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Trisomics from Triploid-diploid Crosses in Self-incompatible *Lycopersicum peruvianum*

II. Transmission of Trisomics*

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Summary. The transmission rate of trisomy was determined for two primary trisomic types, triplo-1 and triplo-3, of the self-incompatible species *Lycopersicum peruvianum*. Chromosome counts in somatic metaphases of root-tip squashes from 112 progeny plants showed that 8 individuals (7.2 %) were trisomic and 104 (92.8 %) were diploid. The average frequency of transmission approximated 2.6 % in triplo-1 and 8.6 % in triplo-3. Data are presented on the karyotype and the morphological features of the 8 trisomics detected in the progenies of triplo-1 and triplo-3 and the various factors affecting the transmission rate of trisomy are discussed.

The transmission rate of trisomy was also determined for the trisomic plant 269 which displayed a complete deletion of the satellited part of chromosome 2 and was characterized by ovate fruits. Out of 18 progeny plants analysed, 8 (44.4 %) were trisomic and 10 (55.6 %) were diploid. Cytological and morphological analyses of the 8 trisomic individuals revealed that only two of them (11.1 %) resembled the parental trisomic. A number of diploid and trisomic progenies exhibited a partial or a complete deletion of the satellited segment of chromosome 2.

Key words: *Lycopersicum peruvianum* - Aneuploidy - Primary Trisomics - Transmission

Introduction

The trisomics of wild species and of primitive forms from many cultivated plants are vigorous and fertile, and have thus been tabulated as being highly tolerant to trisomy (Mooring 1960; Dhillon and Garber 1960; Tsuchiya 1960; Rick and Notani 1961; Burnham 1962; Hermsen et al. 1970). This situation appears to be particularly well illustrated in the genus *Lycopersicum* where Rick and Notani (1961) explained the vigour and fertility of trisomics in the primitive tomato variety 'red cherry' as a part of the plasticity and ability of the species to withstand unfavourable circumstances and where Sree Ramulu et al. (1977) showed that the wild self-incompatible species *L.peruvianum* tolerated certain types of aneuploidy which do not occur in the cultivated tomato species *L.esculentum*.

Such comparative analyses have been extended by us, during the course of a study on the possible relationships between trisomy and the break-down of self-incompatibility (Sree Ramulu et al. 1977), to determine the transmission rate of extra chromosomes in *L.peruvianum*. The values obtained are presented below and are discussed in relation to the rates established by Rick and Barton (1954) for the cultivated tomato and in relation to the various parameters which are known to affect the transmission of the trisomic condition.

Material and Methods

The primary trisomic types, triplo-1 (plant 145) and triplo-3 (plant 220 and plant 172), of *Lycopersicum peruvianum* were chosen for analysing the transmission frequency of extra chromosomes in progenies derived from selfing and also from crosses with a cross-compatible diploid (S_1S_2) used as staminate partner. The trisomic plant 269 ($2n+1$), which sets a few seeds upon selfing, was also included in the study because it displays a modification of chromosome 2 (complete deletion of the satellited arm) and is characterized by ovate-shaped fruits with pointed stylar ends. The progenies analysed in this case were derived from selfing and from crosses with the diploid tester stock S_1S_2 used as pistillate partner. For details on the origin of these three trisomics, reference is made to Sree Ramulu et al. (1977).

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Table 1. Transmission frequency of the extra chromosome in (2n + 1) × (2n + 1) (Triplo-1 and Triplo-3 selfed) and in (2n + 1) × (2n)* of *Lycopersicum peruvianum*

Origin of progeny	Number and percentage of diploids and trisomics in the progenies analyzed							
	Diploids		Trisomics					
			Parental trisomics		Other types		Total	
	no.	%	no.	%	no.	%	no.	%
Triplo-1 (plant 145) selfed	15	100.0	0	0	0	0	0	0
Triplo-3 (plant 220) selfed	25	96.2	1	3.8	0	0	1	3.8
Triplo-3 (plant 172) selfed	13	76.4	3	17.6	1	5.9	4	23.6
Mean for Triplo-3	38	88.4	4	9.3	1	2.3	5	11.6
Triplo-1 (plant 145)♀ × 2n	18	94.7	1	5.3	0	0	1	5.3
Triplo-3 (plant 220) × 2n	17	94.4	1	5.6	0	0	1	5.6
Triplo-3 (plant 172) × 2n	16	94.1	1	5.9	0	0	1	5.9
Mean for Triplo-3	33	94.3	2	5.7	0	0	2	5.7
Total	104	92.8	7	6.3	1	0.9	8	7.2

* 2n: Cross-compatible clone 006 - S_1S_2

All plants were grown under greenhouse conditions. Pollinations were done manually, on the day or the day after anthesis, with fresh pollen obtained from the flowers of plants in a vigorous state of growth. As the trisomics expressed self-compatibility, emasculation of their flowers was carried out one day before crossing them to the diploid clone.

After fruit harvest, the seeds were sown in pots and the chromosome counts on the resulting seedlings were made from root-tip squashes. The root-tips were treated with bromonaphtalene for 75 min. at 60°C, fixed in acetic alcohol (1:3), hydrolised in 1N HCl for 7 min., stained with Feulgen reagent and squashed in 1 % acetocarmine. Pollen fertility was ascertained by means of the acetocarmine technique.

Results

Frequencies of Trisomics in the Progenies Derived from the Self-pollination of Triplo-1 and Triplo-3 and from Crosses of Triplo-1 and Triplo-3 to the Cross-compatible Diploid Clone 006 - S_1S_2

A total of one hundred and twelve plants from the progenies of triplo-1 (plant 145) and triplo-3 (plants 220 and 172) were analysed cytologically. The chromosome counts and karyotype analyses performed on these 112 plants (Table 1) shows that 8 individuals (7.1 %) were trisomic and 104 (92.8%) diploid.

In all the progenies of crosses between the trisomics and the diploid clone (triplo-1 × 006 - S_1S_2 and triplo-3 × 006 - S_1S_2), trisomics were recovered. The frequencies of occurrence varied between 5 % and 6 %.

A different situation was met in the case of the progenies obtained through self-pollination since trisomics were only recorded among the offsprings of triplo-3. The frequency of occurrence ranged from 3.8 % for plant 220 to 23.6 % for plant 172.

Morphology and Fertility of Trisomics Detected in the Progenies of Triplo-1 and Triplo-3

Among the 8 trisomics, 7 displayed essentially the same morphological features as those of the parent trisomics; the one individual found to differ phenotypically from its trisomic parent was derived from the self-pollination of plant 172 (triplo-3). The pollen fertility of the trisomics varied from 43.8 % to 95.7 %, but no relationship could be established between the origin (progeny from selfing or from crosses to 006 - - S_1S_2) or the nature of the trisomic (triplo-1 or triplo-3) and the level of pollen fertility expressed by the trisomics. Tests of self-pollinations showed that all the trisomics were self-incompatible.

Essential Features of the Progenies of the Trisomic Plant 269 Characterized by a Modification of Chromosome 2

In the trisomic plant 269, derived from the cross between the triploid ($S_1S_2S_4$) and the diploid genotype,

Table 2. Types and frequencies of plants among the progeny of trisomic plant 269 (2n + 1) derived from selfing and from crosses between the trisomic and the diploid clone, 006 - S_1S_2 in *Lycopersicum peruvianum*

Origin of the progeny	Diploids					Trisomics					
	Normal karyotype	Modified karyotype		Total		Parental karyotype (whole deletion of satellited part)		Other karyotype		Total	
		Whole deletion of satellited part	Partial deletion of satellited part	no.	%	no.	%	Partial deletion of satellited part	Without deletion	no.	%
2n + 1 selfed	1	0	1	2	28.6	1	14.3	2	2	5	71.5
(2n + 1) × 2n	5	3	0	8	72.7	1	9.1	0	2	3	27.3
Total	6	3	1	10	55.6	2	11.1	2	4	8	44.4

$S_{10}S_{11}$, one of the homologues of chromosome 2 (satellited chromosome) exhibited a whole deletion of its satellited region. The fruits formed by this trisomic had pointed stylar ends and displayed the ovate shape which is known to be governed in *L.esculentum* by genes located on chromosome 2 (Rick and Butler 1956).

The seeds obtained after the self-pollination of plant 269 or in crosses between this trisomic and the cross-compatible diploid tester, 006 - S_1S_2 germinated at approximately a 70% success rate. The resulting seedlings were very weak and grew slowly with only 50% surviving to maturity. Of the 18 plants analysed, 8 (44.4%) were trisomic and 10 (55.6%) were diploid (Table 2).

Among the 8 trisomics, 2 resembled the parent trisomic with respect to karyotype (whole deletion of the satellited region in one of the two homologues of chromosome 2), morphology and fruit shape. The remaining 6 trisomics differed from the parent trisomic and were either normal, without any deletion of the satellite part, or only exhibited a partial deletion of the satellited region of one of the homologues of chromosome 2.

Of the 10 diploids, 3 were characterized by a whole deletion of the satellited region of one of the homologues of chromosome 2 and one displayed a partial deletion of the satellited region.

All trisomic and disomic plants with whole or partial deletion of the satellited region were weak, slow growing, and dwarf. Pollen fertility in these plants was irregular and ranged from 28% to 74%.

All plants in the populations studied were self-incompatible.

Discussion

The Transmission Rate of Trisomy

It appears from the present study with *L.peruvianum* that the average rate of transmission of the extra chromosome to the progenies of triplo-1 and triplo-3 was lower than those of *Datura stramonium, Nicotiana sylvestris, Hordeum vulgare, Hordeum spontaneum, Secale cereale* and *Lotus pedunculatus* (Blakeslee and Avery 1938; Goodspeed and Avery 1939; Tsuchiya 1960, 1967; Chen and Grant 1958 b; Hermsen 1970; Khush 1973). However, when compared with the frequency in *L.esculentum* for triplo-1 and triplo-3 (Rick and Barton 1954), the percentage of transmission found for the same chromosomes in *L.peruvianum* was approximately the same. Hence it seems that the tolerance of *L.peruvianum* towards certain types of aneuploidy (Sree Ramulu et al. 1977) which are not accepted by the cultivated tomato is not associated, in the case of extra-chromosomes tolerated by the two species, to a higher rate of transmission of trisomy in the wild species.

Only guesses can be made at the moment for explaining the relatively low transmission frequency of the trisomic condition in *L.peruvianum*. It is well known that, in the absence of selection forces, the transmission rate should theoretically approximate 50% in the case of crosses between trisomics (2n + 1) and diploids (2n) and that upon self-pollination, (2n + 1) × (2n + 1), the progenies of trisomics should consist of 2n, 2n + 1 and 2n + 2 individuals in the ratio of 1 : 2 : 1. In practice, however, these expectations are never realized and the reduction in transmission frequency may be due to a variety of such different factors as the elimination of the extra-chromosome during meiosis, megaspore replacement, reduced viability of n + 1 gametes and malformation of embryos, endosperms or seed coats. Growing conditions (Rajhathy 1975) and the extension of germination times (Blakeslee and Avery 1938; Goodspeed and Avery 1939; Tsuchiya 1960; Khush 1973) also exert influence on transmission rates and upon final proportion of aneuploids among the offsprings of trisomics. It is probable that pollen abortion, which averaged 30% in the parental trisomics (Sree Ramulu et al. 1977), and reduction in seed germinability (13% of all seed sown failed to germinate) contributed, in the present study, to the deficit of trisomics among the progenies of triplo-1 and triplo-3. It also appears, in view of the fact that no trisomics were recorded among the progenies resulting from self-pollination of triplo-1, that inbreeding in an allogamous species such as *L. peruvianum* reduces the probability to recover trisomics.

Such considerations do not hold true in the case of the trisomic plant 269 which yielded more trisomics upon selfing than when crossed to the normal diploid clone and for which the average transmission rate approximated 44%. It must be noted however, that plant 269 combined trisomy and a deletion of the satellited region of chromosome 2 and that most of its progenies, whether diploid or trisomic, expressed considerable weakness and growth retardation. It is possible that under such circumstances very little selection operated against the transmission of trisomy which, in view of the very high frequency of trisomics among the progenies resulting from selfing (Table 2), even appears to have benefited from a selective advantage of n + 1 pollen grains.

The Influence of Chromosome Length

Transmission rates are known to vary from one chromosome to an other and Einset (1943) established, in maize, a correlation between chromosome length, univalent frequency at metaphase I and the transmission rate of the extra chromosome; the trisomics involving longer chromosomes formed more trivalents, less laggards and the transmission frequency was higher. This correlation does not seem to hold true in such plant species as *L. esculentum* (Rick and Barton 1954) and *Lotus pedunculatus* (Chen and Grant 1968a, b). It is, at the best, only partly valid in the case of *L. peruvianum* where triplo-1 (length of chromosome 1 in somatic metaphase : 3.23 ± 0.06 mμ) formed more trivalents than triplo-3 (length of chromosome 3 : 2.34 ± 0.04 mμ), but transmitted its trisomic condition at a rate (2.6%) which is lower than that of triplo-3 (8.6%). In addition, no relationship could be established between chromosome lengths and the frequency of PMC with univalent laggards (see Sree Ramulu et al. 1977). Chen and Grant (1968 a, b) interpreted a negative relation between chromosome length and transmission rate in *Lotus* by the assumption that the trisomics involving longer chromosomes display greater amounts of genic unbalance which leads to the abortion of a larger proportion of n + 1 gametes and 2n + 1 embryos.

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