

NATURE OF POLYPLOIDY IN SOME 48-CHROMOSOME
SPECIES OF THE GENUS SOLANUM,
SECTION TUBERARIUM

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CHROMOSOME numbers have been reported for 116 species in the section Tuberarium of the genus *Solanum*. An euploid series with 24, 36, 48, 60 and 72 somatic chromosomes exists. PRAKKEN and SWAMINATHAN (1952) concluded from the available evidence that the basic chromosome number in the genus is 12 and not 6 as suggested by some authors. Species with 48 chromosomes will, on this basis, be tetraploids and tetraploid species are present in the taxonomic series *Acaulia* Juz., *Conicibaccata* Bitt., *Longipedicellata* Buk., and *Tuberosa* Rydb. Both native and cultivated species with 48 chromosomes occur in the series *Tuberosa* to which the commercial potato (*Solanum tuberosum*), a tetraploid, belongs. Nineteen tetraploid species are so far known in the section Tuberarium (SWAMINATHAN and HOWARD 1953).

STEBBINS (1947, 1950) has pointed out that it is by no means easy to classify a naturally existing polyploid species into one or the other of the two rigidly contrasting categories usually recognized, namely auto- and allo-polyploids. Such a task is further complicated in potato species since (1) any set of 12 chromosomes is usually capable of pairing with any other set in species hybrids (HOWARD and SWAMINATHAN 1952), and (2) genetic studies are difficult owing to various causes among which the following are some of the more important. First, all potato varieties are heterozygous for many of the characters studied and homozygous plants can only be obtained, if at all, by several years of selfing. Secondly, among the seedlings derived from selfing a variety or from crossing two varieties there is usually a varying percentage of degenerate individuals which may affect genetic segregations for the character being studied. Thirdly, there is the difficulty that among the offspring many may not flower, or, if they do, may have pollen and ovule sterility. Fourthly, segregations are often complex owing to the polyploid constitution of the potato; and fifthly, bud mutations and chimaeras occur frequently. Studies on this problem are nevertheless called for since any information obtained is of considerable interest to potato breeders.

MATERIAL AND METHODS

The following species and varieties possessing 48 chromosomes were used in the study.

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Series Acaulia: *Solanum acaule* varieties Bukasov and Recoba.

Series Longipedicellata: *S. longipedicellatum* C.P.C. 28.

Series Tuberosa: *S. andigenum* C.P.C. 1384.

S. tuberosum varieties Duke of York, Gladstone and Cl.B. 72 (the last mentioned is a selection of Mr. J. CLARK of Ireland which includes in its parentage the varieties Craigs Defiance, Ballydoon and Katahdin.)

The somatic chromosomes were studied following the use of the 8-hydroxyquinoline pretreatment method of TJIO and LEVAN (1950). The schedule adopted was somewhat modified (SWAMINATHAN 1950). Meiotic configurations were studied in microsporocytes which had been fixed in acetic alcohol (3 absolute alcohol : 1 acetic acid) to which a few drops of a saturated solution of ferric chloride had been added. Squashing in a drop of acetocarmine gave satisfactory preparations.

Chromosome doubling was induced in *S. acaule*, *S. longipedicellatum* and *S. tuberosum* by the colchicine-agar seed treatment method (SWAMINATHAN 1950).

Definition of terms

The following terminology as proposed by STEBBINS (1947, 1950) is considered to be the most satisfactory.

Autopolyploid: The constituent genomes are completely homologous, the progenitor being a fertile species.

Segmental allopolyploid: Contains two pairs of genomes which possess in common a considerable number of homologous chromosomal segments or even whole chromosomes, but differ from each other in respect to a sufficiently large number of chromosome segments, so that the different genomes produce sterility when present together at the diploid level.

Genomic allopolyploid: Contains two or more sets of very different genomes and the only type of pairing which normally occurs is that between similar chromosomes of the same genome.

Autoallopolyploid: Combines the characteristics of the preceding types. Plants belonging to this group will have the constitution AAAABB, etc.

These terms are used in this paper in the above senses.

RESULTS

a. *Somatic chromosomes.* The somatic chromosomes of *S. tuberosum* (var. Duke of York) and *S. longipedicellatum* (C.P.C. 28) were examined and classified using over-all length, position of centromeres, secondary constrictions and presence of satellites as diagnostic characters. The chromosomes fell into seven different groups (table 1). Each of these species had two chromosomes bearing satellites in their short arms and two chromosomes with secondary constrictions in their long arms (figs. 1 and 2). No conspicuous differences between the idiograms of the two species could be detected.

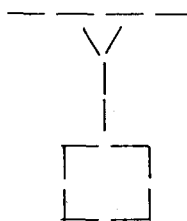


b. *Meiosis.* The chromosomes are usually associated as bivalents at diaki-

TABLE 1
Somatic chromosomes of *S. tuberosum* and *S. longipedicellatum*.

Description	Length in microns	No. of chromosomes in	
		<i>S. tuberosum</i> (Duke of York)	<i>S. longipedicellatum</i> (C.P.C. 28)
1. Long chromosomes with sub-median centromere and satellites in the short arm	3.0 to 3.5	2	2
2. Long chromosomes with sub-median centromere and secondary constriction in the long arm	3.0 to 3.5	2	2
3. Long chromosomes with sub-terminal centromere	3.0 to 3.5	8	6
4. Medium length chromosomes with sub-median centromere	2.0 to 3.0	8	8
5. Medium length chromosomes with median centromere	2.0 to 3.0	4	4
6. Short chromosomes with median centromere	1.5 to 2.0	4	0
7. Chromosomes of varying lengths with sub-median centromere	1.0 to 2.5	20	26

nesis and at metaphase I in *S. acaule* and *S. longipedicellatum*. Occasionally, 23_{II} and 2_I may be present (figs. 3 and 4). Multivalents occurred in *S. andigenum* and *S. tuberosum* and the mean pairing frequency at M I in these two species was $2.70_I + 19.74_{II} + 0.11_{III} + 1.37_{IV}$ (27 cells) and $2.227_I + 18.61_{II} + 0.166_{III} + 2.0_{IV}$ (18 cells) respectively. Two M I plates with univalents, bivalents, trivalents and quadrivalents are shown in figures 5 and 6. The chiasma frequency found at M I in the four species examined is given in table 2.

The quadrivalents observed in *S. andigenum* and *S. tuberosum* were of the following types:

Type	Number in	
	<i>S. andigenum</i>	<i>S. tuberosum</i>
	12	16
	4	5
	21	15

A dicentric bridge and an acentric fragment were twice observed at anaphase I in *S. longipedicellatum* (fig. 7). Metaphase II and subsequent stages were regular in *S. acaule* and *S. longipedicellatum* (fig. 8). In *S. andigenum* and *S. tuberosum*, however, restitution nuclei were formed in 2 to 3% of cells leading to the formation of dyads. Eleven percent of metaphase II plates in *S. andigenum* and 17% in *S. tuberosum* had unbalanced chromosome numbers.

c. *Studies in induced polyploids.* Chromosome doubling was induced by colchicine treatment of seeds in *S. tuberosum* (var. Gladstone), *S. acaule*

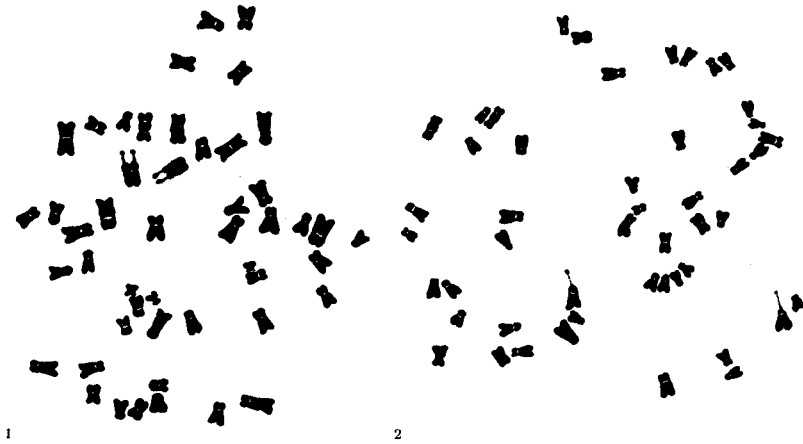


FIGURE 1.—Somatic chromosomes of *S. tuberosum*, variety Duke of York ($\times 1500$).
 FIGURE 2.—Somatic chromosomes of *S. longipedicellatum*, C.P.C. 28 ($\times 1200$).

(var. Recoba and Bukasov) and *S. longipedicellatum* (C.P.C. 28). Octoploid *S. acaule* and *S. longipedicellatum* plants had thicker leaves with a lower length/breadth index, with more prominent hairs and with larger stomata. They were late to commence flowering and had larger flowers with calyx more hairy, with the pedicels thickened and with the anthers thicker but shorter. These plants were vigorous, fertile and showed a good fruit setting both spontaneously and after crossing with *S. tuberosum* (SWAMINATHAN 1951). In contrast, octoploid *S. tuberosum* plants were dwarf, unhealthy in appearance and never flowered. The chromosome associations at M I of meiosis in octoploids of *S. acaule* and *S. longipedicellatum* were either quadrivalents, bivalents or univalents.

Seeds of F_1 *S. demissum* \times *S. tuberosum* ($2n = 60$) were treated with colchicine to determine the nature of the plants with 120 chromosomes. They were, in general, more vigorous than octoploid *S. tuberosum* plants, formed flowers and set a few seeds (5 seeds per berry).

d. *Studies in hybrids between induced polyploids and S. tuberosum*. 1. Octoploid *S. longipedicellatum* \times *S. tuberosum* (Katahdin). This cross succeeded easily whereas no seeds could be obtained following crosses between normal

TABLE 2
Chiasma frequency at M I in tetraploid species.

Species	No. of PMC's examined	No. of configurations with xta					Chiasmata		
		0	1	2	3	4	Total	Per cell	Per bi- valent
<i>S. acaule</i>	20	4	173	305	0	0	783	39.15	1.63
<i>S. andigenum</i>	25	73	231	305	16	21	973	36.04	1.50
<i>S. longipedicellatum</i>	15	8	206	150	0	0	506	33.75	1.40
<i>S. tuberosum</i>	18	41	156	202	21	15	663	36.80	1.53

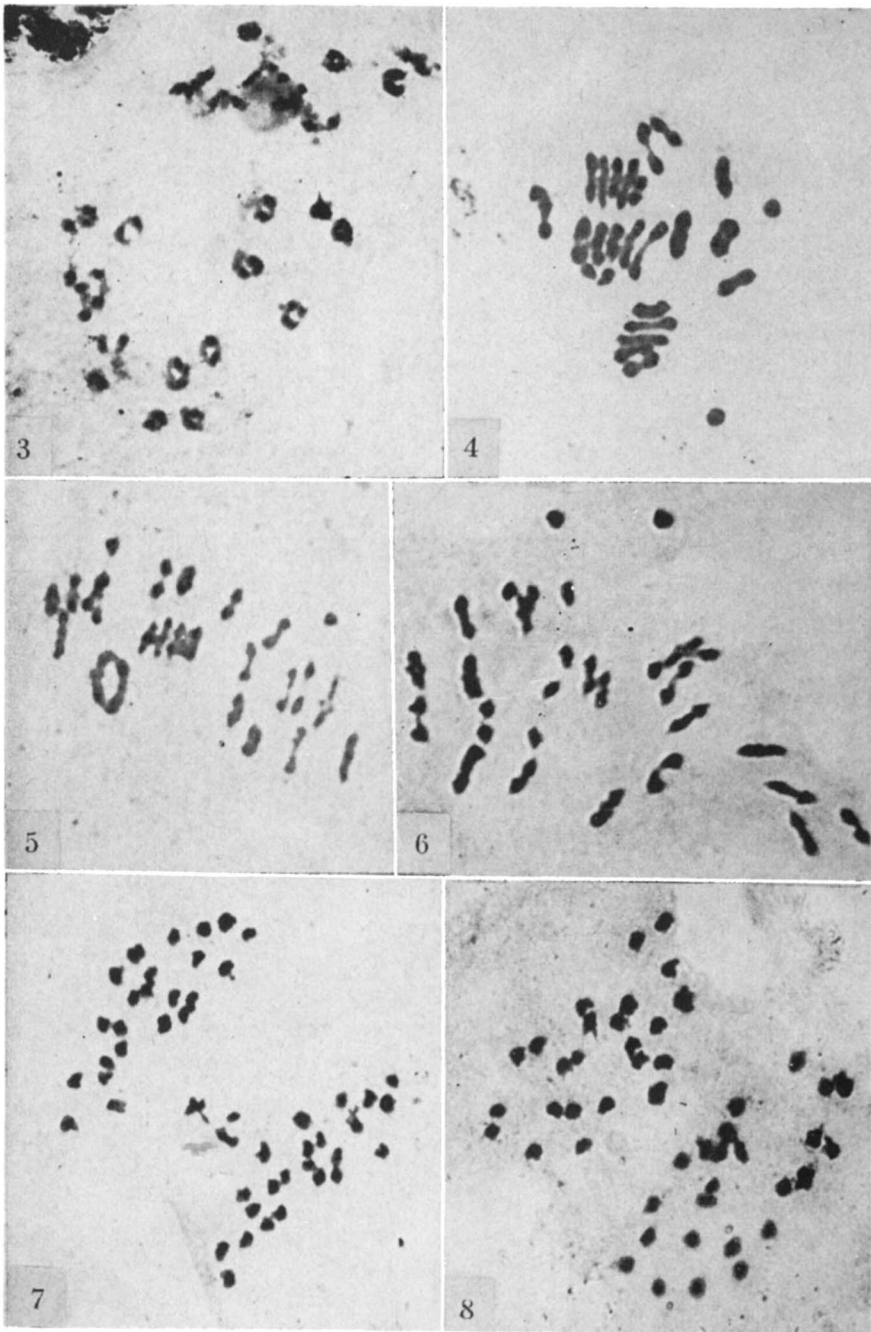


FIGURE 3.—Diakinesis in *S. longipedicellatum*. 24_{II} . FIGURE 4.—First metaphase in *S. longipedicellatum*. $2_I + 23_{II}$. FIGURE 5.—First metaphase in *S. andigenum*. $1_I + 18_{II} + 1_{III} + 2_{IV}$. FIGURE 6.—First metaphase in *S. tuberosum*. $2_I + 19_{II} + 2_{IV}$. FIGURE 7.—First anaphase in *S. longipedicellatum* showing a dicentric bridge and an acentric fragment. FIGURE 8.—Second metaphase in *S. longipedicellatum*. $24 + 24$ segregation.

S. longipedicellatum ($2n = 48$) and *S. tuberosum*. The F_1 hybrids were healthy and flowered but did not produce seeds on selfing. Meiosis was studied in one hybrid plant which had the expected chromosome number $2n = 72$. There was at M I a mean frequency per plate of $2.3_{\text{I}} + 34.65_{\text{II}} + 0.1_{\text{IV}}$ (20 cells). The average number of chiasmata per nucleus and per potential bivalent were 49.05 and 1.36 respectively. At M II, each of the 12 plates examined had 36 chromosomes. Seventy-five percent of the pollen was stainable.

The hybrid plants with $2n = 72$ would have 48 chromosomes of *S. longipedicellatum* and 24 of *S. tuberosum*. The nearly regular bivalent formation in them may be due to the pairing of the chromosomes of the two species among themselves, since normal *S. longipedicellatum* and haploid *S. tuberosum* (IVANOVSKAJA 1939) form 24 and 12 bivalents respectively.

TABLE 3
Chromosome pairing at M I in (F_1 *S. acaule* $8x \times S. tuberosum$) \times
S. tuberosum, $2n = 60$.

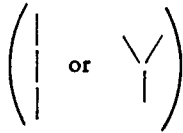
No. of cells	Configuration					
	I	II	III	IV	V	
1	4	14	6	0	2	
1	3	15	6	1	1	
1	7	13	6	1	1	
1	4	17	6	1	0	
1	14	12	6	1	0	
1	7	17	5	1	0	
1	6	19	4	1	0	
1	8	17	6	0	0	
2	6	18	6	0	0	
1	9	18	5	0	0	
1	7	19	5	0	0	
3	5	20	5	0	0	
1	14	17	4	0	0	
3	8	20	4	0	0	
1	6	21	4	0	0	
1	5	23	3	0	0	
2	7	22	3	0	0	
Total	23	159	422	111	6	4
Mean		6.913	18.347	4.826	0.261	0.1765

2. Octoploid *S. acaule* \times *S. tuberosum*. Like the octoploid plants of *S. longipedicellatum*, those of *S. acaule* could be easily crossed to *S. tuberosum*, while crosses involving the undoubled plants did not succeed. Thirty-two berries were obtained from the 86 crosses made in 1950 between octoploid *S. acaule* and varieties of *S. tuberosum*. Each berry contained, on an average, 31 seeds. The F_1 hybrids, raised in 1951, had broader leaves with many interjected leaflets and a prominent pedicel articulation when compared with *S. acaule* in which the articulation is almost obsolete.

Meiosis was studied in one F_1 plant which had the chromosome number $2n = 72$. There was at M I a mean frequency of $1.8_{\text{I}} + 34.7_{\text{II}} + 0.2_{\text{IV}}$ (20 cells). The mean chiasma frequencies per nucleus and per bivalent were 51.15 and

1.42 respectively. Sixty-four percent of the pollen was stainable. The hybrids could be backcrossed to *S. tuberosum* easily and four berries obtained in such crosses had 57, 62, 68 and 91 seeds respectively.

3. (F_1 *S. acaule* \times *S. tuberosum*) \times *S. tuberosum*. The plants of this cross resembled *S. tuberosum* in leaf shape, pedicel articulation and other morphological characters. One plant was examined cytologically and was found to have 60 somatic chromosomes. There was a mean frequency of $6.91_I + 18.347_{II} + 4.826_{III} + 0.26_{IV} + 0.176_V$ at M I. The detailed data are given in table 3. A striking feature of chromosome association at M I in this plant was the presence of several trivalents (range 3 to 6), which had not been observed in other pentaploid hybrids such as F_1 *S. demissum* \times *S. tuberosum* (HOWARD and SWAMINATHAN 1952). There were two pentavalents and six trivalents on one plate (fig. 9). All the trivalents observed were of the chain types



The pentavalents were also simple chains. The mean number of chiasmata per plate was 41.04.

Chromosome distribution was very irregular at M II. Among the 24 cells examined, two had 27 chromosomes; two, 28; four, 29; six, 30; four, 31; two, 32; three, 33; and one, 35. Two plants in which the pollen was examined had 52 and 64% good pollen. These plants could again be easily backcrossed to *S. tuberosum*. Each berry from such a cross contained, on an average, 41 seeds.

The 72-chromosome plants of the cross octoploid *S. acaule* \times *S. tuberosum* would have 48 *acaule* and 24 *tuberosum* chromosomes. Their gametes will probably have 24 *acaule* + 12 *tuberosum* chromosomes in view of the fairly regular meiosis in the plants. A pentaploid hybrid resulting from the fusion of such a gamete with a normal *S. tuberosum* gamete will have 24 *acaule* and 36 *tuberosum* chromosomes. The simplest explanation of the occurrence of about 5 trivalents per plate at M I in the pentaploid hybrid would thus be that they are formed following multivalent association of some of the chromosomes of the 3 basic sets of *S. tuberosum* present.

e. *S. acaule* ($2n = 48$) \times *S. simplicifolium* ($2n = 24$). The triploid F_1 plants from the cross *S. acaule* \times *S. simplicifolium* were vigorous and had compound leaves (*S. acaule* has compound leaves and *S. simplicifolium*, simple leaves—fig. 12). There was a mean frequency of $8.85_I + 9.0_{II} + 3.05_{III}$ at M I (20 cells). The plants were both pollen and ovule sterile. Amphidiploid plants were produced by treating F_1 seeds with colchicine (SWAMINATHAN 1950). There were $0.4_I + 35.8_{II}$ per plate (25 cells) at M I in the amphidiploid. At M II, 30 cells had 36 chromosomes, one had 37 and another 35. The subsequent stages were regular. Pollen fertility was about 61%. The plants were self-fertile and set berries spontaneously. The berries contained, on an average, 101 seeds.

The subsequent generations of this amphidiploid grown in 1951 and 1952 consisted of vigorous and fertile plants which were uniform in growth habits.

f. The backcross hybrid (amphidiploid *S. acaule* × *S. simplicifolium*) × *S. simplicifolium*. Crosses were made between amphidiploid *S. acaule* × *S. simplicifolium* and *S. simplicifolium* in 1950. Several of the berries obtained had nothing but shrivelled seeds whereas one berry had 3 good seeds which were sown in 1951. Two seeds germinated and gave rise to healthy plants. One

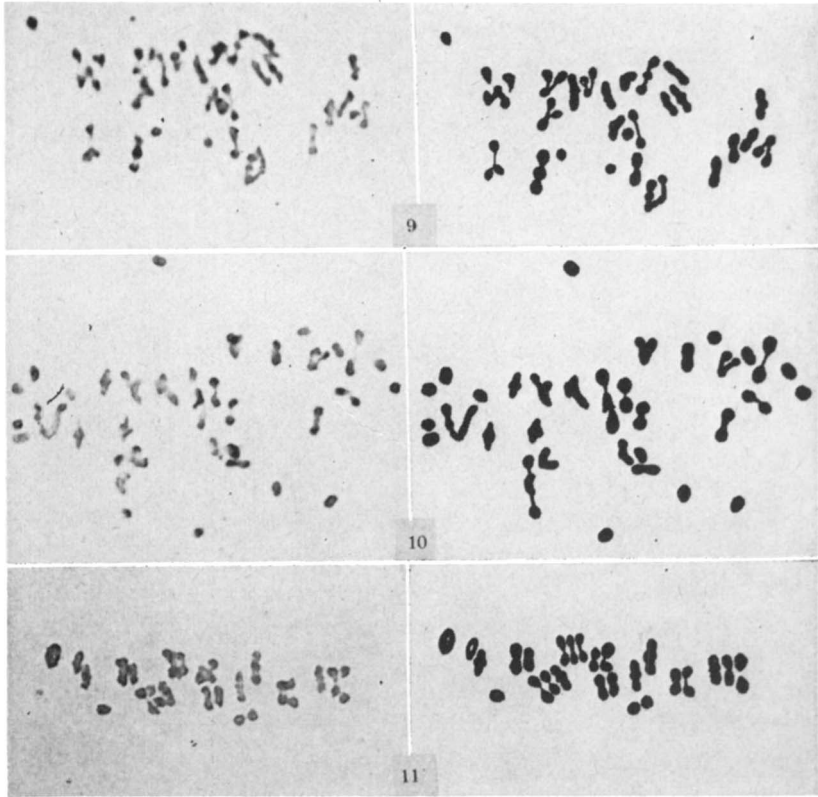


FIGURE 9.—First metaphase in (F_1 *S. acaule* × *S. tuberosum*) × *S. tuberosum*. $4_I + 14_{II} + 6_{III} + 2_V$. FIGURE 10.—First metaphase in (F_1 *S. acaule* × *S. tuberosum*) × *S. tuberosum*. $14_I + 12_{II} + 6_{III} + 1_{IV}$. FIGURE 11.—First metaphase in AD6.151. $3_I + 22_{II}$. (All photomicrographs × 1200.)

(plant no. A.D.6.151) had simple leaves and the other (A.D.6.152) had compound leaves (fig. 12). Chromosome counts in root tips and PMC squashes showed that A.D.6.151 had $2n = 47$ and A.D.6.152, $2n = 48$.

There was at M I in A.D.6.151 a mean frequency of $4.1_I + 20.1_{II} + 0.9_{III}$ (50 cells). A M I plate of this plant is shown in fig. 11. Fourteen of the 40 M II nuclei studied had 24 chromosomes whereas in the rest, the number ranged from 21 to 27. The plant had 8% good pollen and it produced no seed following either selfing or crosses with the sister plant and *S. tuberosum*. Plant A.D.6.152, on the other hand, was fertile and produced seeds in crosses

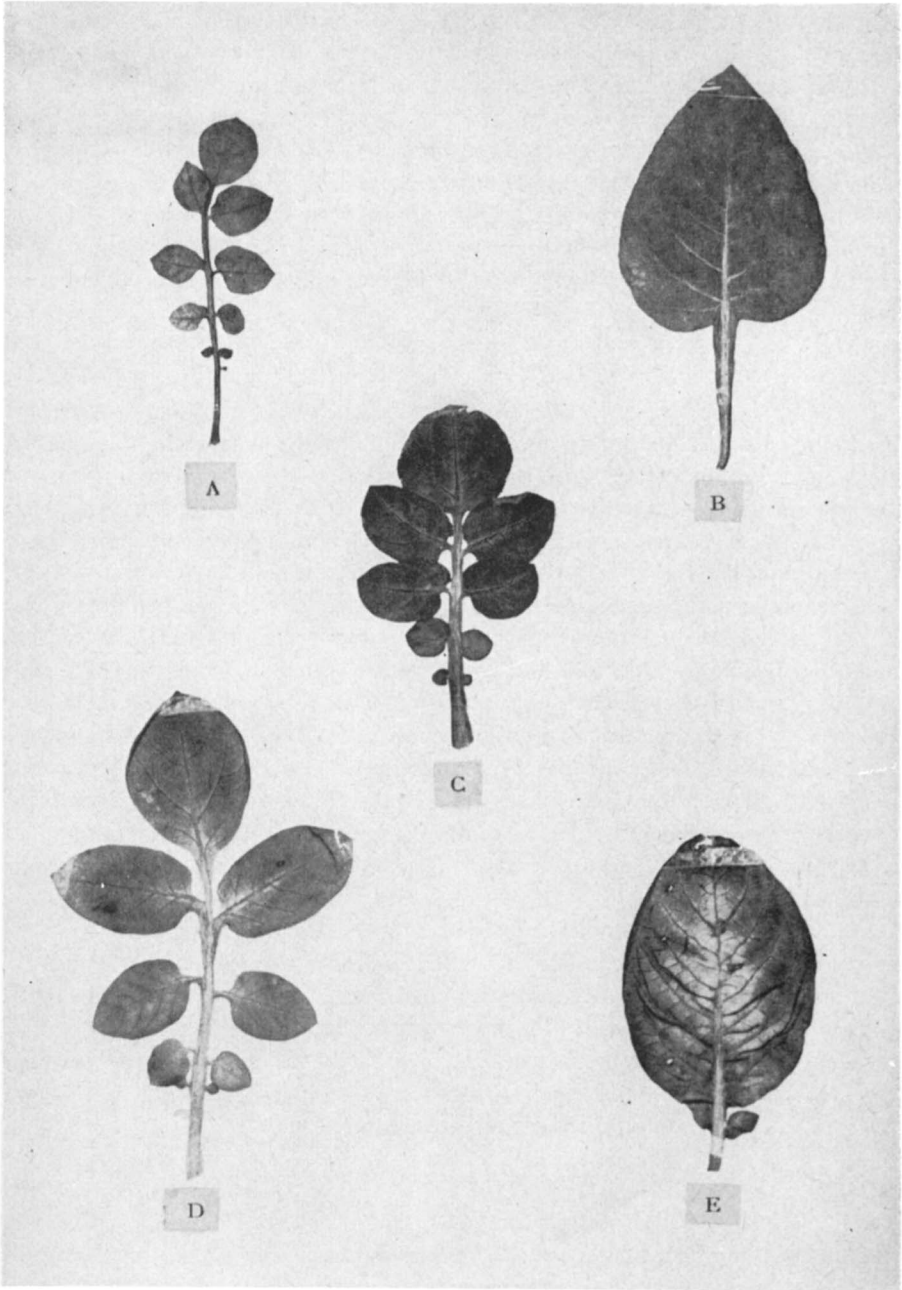


FIGURE 12.—Leaves of A. *S. acaule*; B. *S. simplicifolium*; C. Amphidiploid *S. acaule* \times *S. simplicifolium*; D & E. Two plants of the cross (amphidiploid *S. acaule* \times *S. simplicifolium*) \times *S. simplicifolium*; D. Plant No. AD6.152; E. Plant No. AD6.151.

with *S. tuberosum*. There were $1.2_I + 23.08_{II} + 0.08_{III} + 0.1_{IV}$ at M I (50 cells). The chromosome number was regular at M II in 20 of the 24 plates examined. The plant had 61% good pollen.

It was surprising that one plant of this backcross should have 47 chromosomes in view of the rarity of unbalanced gametes in amphidiploid *S. acaule* \times *S. simplicifolium*. The cross was repeated in 1951 using the second generation amphidiploid plants as mother parents. Three berries containing a total of 8 seeds were obtained and these seeds were sown in 1952. All of them germinated and the plants had compound leaves and a somatic chromosome number of 48. The plants had 60 to 70% good pollen and in one plant there were $3.6_I + 21.4_{II} + 0.4_{IV}$ (5 cells) at M I.

Origin of the simple leaf plant

It was found in studies on the inheritance of leaf type (compound or simple) in diploid species, that those with compound leaves have the genotype *LL* (*L* being a dominant factor for compound leaf) and *S. simplicifolium* has the genotype *ll* (SWAMINATHAN 1952). If *S. acaule*, a tetraploid, has the genotype *LLLL*, its gametes will have *LL* and the triploid hybrid from a cross between it and *S. simplicifolium* will be *LLl*. The amphidiploid will be *LLLLll*. A balanced gamete of the amphidiploid will have *LLl* on the assumption that the 36 bivalents usually formed in it result from pairing within the complements of *S. acaule* and *S. simplicifolium* respectively. The tetraploid plant resulting from backcrossing the amphidiploid to *S. simplicifolium* will have the genotype *LLll* and will have compound leaves. The 47-chromosome backcross plant will have the genotype *Lll* if the gamete of the amphidiploid parent had been deficient for one chromosome with the locus *L*, and should still possess compound leaves since it has been found from studies in amphidiploid *S. macolae* \times *S. simplicifolium* that plants simplex for *L*, i.e., *Llll*, have compound leaves.

The formation of a simple leaf plant in the backcross can be explained if *S. acaule* is disomic for *L*. The F_1 hybrid in such a case will be *Ll* and the amphidiploid *LLll*. The balanced gametes of the amphidiploid will have *Ll*, while a deficient gamete with the chromosome carrying *L* absent will have only *l* and such a gamete on being fertilized by *S. simplicifolium* pollen will give rise to a plant with simple leaves. These results thus suggest that with reference to locus *L*, *S. acaule* behaves as a functional diploid.

DISCUSSION

STEBBINS (1950) has described in great detail the occurrence and characteristics of polyploids and has pointed out the difficulties in classifying them. He has recognized four types of polyploids: autopolyploids, segmental allopolyploids, true allopolyploids and autoallopolyploids. These are only modal types and may be connected by several intermediate categories.

Chromosome associations at the first division of meiosis are the usual source of information concerning the type of polyploidy in a given plant. Presence of

multivalents is considered to indicate autopolyploidy and their absence, allopolyploidy. However, MÜNTZING and PRAKKEN (1940) and GILES and RANDOLPH (1951) have proposed for two different reasons that the absence of multivalents should not be treated as evidence of allopolyploidy. The former authors found a genotypically controlled tendency to form only bivalents in an autopolyploid *Phleum*. The latter authors made a study of the frequency of quadrivalents in a strain of autotetraploid maize at the beginning and end of a ten year period. They found that there were fewer quadrivalents and more bivalents at the end of the period than at the beginning.

The occurrence of tetrasomic ratios of inheritance provides evidence of autotetraploidy. Genetic ratios again may not provide absolute proof of the nature of origin of long established plants since the initially homologous genes lying in the different chromosome sets of a polyploid may mutate in different directions and gradually become so distinct as to be no longer allelic. Such a differentiation may eventually transform a polyploid into a species that has most genes represented only once in the gametes. Also, different loci may segregate differently in segmental allopolyploids so that any conclusions drawn from the study of one or two factors may be misleading.

These limitations will have to be borne in mind while discussing the mode of the origin of a polyploid plant from evidence obtained in present day studies. Such studies, however, show the relationship between the component genomes of a polyploid plant as it exists today, and in a polyploid which is also a crop plant, this knowledge facilitates the formulation of a rational approach to current breeding problems. The available data relating to four *Solanum* species are summarized below.

S. acaule

This species is highly fertile (pollen and seed) and regularly forms 24 bivalents and no quadrivalents at M I of meiosis. Octoploid *S. acaule* forms quadrivalents and as LAMM (1945) has pointed out, it is hence unlikely that the formation of bivalents in tetraploid *S. acaule* is determined by genotypic control. While no genetic study has been reported in this species, the data presented herein suggest that it behaves as a functional diploid with reference to locus *L*.

The triploid hybrids from crosses between *S. acaule* and diploid species have a high trivalent frequency (3 to 7), which led PROPACH (1937) to suggest that *S. acaule* is really an autotetraploid. However, the fact that amphidiploid *S. acaule* × *S. simplicifolium* forms only bivalents and the hybrid between octoploid *S. acaule* and *S. tuberosum* forms very few quadrivalents, suggest that the two genomes in a gamete of *S. acaule* are well differentiated. No diploid species has so far been found in the taxonomic group Acaulia. JUZEPČUK (1937) considers Acaulia to be the most recently formed series, since the pedicel articulation is almost obsolete and the corolla lobes are very much fused together. It is probable that *S. acaule* arose as a segmental allotetraploid from diploid species belonging to other taxonomic groups in *Solanum*.

S. longipedicellatum

This species has two satellited chromosomes, usually forms 24 bivalents and is fertile. One clone was heterozygous for an inversion. Octoploid plants are vigorous, form quadrivalents and are seed fertile. The hybrid between octoploid *S. longipedicellatum* and *S. tuberosum* forms mostly bivalents. Also, as in *Acaulia*, no diploid species have so far been recorded in the series *Longipedicellata*. Hence this species seems to be a segmental allotetraploid or a genomic allotetraploid.

S. andigenum

The name *S. tuberosum* was given to the European potato by BAUHIN in 1596 and that name was retained by LINNAEUS. JUZEP CZUK and BUKASOV (1929) grouped the Andean tetraploid varieties into a new species, *S. andigenum*, since these varieties form tubers best under short day conditions and the authors considered that they had had an independent origin from that of *S. tuberosum*. SALAMAN (1937) and HAWKES (1944), however, suggested that the two species were not markedly distinct and that they had had a common origin. VAN DER PLANK (1946) adduced evidence to suggest that the first European potatoes were short day types and he concluded that the new name *S. andigenum* is not justifiable since the chief characteristic of the plants of this species is their short day reaction. HAWKES and DRIVER (1946) agreed with the views of VAN DER PLANK and recently CORRELL (1952) has also listed *S. andigenum* as a synonym of *S. tuberosum*.

Varieties of *S. andigenum* can be easily crossed reciprocally with *S. tuberosum* and the hybrids are fertile. One to two quadrivalents are formed at M I in *S. andigenum* (maximum—4 quadrivalents). The meiotic behavior is hence quite similar to that found in varieties of *S. tuberosum*. Since there could thus be no objection on taxonomic or cytogenetical grounds for *S. andigenum* being considered as a subspecies or variety of *S. tuberosum*, the following discussion as to the nature of polyploidy in *S. tuberosum* would likewise apply to *S. andigenum*.

S. tuberosum

Floral characters. FUKUDA (1927) suggested that *S. tuberosum* arose from a single species since the floral characters in the various varieties have remained constant during the past 300 years. LONGLEY and CLARK (1930) pointed out that there was no need to suppose that more than one type of calyx and corolla were involved in the early ancestry and that it would be possible for a dominant type of flower to be carried unchanged through several generations of inbreeding especially if it was linked with desirable economic characters. All the varieties investigated by LUNDEN (1937) segregated for flower color and this was considered by him to point to the autotetraploid nature of the cultivated potato.

Somatic chromosomes. ELLISON (1935) found that the somatic chromosomes of *S. tuberosum* could not be classified into groups of four by their size.

His results are very misleading since he reported differences between the chromosomes of the varieties Langworthy and Golden Wonder. These should have similar somatic chromosome complements since Golden Wonder has been shown to be a periclinal chimaera with an inner core of Langworthy (CRANE 1936). LAMM (1945) who found 4 chromosomes with satellites in autotetraploid *S. rybinii* suggested that the presence of only two such chromosomes in *S. tuberosum* might be due to amphiplasty (NAVASHIN 1928). It appears that the study of somatic chromosomes will not provide much evidence concerning the nature of polyploidy in Solanum species.

Meiosis. It would appear from the data of authors other than CADMAN (1943)—table 4—that in *S. tuberosum* there occurs a mean trivalent + quadrivalent frequency of between 2 and 3 per plate as compared with about 4 to 6 in artificially produced autotetraploids (SWAMINATHAN 1952) and 0 in *S. acaule* and *S. longipedicellatum*. THOMAS (1946) reported that in *S. tuberosum* only two true quadrivalents per plate occur and he suggested that several

TABLE 4
Frequency of multivalents at M I in S. andigenum and S. tuberosum.

Species and variety	No. of cells with a quadrivalent (+ trivalent) frequency of										Multivalents		Reference
	0	1	2	3	4	5	6	7	8	9	Mean per nucleus	Coefficient of realization	
<i>S. tuberosum</i>													
Flourball	1	0	4	5	13	15	15	11	4	2	5.24	0.436	CADMAN (1943)
Deodara	1	1	3	5	7	3	0	0	0	0	3.25	0.27	LAMM (1945)
36/200	1	8	8	2	1	0	0	0	0	0	1.70	0.14	" "
Cl. B72	1	5	6	3	2	1	0	0	0	0	2.16	0.18	Present study
<i>S. andigenum</i>													
C.P.C.1384	8	8	4	4	3	0	0	0	0	0	1.48	0.12	" "

workers had failed to distinguish between primary and secondary associations. It is difficult to judge whether the quadrivalents observed are formed in a random manner or whether particular chromosomes always form them, since it is not possible to identify the individual chromosomes from morphological characters.

LONGLEY and CLARK (1930), MEURMAN and RANCKEN (1932) and ELLISON (1936) have all suggested that the irregularities of meiosis frequently observed in *S. tuberosum* (like dyad formation, asynapsis, etc.) could be explained if it was assumed that the species had originated as a hybrid between two species whose chromosomes did not pair fully. LAMM (1945) pointed out that similar irregularities occur in synthetic autotetraploids.

Sterility. KOMAROV (1931) suggested that the sterility of many cultivated varieties as contrasted with the fertility of many of the wild species, indicates a hybrid origin of the former. ELLISON (1936) on the other hand, has shown that several cultivated varieties are highly fertile when grown under favorable conditions.

Study of a haploid. IVANOVSKAJA (1939) obtained a single haploid (technically "polyhaploid") plant of *S. tuberosum* var. Aurora. Usually 12 bivalents were present at M I in this plant but occasionally 11 bivalents and 2 univalents occurred. Bridges and fragments were observed in 7% of the sporocytes at anaphase I, indicating some differentiation of the two genomes in the gametic set of *S. tuberosum*. The haploid produced 3 seeds in 12 berries. IVANOVSKAJA (1939) concluded from these observations that *S. tuberosum* is an allotetraploid. LEWIS (1943) has, however, pointed out that it is to be expected that haploid *S. tuberosum* plants will be self-incompatible like the majority of diploid *Solanum* species.

Study of species hybrids. The pairing behavior of the chromosomes of the two genomes in the gametic set of *S. tuberosum* can be inferred from hybrids such as the tetraploids obtained from the cross *S. tuberosum* × diploid species (due either to the functioning of unreduced gametes in the diploid parent or the use of autotetraploids of diploids) and from the hexaploid hybrids, octoploid *S. acaule* × *S. tuberosum* and octoploid *S. longipedicellatum* × *S. tuberosum*. All the results agree in showing that the chromosomes of the two genomes may pair to form approximately 12 bivalents. The pentaploid hybrid, (octoploid *S. acaule* × *S. tuberosum*) × *S. tuberosum*, provides some evidence as to the nature of the chromosome association in a triploid complement of *S. tuberosum*. The maximum frequency in a cell of 6 trivalents and 2 pentavalents suggests that 8 chromosomes of each of the 3 sets of 12 can associate together.

Behavior of polyploids. Octoploid plants of *S. tuberosum* are dwarf and weak in contrast to such plants of *S. acaule* and *S. longipedicellatum*, which are large and vigorous. Decaploid (*S. demissum* × *S. tuberosum*, $2n = 120$) plants have more vigor than octoploid *S. tuberosum* which may be considered as evidence in support of the general view that species hybrids suffer less from chromosome doubling than true species.

Effect of inbreeding. KRANTZ (1946) found that results from inbreeding commercial potato varieties are more explicable on an autotetraploid than on an allotetraploid basis.

Genetic results. MÜLLER (1930) first pointed out that the potato, owing to its tetraploid nature, does not behave genetically in the same way as a diploid. Prior to that time, all results had been interpreted on a simple, disomic basis. ASSEJEVA and NICOLAEVA (1935) obtained evidence for the occurrence of several duplicate factors controlling plant and tuber color. It appeared probable that some of these duplicate factors were allelomorphic. The occurrence of tetrasomic inheritance in the commercial potato was clearly established by LUNDEN (1937). He found, besides typical tetrasomic ratios of inheritance for certain loci, double reductional segregation, i.e., random chromatid segregation, at the following loci. (a) In reciprocal crosses of the type $Pppp \times pppp$ and $Dddd \times dddd$ (P is a factor for purple pigmentation and D , a factor needed for the development of plant color), P segregated as $1 P : 1 p$ while D segregated as $13 D : 15 d$. (b) Duplex $RRrr$ individuals were found in backcross

progenies of the type $Rrrr \times rrrr$ (R is a factor for red color). (c) Nulliplex $dddd$ offspring occurred in $DDDd \times dddd$ crosses. CADMAN (1942) found double reductional division at the Nx locus (gene Nx controls the top necrotic reaction to virus X). Since the publication of LUNDEN'S (1937) paper, segregations for various characters in commercial varieties have been explained on a tetrasomic basis. Simplex genotypes have been assigned in many instances without any other evidence of tetrasomic inheritance and in such cases, it is equally likely that the inheritance is disomic.

To summarize the results of the cytogenetical studies in *S. tuberosum* outlined so far: (a) genetical results suggest that several presumably unlinked loci show tetrasomic inheritance, and (b) cytological results show that first, 12 bivalents are formed in a haploid plant; secondly, a triploid complement may form up to 8 trivalents; and thirdly, a maximum frequency of 5 quadrivalents (9 according to the data of CADMAN 1943) and a mean number of 2 to 3 quadrivalents per metaphase I plate occur in some varieties. The lower quadrivalent frequency at the tetraploid level in comparison with the bivalents in the haploid and trivalents in the triploid may be due to some degree of preferential pairing in the tetraploid caused by a slight differentiation of some of the chromosomes. The extent of differentiation may vary in different varieties probably depending upon the degree of hybridization involved in their evolution. This may lead to significant differences in the multivalent frequencies observed in different varieties. The low chiasma frequency (less than 2 per bivalent) found in *Solanum* species may also partly lead to the realization of potential quadrivalents in the form of bivalents or trivalents and univalents.

These results would suggest that *S. tuberosum* probably arose as an autotetraploid. However, at this distance from the period of its evolution and with much hybridization work having been done in the breeding of commercial varieties, it would be futile to expect representatives of this species to behave strictly in conformity with the classical definition of autopolyploids. For all practical purposes, we may consider the current commercial varieties as segmental allotetraploids. Whether the term "segmental allotetraploid" can be applied to *S. tuberosum* in the evolutionary sense, as STEBBINS (1950) has proposed, can only be decided after several haploid plants of this species have been obtained and data concerning their fertility are available.

The fact that *S. tuberosum* seems essentially to be an autotetraploid will have some major implications in potato breeding programs. The production of homozygous breeding lines will be a slow process and a good proportion of the inbred plants may be aberrant owing to the possibility for the accumulation of deleterious lethal factors in a vegetatively propagated crop like the potato. It may consequently be difficult to perform several generations of continuous inbreeding. Desirable genes like the ones giving top-necrotic reaction to virus X (COCKERHAM 1943) and resistance to wart (LUNDEN 1950) seem to be present in the varieties possessing them in the simplex state and the breeder will require both much space and patience to get these genes in the triplex or quadruplex conditions. On the other hand, the existence of the possibility to

produce plants quadruplex for a particular gene is a definite advantage in instances where the genes have an additive effect.

SUMMARY

1. *Solanum longipedicellatum* and *S. tuberosum* have two chromosomes with satellites and two with secondary constrictions in their long arms.

2. *S. acaule* and *S. longipedicellatum* invariably form 24 bivalents at metaphase I of meiosis in microsporocytes. Some multivalents (± 2) occur in *S. andigenum* and *S. tuberosum*.

3. Octoploid plants of *S. acaule* and *S. longipedicellatum* are vigorous and fertile, while those of *S. tuberosum* are dwarf and fail to flower. Decaploid plants of F_1 *S. demissum* \times *S. tuberosum* with 120 chromosomes are vigorous but weakly fertile. Associations higher than quadrivalents have not been observed in octoploid *S. acaule* and *S. longipedicellatum*.

4. Thirty-six bivalents occur at M I in the hexaploid plants from crosses between octoploid *S. acaule* and *S. longipedicellatum* (pistillate parents) and normal *S. tuberosum* (pollen parent).

5. A maximum frequency of 2 pentavalents + 6 trivalents occurs in the pentaploid hybrid, (F_1 octoploid *S. acaule* \times *S. tuberosum*) \times *S. tuberosum*. This suggests that 8 chromosomes of the 3 sets of *S. tuberosum* present in the hybrid may form trivalent associations.

6. The amphidiploid from the cross *S. acaule* \times *S. simplicifolium* is fertile in contrast to the complete sterility of the triploid hybrid. Thirty-six bivalents are present at M I.

7. Two plants from the backcross (amphidiploid *S. acaule* \times *S. simplicifolium*) \times *S. simplicifolium* had the chromosome numbers $2n = 48$ and 47 respectively. The 48-chromosome plant had compound leaves like *S. acaule* and the 47-chromosome plant had simple leaves like *S. simplicifolium*. This suggests that *S. acaule* has the factor *L*, needed for the development of the compound leaf, in only 2 of its 4 genomes.

8. The available data suggest that (a) *S. acaule* and *S. longipedicellatum* are segmental allotetraploids, (b) *S. andigenum* and *S. tuberosum* are autotetraploids though the current commercial varieties can be considered as segmental allotetraploids, and (c) both on taxonomic and cytogenetical grounds *S. andigenum* can be treated as a sub-species of *S. tuberosum*.

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