i>s</i>	<i>o</i>	—	3	0	3
			<i>s</i>	—	—	1	1	2
			<i>s</i>	—	<i>d</i>	0	3	3
					<u>70</u>			

(*d*) In order to obtain information about the genetic constitution of the back-cross plants, seeds from these plants were harvested and their progenies tested to determine whether the BC plants had been heterozygous for *s*, *o* or *d*. In this way the progenies of 75 green (*sulf*⁺) and 70 yellow-green speckled (*sulf*^{*vag*}) BC plants have been analysed for the occurrence of segregation for *s*, *o* and *d*. The analysis is given in table 3. From these results the frequency of crossing-over between the *sulf* locus (and the break points of T1-2 and T2-11) and the markers *s*, *o* and *d* has been determined (table 4). Moreover, the frequency of cross-over events in the different regions of chromosome 2 (break points—*sulf*, *sulf*—*s*, *s*—*o*, *o*—*d*) can be determined (table 5).

The determination of the linkage relations between *sulf* and different markers in chromosome 2 has led to the following results:

(1) The break points of T1-2 as well as T2-11 and *sulf* are absolutely linked. Regarding linkage with *sulf* there is no difference between the break points of T1-2 and T2-11.

TABLE 4

Determination of crossing-over frequency between the sulf locus (and the breakage points of T1-2 and T2-11) and the markers s, o, d

Presence of the wild-type or the mutant allele due to crossing-over (single or multiple)	
75 R ₁ plants <i>sulf</i> ⁺ , green	70 R ₁ plants <i>sulf</i> ^{var} , yellow-green speckled
<i>d</i> ⁺ — <i>d</i> Number of progenies not segregating for <i>d</i> (13+12+17+2 =) 44 out of 75 = 58.7%	Number of progenies segregating for <i>d</i> (14+11+10+3 =) 38 out of 70 = 54.3%
Total: 82 out of 145 = 56.6%	
<i>o</i> ⁺ — <i>o</i> Number of progenies not segregating for <i>o</i> (12+17+4+2 =) 35 out of 75 = 46.7%	Number of progenies segregating for <i>o</i> (11+10+1+3 =) 25 out of 70 = 35.7%
Total: 60 out of 145 = 41.4%	
<i>s</i> ⁺ — <i>s</i> Number of progenies not segregating for <i>s</i> (17+2+3+2 =) 24 out of 75 = 32.0%	Number of progenies segregating for <i>s</i> (10+3+2+3 =) 18 out of 70 = 25.7%
Total: 42 out of 145 = 29.0%	

(2) The order of genes in chromosome 2 is: *sulf*—*s*—*o*—*d*. The distances determined are:

break points, *sulf*—*s*: 29.0
break points, *sulf*—*o*: 41.4
break points, *sulf*—*d*: 56.6.

TABLE 5

Frequency of crossing-over events in bivalents, the chromatids of which have contributed to 75 green plants and 70 yellow-green speckled plants

		Number of crossing-over events	
		Test of green plants	Test of yellow-green speckled plants
in Region 1	13+4+2+2 = 21		14+1+3+3 = 21
in Region 2	12+3+2 = 17		11+2+3 = 16
in Region 3	17+2+3+2 = 24		10+3+2+3 = 18
in Region 4	0 = 0		0 = 0

(3) Of all known genes in chromosome 2, *sulf* is the locus which lies closest to (or even within) the heterochromatic part of the chromosome, and thus represents the beginning of the linkage map of chromosome 2 (fig. 1).

(4) There is no crossing-over between the break points and *sulf*; therefore the exact position of these markers to each other is at the moment still uncertain. Nevertheless it seems probable that the *sulf* locus lies at the very beginning of the euchromatic part of the chromosome in the transition region between the heterochromatic and the euchromatic part of the long arm (fig. 1).

4. DISCUSSION

In *sulf*⁺*sulf* heterozygotes of the tomato paramutation (= somatic conversion) takes place which leads to a heritable change of the wild type allele *sulf*⁺. Many genetic results found in our previous work on this phenomenon fit into the hypothesis that the paramutation of *sulf*⁺ is the result of the heterochromatinisation of this gene leading to an inhibition of the normal action of the *sulf*⁺ allele. This inhibition is either complete (leading to *sulf*^{para} alleles, the homozygotes of which have pure yellow leaves) or it is partial (leading to *sulf*^{vag} alleles, the homozygotes of which are yellow-green speckled) (Hagemann, 1968, 1969a). Knowledge of the exact position of the *sulf* locus within chromosome 2 and thus of the relation to the euchromatic and heterochromatic parts of this chromosome is very important for further studies on the mechanism of paramutation.

Cytogenetic studies by Lesley (1937) and Brown (1949) have indicated the absence of crossing-over in the heterochromatic parts of chromosome 2; heterochromatic areas did not show chiasmata in contrast to euchromatic parts. Further evidence for this was presented by Barton (1951) and Moens and Butler (1963). These authors demonstrated that no crossing-over occurs between the centromere and the satellite, whose length varies significantly among different tomato varieties and therefore represents a good cytological marker; heteromorphic satellites always separate reductionally at first anaphase. The results of Moens and Butler (1963) and Snoad (1961, 1962, 1965) demonstrate the absence of crossing-over in the heterochromatic part of the long arm too. Snoad compared the crossing-over frequency between the marker *s* and eight interchange points within the centric heterochromatin of chromosome 2. The recombination values were practically equal; they did not increase with increasing distances between *s* and the particular break points which were determined cytologically. Thus crossing-over between *s* and the break points is a function of the length of euchromatin between *s* and the centromere, and this is equal for all interchanges studied. Snoad found an average recombination value between *s* and the break points of 38 units. Using heteromorphic satellites as cytological markers, Moens and Butler (1963) have calculated 31 units for the map distance between centromere and *s*. Finally, the latest linkage map of the tomato (TGC 1968) gives 30 units for the distance between centromere and *s*.

The experiments reported in this paper demonstrate absolute linkage between the *sulf* locus and the interchange points of T1-2 and T2-11, which are in the centric heterochromatin of chromosome 2 (fig. 1). These results lead to the conclusion that the *sulf* locus lies in the transition region between the heterochromatic and the euchromatic part of the long arm or even within the heterochromatic part of chromosome 2.

The recombination value of 29 units for the distance between *s* and *sulf* (or the interchange points) found in our experiments agrees very well with the results reported by Moens and Butler (31 units), in TGC 1968 (30 units) and also with Snoad's results (*s*—break point T1-2: 36 per cent., *s*—break point T2-11: 32 per cent., Snoad, 1965).

The results of the experiments to localise the *sulf* locus support our working hypothesis, that the paramutation of the *sulf*⁺ allele to a *sulf* mutant allele is the result of the heterochromatinisation of *sulf*⁺. The position of the locus in the transition region between the euchromatic and the hetero-

PLATE 1.

Pachytene in which each of the twelve chromosome pairs can be identified. $\times 3500$.

2.—D 48 (T2-11) $\times 500$.

3.—D 58 (T1-2) $\times 5000$.

chromatic part of the long arm of chromosome 2 seems to be particularly sensitive to a spreading effect of neighbouring heterochromatin.

Experiments are under way to test this hypothesis further. Of particular interest in this connection are changes in the amount of neighbouring heterochromatin and changes in the spatial relationship between *sulf* and the nucleolar organiser.

At present several other systems of paramutation are studied in higher plants, in particular paramutation at the *R* locus in maize (Brink, 1964; Brink, Styles and Axtell, 1968) and at the *B* locus in maize (Coe, 1966); cf. the survey in Hagemann (1969a). Although the details of the cytogenetic situation at these loci are different from that at the *sulf* locus of the tomato, for both systems hypotheses have been worked out which also assume the involvement of repressing, heterochromatic elements in the process of paramutation.

5. SUMMARY

1. The *sulfurea* (*sulf*) locus of *Lycopersicon esculentum* is characterised by the occurrence of paramutation (= somatic conversion): In vegetative cells of *sulf*⁺*sulf* heterozygotes the wild type allele *sulf*⁺ is heritably altered to a *sulf* mutant allele under the influence of the mutant *sulf* allele which is already present in the heterozygous nucleus. The *sulf* series influences the leaf colour of tomato plants: *sulf*⁺ determines green leaves, *sulf*^{pure} pure yellow, and *sulf*^{vag} yellow-green speckled leaves. Studies with trisomics (triplo-2) have proved that the *sulf* locus is on chromosome 2, the nucleolar chromosome of the tomato.

2. The markers *d* and *aw*, located in the distal part of the long arm, give free recombination with *sulf* (table 1), thus indicating the position of *sulf* in the neighbourhood of the centromere.

3. Crosses between *sulf* homozygotes and two translocation lines, T1-2 and T2-11 (D 58 and D 48), with their interchanges points in the heterochromatin of chromosome No. 2 (plate 1) led to the localisation of *sulf*.

4. The break points (of T1-2 and T2-11) and the *sulf* locus are absolutely linked; no crossing-over occurs between them (table 2).

5. The order of genes in chromosome 2 is: *sulf*—*s*—*o*—*d*. Of all known genes in chromosome 2, *sulf* is the locus which lies closest to (or even within) the heterochromatic part; *sulf* marks the beginning of the genetic map of chromosome 2. The distance: break points, *sulf*—*s* is 29 units (tables, 3-5).

6. The position of *sulf* seems to be to the right of the break points, and it is assumed that *sulf* lies in the transition region between the heterochromatic and the euchromatic part of the long arm of chromosome 2 (fig. 1).

7. The results reported support our working hypothesis that the paramutation (= somatic conversion) of *sulf*⁺ is the result of the heterochromatinisation of *sulf*⁺. The *sulf* locus in this peculiar position seems to be particularly sensitive to a spreading effect of neighbouring heterochromatin.

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