STUDIES ON THE CYTOLOGY OF OXALIS TUBEROSA AND TROPAEOLUM TUBEROSUM

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ABSTRACT. Chromosome numbers are reported for the cultivated tuber-bearing species *Oxalis tuberosa* Mol. (Oxalidaceae) and *Tropaeolum tuberosum* Ruiz & Pavon (Tropaeolaceae) from Peru. Chromosome numbers for *O. tuberosa* fall in the range 2n = 58–66 and for *T. tuberosum* a new count of 2n = 52 is established. Both species show multivalent formation and other meiotic abnormalities which suggest a possible autopolyploid origin.

Oxalis tuberosa Mol. and *Tropaeolum tuberosum* Ruiz & Pavon are two tuber-bearing minor crop plants which are cultivated in the Andes of Bolivia, Peru, Ecuador, Colombia and Venezuela. Although cultivation has declined in recent times *O. tuberosa* is still an important element in the diet of Indian communities in remote areas where it is often cultivated on hillside terrace systems in rotation with potato and ulluco (*Ullucus tuberosus* Loz.). Storage potential is increased by soaking the tubers followed by exposure to the sun and night frosts to give the dried tuber "oca chuño". *Tropaeolum tuberosum* is cultivated less frequently but is apparently employed as a diuretic and for other medicinal purposes in addition to its use as a food tuber. Hodge (1951) and Leon (1964) give details of cultivation and Gibbs (1976) has reported on the breeding system of *O. tuberosa*.

Materials and Methods

Oxalis tuberosa buds were fixed from flowering plants in the collection maintained at Huancayo (Experimental Station of the International Potato Centre, Lima) derived from accessions of native cultivars from localities in the surrounding Central Sierra, viz., Tarma (746/6), Ingenio (747/8–10), Huasa Huasi (748/3–5) and Huancayo (741/6).

Tropaeolum tuberosum flower buds came from the following sources: a field crop at Cuyo Cuyo (CY2), Department of Puno; cultivated plants at Huancayo grown from tubers from Huasa Huasi (748/1T), Department of Huancayo, and Bambamarca (743/1T), Department of Cajamarca; cultivated plants grown at the University Botanic Garden, St Andrews, (a) of a long established horticultural cultivar (135/68) and (b) from tubers originally from Puno (749/1T).

All buds were fixed in 3:1 ethanol/glacial acetic acid and anther squashes were prepared by standard aceto-carmine or aceto-orcein techniques. Attempts to study mitosis in root-tips were unproductive.

Results

Meiosis in *Oxalis tuberosa* presents a range of abnormalities which include multivalent formation, irregular disjunction, lagging chromosomes and secondary associations. Chromosome numbers vary from 2n = 58–66. In some buds 100% abortive pollen was observed.

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Meiosis in *Tropaeolum tuberosum* presents abnormalities very similar to those encountered in *Oxalis tuberosa*, although a relatively stable chromosome number of 2n = 52 was observed. Again, considerable numbers of malformed pollen grains occur.

The meiotic configurations encountered in the two species are set out in Table 1 and illustrated in Fig. 1 a–e.

Discussion

The frequency of multivalent formations and of secondary associations suggest that both *O. tuberosa* and *T. tuberosum* are possibly of autopolyploid origin. A series of basic chromosome numbers has been proposed for the genus *Oxalis*, x = 5, 6, 7, 9, 11 (Darlington & Wylie, 1955), and the counts obtained for *O. tuberosa* indicate that it is a hexaploid of the x = 11 series showing much aneuploid instability. *T. tuberosum* is perhaps best regarded as a tetraploid species of the x = 13 series proposed by Huynh (1967)—see below.

Previous counts for *O. tuberosa* are 2n = 14 (Heitz, 1927), 2n = 63–68–70 (Kostoff *et al*, 1935), 2n = 66 (Cárdenas & Hawkes, 1948) and 2n = 66 (Marks, cited by Smith, 1976). The present counts are in accord with these apart from the anomalous number recorded by Heitz. Obviously multivalent formation and lagging chromosomes have led to considerable numerical instability which has been protected from the action of natural selection because of asexual propagation by tubers. Indeed, in both species dealt with in this paper the association of polyploidy with asexual reproduction by tubers is a significant feature. As with *Tropaeolum tuberosum* (see below) it must be assumed that the tuber-bearing habit in *O. tuberosa* preceded polyploidy but although herbarium specimens from apparently non-cultivated areas have been cited (Macbride, 1949) nothing is known of their cytology or extent of tuber formation, or indeed if they represent wild forms or merely escapes from cultivation.

The high pollen infertility observed in this investigation is interesting since Gibbs (1976) reported successful pollinations between the floral morphs (*O. tuberosa* is a tristylous species) and, furthermore, the physiological incompatibility system was found to be largely intact. Although considerable pollen sterility was also found in the plants used in the pollination experiments (2–79% sterile pollen) apparently sufficient viable pollen was produced to obtain some seed set.

Previous chromosome counts for *Tropaeolum tuberosum* are 2n = 42 (Sugiura, 1936a & b) and 2n = 48 (Marks, cited by Smith, 1976). The new count of 2n = 52 reported here is well established since it is based on native cultivars from northern, central and southern Peru and also on a long established horticultural cultivar in Britain. It also fits well with the albeit sparse cytological data available for the genus at sectional level. Thus, Sparre (1968) in his detailed monographic studies on *Tropaeolum* has grouped *T. tuberosum* in sect. Mucronata together with *T. longiflorum* Killip, *T. crenatiflorum* Hooker, *T. purpureum* Killip and *T. cochabambae* Buch. This section is morphologically very homogeneous and palynological studies (Huynh, 1968) also support the grouping in that the pollen type C_2 is confined to it.

TABLE 1

Meiotic configurations and chromosome numbers in *Oxalis tuberosa* and *Tropaeolum tuberosum*

Plant	Meiotic configuration IV	III	II	I	No. of cells	2n	Stage & notes
O. tuberosa							
748/3	4		24		1	64	MI
748/4					1	66	AI, 31–31 disjunction with two lagging biv.
748/5	1		28		1	60	MI
747/10		3	24	10	1	67	MI
					1	c66	AI
741/6					1	65–66	AI
746/6					1	57–58	AI
					1	58	TI, 31–27 irregular disjunction
747/8					1	66	AI, 34–31 with one lagging univ.
					1	66	AI, 34–32
T. tuberosum							
743/1T			26		1	52	All cells of *T. tuberosum* at MI
747/1T			26		2	52	
	1		24		2	52	
	1		22		1	48	
748/1T	2		22		1	52	
	1	4	18		1	52	
	1	3	19	1	1	52	
	1	1	20	1	1	52	
	1		22	1	1	52	
		2	23		2	52	
		2	22	2	1	52	five 2ndry assocs each of two biv. and one of three biv.
		1	23	2	1	52	three 2ndry assocs each of two biv.
			26		2	52	one cell shows four 2ndry assocs each of two biv.
	3		26		1	64	
		21		1	1	64	anomalous cell showing almost complete triv. assoc.
			25	1	1	51	
			21	1	1	43	
749/1T			26		1	52	
CY 2	1		24		1	52	
		2	23		1	52	
			26		1	52	
garden cultivar	1		24		2	52	
(135/68)		2	23		1	52	

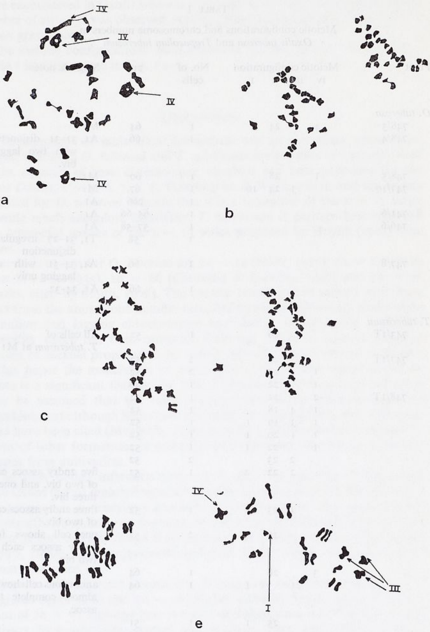

FIG. 1. Camera lucida drawings of meiosis in PMC × approx. 1200. a, b, c, *Oxalis tuberosa*: a, plant 748/3, MI, 4_{iv} 24_{ii} (2n = 64); b, 746/6, TI, irregular disjunction, n = 31 at l.h. pole, n = 27 at r.h. (2n = 58); c, 747/8, TI, irreg. disj., n = 34 at l.h. pole, 31 at r.h., with 1 laggard in the centre (2n = 66); d, e, *Tropaeolum tuberosum* (2n = 52): d, 743/1T, MI, 26_{ii}; e, 748/1T, MI, 1_{iv} 3_{iii} 19_{ii} 1_{i}.

The cultivated forms of *T. tuberosum* are the only tuber-bearing plants in the section and the remaining species are all annual. Huynh (1967) reported chromosome counts of 2n = 26 for *T. cochabambae*, 2n = 28 for *T. pubescens* (sect. Serrato-ciliata) and 2n = 52 for *T. tricolor* (sect. Chilensia). On the basis of these counts Huynh proposed a base number of x = 13 as an addition to the previously established x = 7 for *Tropaeolum*. He also suggested that in view of the cytological disparity between *T. tuberosum* (2n = 42, according to Sugiura, 1936a & b) and *T. cochabambae* (2n = 26) sect. Mucronata might require further subdivision as the cytology of other species became known. The new count of 2n = 52 for *T. tuberosum*, however, removes this ambiguity and reinforces the homogeneity of Sparre's sect. Mucronata, with *T. tuberosum* as a probable tetraploid in an x = 13 series. It would seem that the often cited count by Sugiura, based on sectioned rather than squash preparations, is erroneous.

The polyploid nature of *T. tuberosum* in such a series suggests some interesting possibilities for the origin of the tuber-bearing cultivar. Sparre (1973) has recognised two subspecies for *T. tuberosum*: subsp. *tuberosum*, the widely cultivated form, and subsp. *silvestre*, a naturally occurring form. The two subspecies are largely sympatric in Ecuador, Peru and Bolivia, and as Sparre himself admits, the differences between them are slight, viz:— somewhat smaller leaves, more slender habit and, most strikingly, lack of tubers in subsp. *silvestre*. Perhaps floral abnormalities* and marked levels of pollen sterility in subsp. *tuberosum* may also be diagnostic features. It is tempting to suggest that the cultivated form has been derived from subsp. *silvestre* by autopolyploidy and protected from sterility problems by asexual tuber propagation, but segmental allopolyploidy following hybridisation with another closely related species (*T. cochabambae*?) cannot be discounted, nor can evolution at the homoploid level. To resolve the problem cytological studies of the tuberless subsp. *silvestre* are needed and, meantime, the new count should be referred strictly to *T. tuberosum* subsp. *tuberosum*.

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References

Cárdenas, M. & Hawkes, J. G. (1948). Número de cromosomas en algunas plantas nativas cultivadas por los indios de los Andes. *Revista de Agricultura* (*Cochambamba*) 5(4):30–32.

Darlington, C. D. & Wylie, A. P. (1955). *Chromosome Atlas of Flowering Plants*. London.

* We have found supernumerary petals and stamens and 4–5 ovary loculi and stigmatic lobes to be common in our material and this seems to have been the case with others, e.g. Harrison *et al* (1969) depict a 5-lobed ovary. However, the original illustration by Ruiz & Pavon (*Flora Peruviana et Chilensis* 3, 314, Fig. 6, 1802) has a normal flower as does *Bot. Mag.* t. 3714 (1840).

GIBBS, P. E. (1976). Studies on the breeding system of Oxalis tuberosa Mol. *Flora* 165:129–138.

HARRISON, S. G., MASEFIELD, G. B. & WALLIS, M. (1969). *The Oxford Book of Food Plants*. Oxford.

HEITZ, E. (1927). Ueber multiple und aberrante Chromosomenzahlen. *Abhandl. Naturwiss. Vereins Hamburg* 21 (3–4):47–57, cited in Federov, A. (ed.) (1969). *Chromosome Numbers of Flowering Plants*. Leningrad.

HODGE, W. H. (1951). Three native tuber foods for the high Andes. *Economic Botany* 5:185–201.

HUYNH, K. L. (1967). Caryosystématique dans le genre Tropaeolum L.: I. T. cochabambae Buch., T. pubescens HBK et T. tricolor Sweet. *Bull. Soc. Bot. Suisse* 77:309–313.

——(1968). Morphologie du pollen des Tropaeolacées et des Balsaminacées I. *Grana Palyn.* 8:88–184.

KOSTOFF, D., DOGADKINA, H. & TICHONOWA, A. (1935). *Dokl. Acad. Nauk. URSS* 3(8):401, cited in Darlington, C. D. & Wylie, A. P. (1955). *Chromosome Atlas of Flowering Plants*. London.

LEON, J. (1964). *Plantas Alimenticias Andinas. Instituto Interamericano de Ciéncias Agricolas. Boletin Tecnico no. 6*. Lima.

MACBRIDE, J. F. (1949). Oxalis tuberosa in Oxalidaceae, *Flora of Peru, Field Mus. Nat. Hist., Bot. Ser.* 13(3):598–599.

SMITH, P. M. (1976). Minor crops, in Simmonds, N. W. (ed.). *Evolution of Crop Plants*. London & New York.

SPARRE, B. (1968). Preliminary report on the taxonomy of the Tropaeolaceae. *Grana Palyn.* 8:97–114.

——(1973). Tropaeolaceae in *Flora of Ecuador* (Sparre, B. & Harling, G., eds.) *Opera Bot.*, ser. B, 2:2–30.

SUGIURA, T. (1936a). A list of chromosome numbers in angiospermous plants. II. *Proc. Imp. Acad. Tokyo*. 12:144–146.

——(1936b). Studies on the chromosome numbers in higher plants with special reference to cytokinesis, 1. *Cytologia* 7:544–595.