CHROMOSOME COUNTS IN THE VARIETIES OF *SOLANUM TUBEROSUM* AND ALLIED WILD SPECIES[1]

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As far as has been determined, the species in the *Solanaceae* have a basic haploid chromosome number of 12. BÖNICKE (1911) has shown that the haploid chromosome number in both *Datura Stramonium* L. and *Datura Tatula* L. is 12. BLAKESLEE (1921) reports tetraploid mutations in *Datura Stramonium* with the haploid chromosome number 24. BLAKESLEE and BELLING (1924) produced experimentally, by means of cold, tetraploid plants of *Datura Stramonium.* WINKLER (1910) reports that the chromosome number is 36 in the haploid cells of *Solanum nigrum* L. and 12 in the haploid cells of *Solanum lycopersicum* L. WINKLER (1916) produced tetraploids artificially in these two *Solanum* species from dehydrated callus tissue and as graft hybrids. From callus tissue dehydrated with chloral hydrate, adventitious buds arose whose cells contained the 4X chromosome number. In his grafting experiments, a tetraploid sprout was produced at the union of a wedge-shaped piece of nightshade scion with tomato stock. After union had taken place, a cut was made at the level of the union so that the tomato tissue was in the middle of the cut surface and the nightshade tissue was on both sides. All axial buds were removed to allow adventitious buds to grow on the cut surface. Periclinal and sectorial chimeras appeared and in one case a periclinal chimera proved to be a tetraploid branch. WINKLER produced a true tetraploid tomato from this branch by cutting the stem across and forcing adventitious buds from callus tissue. The cells of the tetraploid tomato branch contained 48 chromosomes. In somewhat the same way WINKLER obtained a giant nightshade plant whose cells contained 4X or 144 chromosomes. In connection with the work of BLAKESLEE and of WINKLER in the experimental production of tetraploid plants in the Solanaceae, the work of NĚMEC (1899) with potatoes is of interest. NĚMEC studied the regeneration layer which forms over cut potato tubers and reports that the chromosome number found in the cells of such tissue is surely more than 70.

[1] Papers from the Department of Biology of the MAINE AGRICULTURAL EXPERIMENT STATION, No. 177, and from the Department of Botany of the UNIVERSITY of MICHIGAN, No. 244.

The relative ease with which tetraploidy has been experimentally produced in Solanaceae would suggest that the customary vegetative reproduction of potatoes might easily, of itself, afford an opportunity for the occurrence of tetraploid mutations. By the term tetraploidy, as used in this paper, is meant the doubling of the primitive chromosome group; just how this takes place is not known at the present writing. In view of the fact that, as this paper shows, tetraploidy does occur in some of the cultivated potatoes, it is planned to attempt the artificial production of potato tetraploids from the available diploid types. Such work may give rise to the production of commercial strains of economic value. Tetraploid forms of plants are usually *gigas* forms, and *gigas* forms may possibly produce a greater yield or different quality of tubers than parental types.

It does not appear unlikely that a cytological examination of the cultivated potatoes and their wild allies may determine whether or not tetraploidy has been one of the factors in the evolution of the potato. This is the problem which is dealt with in a preliminary way in this paper. In potatoes the question of pollen sterility is a very important one. It is not impossible that one of the manifestations of sterility may be that some pollen mother cells, failing to undergo the reduction divisions produce non-functional pollen grains, whereas other microspores produced in the same anther by the normal reduction division are functional. It may also be that in certain potato varieties and species-hybrids the chromosomes are irregularly distributed to the two poles during meiosis. Although to date no study has been made of somatic material, such a study is planned for the coming season and thus evidence may be obtained for the solution of the problems suggested. It would be decidedly interesting to find out what plant breeding advances might come about through the repeated intercrossing of tetraploid plants with diploid, with the end in view of securing types with one or more reduplicated chromosomes, thus applying to a vegetatively propagated economic plant some of the results obtained by BLAKESLEE and BELLING with Datura.

The material from which this cytological study in Solanum was made was grown at Aroostook Farm of the MAINE AGRICULTURAL EXPERIMENT STATION by Doctor CHARLES F. CLARK of the Office of Horticultural Investigations, UNITED STATES DEPARTMENT OF AGRICULTURE. Doctor CLARK not only very kindly allowed the writer to have access to the material but also checked over the classification of the various forms and furnished information regarding the original sources of the wild species referred to in this paper. *S. chacoense* Bitter originally came from Paraguay, *S. demissum* Lindl. from Mexico, and *S. Fendleri* Gray and

S. Jamesii Torr. from the Alamo National Forest at Cloudcroft, New Mexico. The material was fixed in ALLEN'S modification No. 15 of BOUIN'S killing fluid. The cytological problem in this paper was suggested to the writer by Doctor KARL SAX of the MAINE AGRICULTURAL EXPERIMENT STATION. Doctor SAX also very kindly assisted the writer during the course of the study.

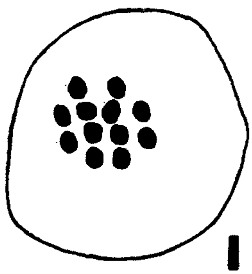


FIGURE 1.—Haploid chromosome group of *Solanum Jamesii* at heterotypic metaphase.

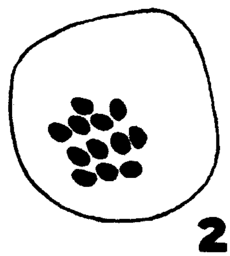


FIGURE 2.—Haploid chromosome group of *Solanum chacoense* at heterotypic metaphase.

As far as is now known the chromosome number of all the cultivated varieties of *Solanum tuberosum* L. and the allied wild species is some multiple of 12. Figures 1 and 2 illustrate that the reduced number of

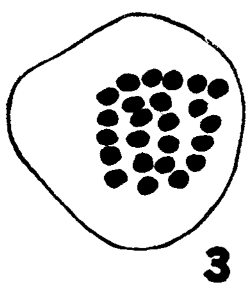


FIGURE 3.—Haploid Chromosome group of *Solanum Fendleri* at heterotypic metaphase.

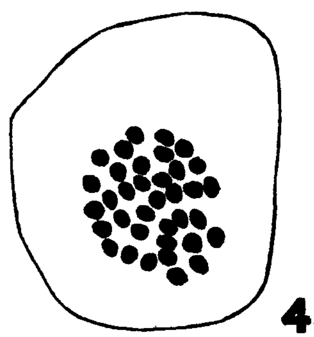


FIGURE 4.—Haploid chromosome group of *Solanum demissum* at heterotypic metaphase.

chromosomes in *Solanum Jamesii* and *Solanum chacoense* respectively is 12. The chromosomes at homotypic metaphase in haploid cells of *Solanum Jamesii* are shown also in plate 1, figure 1. For *Solanum Fendleri*, as shown in figure 3 and plate 1, figure 2, the haploid chromosome number is 24, and for *Solanum demissum* as illustrated in figure 4 and plate 1, figure 3, the haploid chromosome number is 36.

In the cultivated varieties McIntyre and McCormick, 24 is the reduced number of chromosomes. Figure 5 and plate 1, figures 4 and 5 illustrate the heterotypic metaphase as observed in pollen mother cells of the McIntyre variety. There can be no question about the count in this variety as both poles clearly show 24 chromosomes. The two equatorial

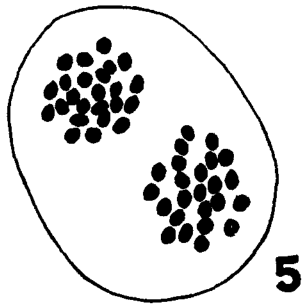


FIGURE 5.—Haploid chromosome groups of the McIntyre variety at homotypic metaphase.

plates are approximately in one plane within the cell. The same clear-cut evidence has been obtained for the McCormick variety, for which figures 6 and 7 represent the heterotypic metaphase. In this case the chromosomes at the two poles were necessarily shown in separate drawings because the two plates were in different planes, one directly beneath the other.

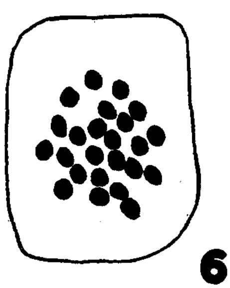


FIGURE 6.—Haploid chromosome group of the McCormick Variety at homotypic metaphase.

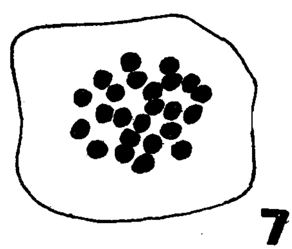


FIGURE 7.—Haploid chromosome group of the McCormick variety at homotypic metaphase.

It is believed that tetraploidy occurs in the Early Ohio variety. Figures 8 and 9 and plate 1, figures 6 and 7 present evidence for this belief. These figures illustrate a pollen mother cell of the Early Ohio variety at heterotypic metaphase. Since both poles of the division figure show unquestionably more than 36 and approximately 48 chromosomes, there can be little doubt that these figures indicate tetraploidy in this variety.

LEGEND FOR PLATE 1

FIGURE 1.—Photomicrograph showing the haploid chromosome group of *Solanum Jamesii* at heterotypic metaphase. The 12 chromosomes of this species are clearly illustrated.

FIGURE 2.—Photomicrograph showing the haploid chromosome group of *Solanum Fendleri* at heterotypic metaphase. The 24 chromosomes of this species are clearly illustrated.

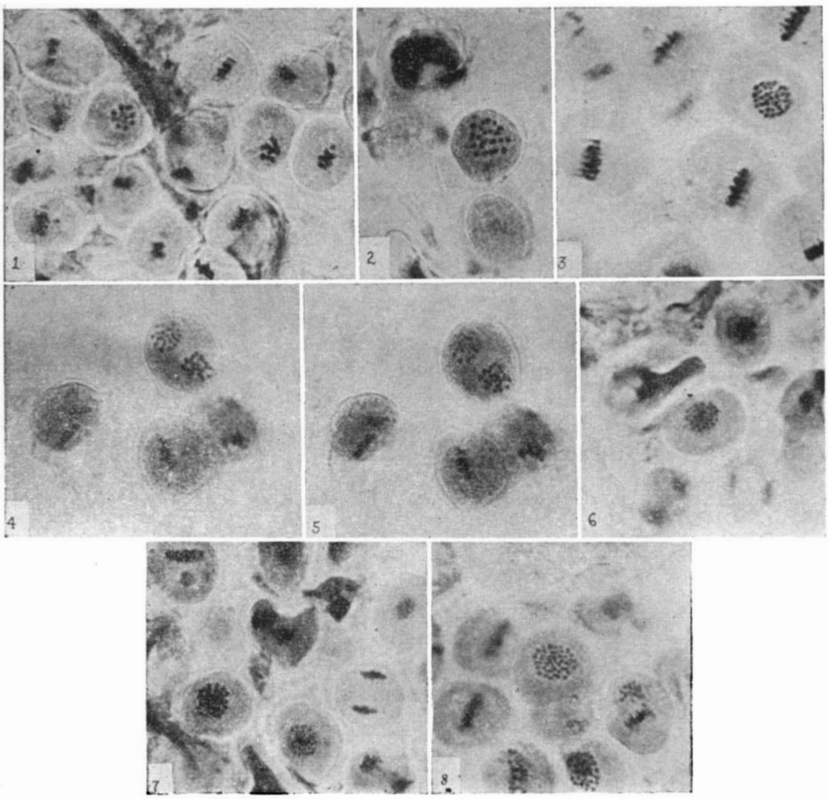
FIGURE 3.—Photomicrograph showing the haploid chromosome group of *Solanum demissum* at heterotypic metaphase. The 36 chromosomes of this species are clearly illustrated.

FIGURES 4 AND 5.—Photomicrographs of a pollen mother cell of the McIntyre variety of the cultivated potato at homotypic metaphase; in figure 4 one of the two equatorial plates is in focus and in figure 5 the other equatorial plate is in focus. These figures show that the haploid chromosome number of this variety is 24, and that the diploid chromosome number is 48.

FIGURES 6 AND 7.—Photomicrographs showing tetraploidy in the Early Ohio variety; figure 6 shows one of the two poles of the homotypic metaphase, and figure 7 shows the other pole of the same cell in focus.

FIGURE 8.—Photomicrograph showing what is believed to represent tetrapoloidy in the Early Rose variety. This figure shows the 48 chromosomes at heterotypic metaphase of the pollen mother cells.

SMITH, HUGH B. CHROMOSOME COUNTS IN *Solanum tuberosum*. PLATE 1.



. At any rate the chromosome number is greater than a triploid form would have.

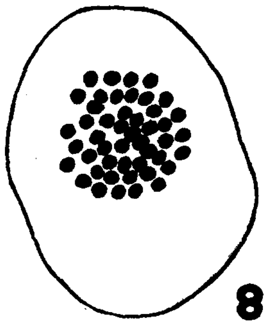


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FIGURE 8.—Haploid chromosome group in the Early Ohio variety at homotypic metaphase, indicating tetraploidy in this variety.

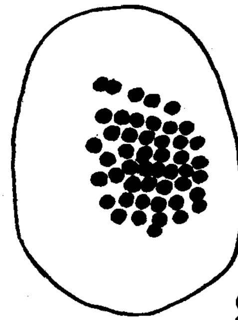

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FIGURE 9.—Haploid chromosome group in the Early Ohio variety at homotypic metaphase, indicating tetraploidy in this variety.

Although the evidence is not so conclusive as that which has just been described for the McIntyre and McCormick varieties, it is, nevertheless, believed that the haploid chromosome number in the Russet Rural and Early Ohio varieties is 24, and that tetraploidy, similar to that in Early Ohio, occurs in the Early Rose and Russet Rural varieties. The evidence

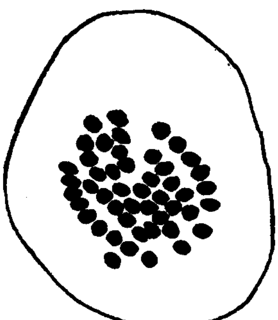

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FIGURE 10.—Haploid chromosome group in the Russet Rural variety at heterotypic metaphase, indicating tetraploidy in this variety.

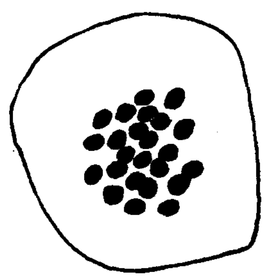

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FIGURE 11.—Haploid chromosome group in the Russet Rural Variety at heterotypic metaphase.

for these tentative conclusions is presented in the following illustrations of heterotypic metaphases. Figures 10 and 11 illustrate respectively the haploid chromosome number of tetraploid and diploid plants of the Russet Rural variety. Figure 12 illustrates the haploid chromosome number of diploid Early Ohio plants, and figures 13 and plate 1, figure 8 illustrate a pollen mother cell of the Early Rose variety at homotypic metaphase and are believed to indicate tetraploidy in this variety.

LUTMAN (1925) reports for the Irish Cobbler, Green Mountain, Lookout Mountain, and Early Rose varieties that the diploid chromosome number, as determined from a study of root tip material, is 36. This does not mean that heterotypic figures would necessarily show less than 24 chromosomes, as 12 may be single chromosomes and 12 of them paired. If this were the case, one would never be able to find 24 chromosomes at both poles of the heterotypic metaphase in these four varieties, and no such counts have been reported.

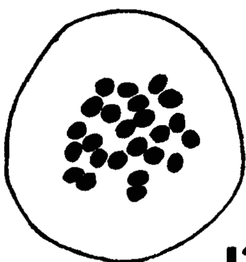
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FIGURE 12.—Haploid chromosome group in the Early Ohio variety at heterotypic metaphase.

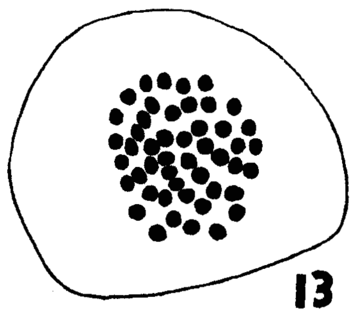
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FIGURE 13.—Haploid chromosome group in the Early Rose variety at heterotypic metaphase, indicating tetraploidy in this variety.

If certain potato varieties are triploid, as is suggested by a count of 36 in somatic cells, one might find in this fact an explanation of at least part of the pollen sterility in the potato. Such a cause of sterility has been shown for Oenothera by GATES (1915), for Datura by BLAKESLEE, BELLING, and FARNUM (1920), for wheat by SAX (1921, 1922, 1922), and for roses by BLACKBURN AND HARRISON (1921). BLAKESLEE, BELLING, and FARNUM have shown that Datura mutants have a relatively high degree of pollen sterility and that the tetraploid form of *Datura Stramonium* is sterile with its parent stock. GATES states that only 11 percent of the pollen grains are viable in *Oenothera gigas* × *lata rubricalyx*. The irregular, 5- and 6-lobed grains, together with many other misshapen and sterile grains, may contain chromosome combinations which are incompatible with development. BLACKBURN AND HARRISON in their work with roses have found that univalents split at heterotypic metaphase and in many cases fail to reach the poles but form supernumerary micronuclei. Thus octads rather than tetrads are often formed and those pollen grains derived chiefly from micronuclei collapse. Such behavior is believed to be due to hybridity. SAX working with wheat has found that the homologous chromosomes of the bivalents in species hybrids separate and pass regularly to the two poles, and univalents, if present, are distributed irregularly to one pole or the other during meiosis. He accounts for sterility in such hybrids on a hypothesis involving, "(1) the numerical and unbalanced relations of the chromosomes resulting from irregular meiotic divisions and (2) the specific interrelations of the parental chromosomes." He believes that the gametes exhibit more and more perfection as their chromosome constitution approaches more and more closely to that of the parental forms.

It has been shown by STOUT and CLARK (1924) that certain of the cultivated potato varieties have more pollen sterility than others. Perhaps the most sterile varieties have 12 univalent chromosomes and have a somatic chromosome number 36 and the least sterile ones have only paired chromosomes and have a diploid chromosome number of 48. The McIntyre and McCormick varieties do not have unpaired chromosomes and the haploid chromosome number in these two varieties is unquestionably 24; therefore, their 2X chromosome number is 48. It is of interest to note that STOUT and CLARK (1924) classify these two varieties as having a relatively high percentage of fertile pollen. Work is in progress to determine whether or not any of the commercial varieties exhibit lagging chromosomes during meiosis.

In this preliminary paper it has been shown that the haploid chromosome number is 12 for *S. Jamesii* and *S. chacoense*, 24 for *S. Fendleri*, and 36 for *S. demissum*. This is evidence that in these wild species of potato the haploid chromosome number is some multiple of 12, just as has been reported for other species of the Solanaceae. The McIntyre and McCormick cultivated varieties, which are characterized by a relatively high percentage of fertile pollen, have a haploid chromosome number of 24 and do not have unpaired chromosomes. Tetraploidy has occurred in the Early Ohio variety as shown by the appearance of haploid cells with approximately 48 chromosomes. The fact presented in this paper that the haploid chromosome number of potato has increased from 12 to 48 indicates that tetraploidy may have been a factor in the development of the cultivated varieties.

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