DET KGL. DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE MEDDELELSER, BIND XVIII, NR. 3

THE ASPECTS OF POLYPLOIDY IN THE GENUS SOLANUM

III: SEED PRODUCTION IN AUTOPOLYPLOID AND ALLOPOLYPLOID SOLANUMS

BY

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1948

Det Kgl. Danske Videnskabernes Selskabs Publikationer i 8vo:

Oversigt over Selskabets Virksomhed,
Historisk-filologiske Meddelelser,
Arkæologisk-kunsthistoriske Meddelelser,
Filosofiske Meddelelser,
Matematisk-fysiske Meddelelser,
Biologiske Meddelelser.

Selskabet udgiver desuden efter Behov i 4to Skrifter med samme Underinddeling som i Meddelelser.

Selskabets Adresse: Dantes Plads 35, København V.

Selskabets Kommissionær: *Ejnar Munksgaard*, Nørregade 6, København K.

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Printed in Denmark.
Bianco Lunos Bogtrykkeri.

I. Material and Methods.

The present paper deals with the seed production in a number of *Solanum* species and their polyploid derivatives. The natural species all belong to the Morella group of the genus *Solanum* (basic chromosome number x = 12). The investigation comprises 7 monobasic species (2 n = 24), viz. *S. nodiflorum* Jacq., *S. nodiflorum* var. *dentatum* var. nov., *S. gracile* Otto, *S. Insulæ-pascalis* Bitter, *S. Dillenianum* Polgár, *S. adventitium* Polgár and *S. nitidibaccatum* Bitter; 9 dibasic species (2 n = 48), viz. *S. villosum* Lam., *S. flavum* Kit. in Reich., *S. miniatum* Bernh. in Reich., *S. alatum* Moench, *S. bengalensis* sp. nov., *S. curtipes* Bitter, *S. retroflexum* Dun., *S. rubrum* Mill. and *S. ochroleucum* Bast.; and finally 7 tribasic species (2 n = 72), viz. *S. nigrum* L., *S. nigrum* var. *chlorocarpum* (Spenn.) Boiss., *S. nigrum* var. *gracile* Raddi, *S. nigrum* var. *humile* (Bernh.) Boiss., *S. nigrum* var. *memphiticum* Mart., *S. Roberti-Eliae* Bitter and *S. Guineense* Lam.

The detailed morphology and the relationship of these species will be described elsewhere (C. A. Jørgensen, in course of publication). However, a brief outline of the classification of the material is necessary also in this paper: The monobasic species are fairly well defined. *S. adventitium* and *S. nitidibaccatum* are unable to cross with the other monobasic species. The others can be crossed with some difficulty, but the hybrids are sterile, except in the cross *S. nodiflorum* (or *S. nodiflorum* var. *dentatum*) × *S. gracile*, where the hybrids produce a few seeds. The hybrid between *S. nodiflorum* and *S. nodiflorum* var. *dentatum* is entirely fertile.—The dibasic species on the other hand are very closely related except for *S. retroflexum*, which also morphologically takes up a rather isolated position in this group, being the only dibasic species with black berries known to us. *S. retroflexum* crosses only with difficulty with the other dibasic species and the fertility of the hybrids is rather poor. The other dibasic species cross readily, the hybrids are quite fertile and regular Mendelian segregations are recorded in F_2. Probably all these species should be considered varieties of *S. villosum*. The dibasic species can be crossed to all of the monobasic species except *S. adventitium* and *S. nitidibaccatum*. The hybrids are completely sterile.—The tribasic species are likewise closely related. However, *S. Guineense* and probably *S. Roberti-Eliae* are somewhat isolated from the *S. nigrum* types. Hybrids between *S. Guineense* and *S. nigrum* show reduced fertility and complicated segregations are recorded in F_2, in which also many sterile plants appear. *S. Roberti-Eliae* has not been crossed to the other tribasic species, but is morphologically rather closely related to *S. Guineense*.

Autotetraploids have been produced experimentally from all of the 7 monobasic species ($2n = 48$ in the tetraploids), from 7 dibasic species ($2n = 96$ in the tetraploids) and from 7 tribasic species or varieties ($2n = 144$ in the tetraploids). Crossings between monobasic species with subsequent chromosome doubling of the hybrid produced 6 amphidiploids ($2n = 48$). From crossings between monobasic and dibasic species, 24 amphidiploids were raised ($2n = 72$). Chromosome doubling of the hybrids between monobasic and tribasic species resulted in 6 amphidiploids ($2n = 96$), and crossings between tribasic S. *nigrum* types and the dibasic *S. villosum* and chromosome doubling of the hybrids gave two amphidiploids ($2n = 120$). The material thus comprises 21 autotetraploids raised from three different chromosome levels and 39 amphidiploids representing four different chromosome levels. The chromosome doubling was induced by a combination of the callus method (JØRGENSEN 1928) and colchicine treatment. A detailed description of the experiments will follow in C. A. JØRGENSEN's paper.

For fertility determinations five typical plants from field plots have been selected and the total number of berries (ripe + unripe) was counted two or three times until the end of the growing season. The number of berries per plant (Tables 1 *a* and 1 *b*) is the average of these 5 plants. The number of seeds per berry (Table 2 *a* and 2 *b*) have been counted in 100 berries taken from typical plants and the average figure calculated. The number of berries per plant multiplied by the number of seeds per berry gives the number of seeds per plant (Tables 2 *a* and 2 *b*). The seed weight is determined from the weight of 1000 seeds, and the seed weight multiplied by the number of seeds per plant is the seed weight per plant (Tables 4 *a* and 4 *b*).

II. Results.

Seed production in autopolyploids. Table 1 *a* shows that in all cases but one (no. 11, *S. alatum*) chromosome doubling results in reduced berry production. On an average, the berry production of the tetraploids of the monobasic group is 51 per cent of the diploid species. In the dibasic group the average is 55 per cent and in the tribasic group 32 per cent only; the tetraploid *S. nigrum* var. *memphiticum* is almost sterile and could not be propagated sexually.

In Table 2 *a* it should first be noted that there is no correlation between the seed number per berry and the chromosome level of the species. The two highest figures (nos. 2 and 21) are from a monobasic and a tribasic species, and the two lowest figures (nos. 14 and 7) from a dibasic and a monobasic species. In the monobasic group the average seed number per berry of the tetraploids is 44 per cent of the diploids, in the dibasic group 37 per cent of the fertility is recovered in the tetraploids and in the tribasic group 8 per cent only. The tetraploid S. *Guineense* produces a large number of big parthenocarpic berries without any seeds. The combined effect of the reduction in the number of berries and in the number of seeds per berry is a very drastic reduction in the fertility of the experimental polyploids as compared with the diploid species (Table 2 *a*, the last 3 columns). In the monobasic and the dibasic group 19 and 21 per cent, respectively, of the fertility of the diploids is on an average recovered, and in the tribasic group 4 per cent only is maintained.

Seed production in allopolyploids. In Tables 1 *b* and 2 *b* the seed production of the amphidiploids (designated 4 n, F_1) is compared with the diploid parent species. It should be kept in mind that the F_1 hybrids are completely sterile except for the hybrids *S. nodiflorum* (or *S. nodiflorum* v. *dentatum*) × *S. gracile* (nos. 23 and 25), which both had a few berries with approx-

Table 1 a.
Number of Berries per Plant, Autopolyploids.

Case no.	2 n*	Species	Berries per Plant		4 n in p.c. of 2 n
			2 n	4 n	
1	24	*S. nodiflorum*	2668	1066	**40**
2		*S. nodiflorum* v. *dentatum*	1462	781	**53**
3		*S. gracile*	1368	871	**64**
4		*S. Insulae-pascalis*	341	125	**37**
5		*S. Dillenianum*	296	16	**5**
6		*S. adventitium*	825	348	**42**
7		*S. nitidibaccatum*	1355	1036	**76**
8	48	*S. villosum*	1203	578	**48**
9		*S. flavum*	915	842	**92**
10		*S. miniatum*	853	459	**54**
11		*S. alatum*	1015	1326	**131**
12		*S. bengalensis*	845	425	**50**
13		*S. curtipes*	2065	814	**39**
14		*S. retroflexum*	2001	476	**24**
15	72	*S. nigrum*	1046	847	**81**
16		*S. nigrum* v. *chlorocarpum*	2826	982	**35**
17		*S. nigrum* v. *gracile*	1688	785	**47**
18		*S. nigrum* v. *humile*	1682	229	**14**
19		*S. nigrum* v. *memphiticum*	1617	+	**0**
20		*S. Roberti-Eliae*	1511	434	**29**

* Somatic chromosome number of the diploid species.

imately 6—7 seeds per berry, and the varietal hybrid *S. nodiflorum* × *S. nodiflorum* v. *dentatum* (no. 22), which gave 55 seeds per berry. One of the most striking features in these tables is the complete sterility of the hybrids *S. nodiflorum* × *S. villosum* (no. 29), *S. gracile* × S. *villosum* (no. 36), *S. gracile* × *S. curtipes* (no. 38) and *S. gracile* × *S. retroflexum* (no. 39). To this group of sterile amphidiploids should be added the hybrids, not recorded in the table, between *S. nodiflorum* and the dibasic species *S. rubrum*, *S. ochroleucum*, *S. flavum*, *S. miniatum* and *S. alatum*, all closely related to *S. villosum*, and those between *S. gracile* and *S. rubrum*, *S. ochroleucum*, *S. flavum*, *S. miniatum*, and *S. alatum*. However, these amphidiploids are only male sterile; in the *S. nodiflorum* hybrids the anthers are transformed into petals, and in the *S. gra-*

Table 1b.
Number of Berries per Plant, Allopolyploids.

Case no.	2 n*	Cross ♀ × ♂	Berries per Plant			4 n, F_1 in p.c. of	
			2 n ♀	2 n ♂	4n, F_1	2 n ♀	2 n ♂
23	48	*S. nodiflorum* × *S. gracile*	2668	1368	267	**10**	**20**
24		*S. nodifl.* × *S. Dillenianum*	2668	296	274	**10**	**93**
25		*S. gracile* × *S. nod.* v. *dentatum*	1368	1462	267	**20**	**18**
27		*S. Insulae-pasc.* × *S. nod.* v. *dentatum*	341	1462	550	**161**	**38**
30	72	*S. nodiflorum* × *S. bengalensis*	2668	845	1747	**65**	**207**
31		*S. nodiflorum* × *S. curtipes*	2668	2065	767	**29**	**37**
32		*S. nodiflorum* × *S. retroflexum*	2668	2001	106	**4**	**5**
33		*S. nod.* v. *dent.* × *S. bengalensis*	1462	845	2194	**150**	**260**
34		*S. nod.* v. *dent.* × *S. curtipes*	1462	2065	1116	**76**	**54**
35		*S. nod.* v. *dent.* × *S. retroflexum*	1462	2001	1722	**118**	**86**
36		*S. gracile* × *S. villosum*	1368	1203	+	**0**	**0**
37		*S. gracile* × *S. bengalensis*	1368	845	46	**3**	**5**
38		*S. gracile* × *S. curtipes*	1368	2065	73	**5**	**4**
39		*S. gracile* × *S. retroflexum*	1368	2001	+	**0**	**0**
40		*S. Insulae-pascalis* × *S. curtipes*	341	2065	1271	**373**	**62**
41		*S. Insulae-pascalis* × *S. retroflexum*	341	2001	952	**279**	**48**
42		*S. Dillenianum* × *S. curtipes*	296	2065	768	**259**	**37**
43	96	*S. nigrum* × *S. nodiflorum*	1046	2668	459	**44**	**17**
44		*S. nigrum* × *S. nod.* v. *dentatum*	1046	1462	702	**67**	**48**
45		*S. nigrum* × *S. gracile*	1046	1368	824	**79**	**60**
46		*S. nigrum* × *S. Insulae-pascalis*	1046	341	616	**59**	**181**
47		*S. nigrum* × *S. nitidibaccatum*	1046	1355	938	**90**	**69**
48		*S. nig.* v. *chlorocarp.* × *S. nitidibac.*	2826	1355	1242	**44**	**92**
49	120	*S. nigrum* × *S. villosum*	1046	1203	820	**78**	**68**
50		*S. nig.* v. *chlorocarp.* × *S. villosum*	2826	1203	424	**15**	**35**

* Somatic chromosome number of the amphidiploid (4 n, F_1)

cile hybrids the anthers contain 100 per cent abortive pollen. When pollinated with diploid *Solanum* species with the same chromosome number, these amphidiploids are fertile on the female side (the amphidiploid *S. gracile* × *S. villosum* for instance, when pollinated with *S. nigrum*, gave 24 seeds per berry).

When the fertile amphidiploids only are considered, the berry production of the polyploids, as seen in Table 1 *b*, is generally

Table 2 a.
Number of Seeds per Plant, Autopolyploids.

Case no.	2 n	Species	Seeds per Berry		4 n in p.c. of 2 n	Seeds per Plant		4 n in p.c. of 2 n
			2 n	4 n		2 n	4 n	
1	24	*S. nodiflorum*	59	27	**46**	157412	28782	**18**
2		*S. nod.* v. *dentatum*	88	34	**39**	128656	26554	**21**
3		*S. gracile*	45	12	**27**	61560	10452	**17**
4		*S. Insulae-pascalis*	52	26	**50**	17732	3250	**18**
5		*S. Dillenianum*	73	24	**33**	21608	384	**2**
6		*S. adventitium*	46	43	**93**	37950	14964	**39**
7		*S. nitidibaccatum*	23	3	**13**	31165	3108	**10**
8	48	*S. villosum*	39	12	**31**	46917	6936	**15**
9		*S. flavum*	37	13	**35**	33855	10946	**32**
10		*S. miniatum*	43	15	**35**	36679	6885	**19**
11		*S. alatum*	42	14	**33**	42630	18564	**44**
12		*S. bengalensis*	45	21	**47**	38025	8925	**23**
13		*S. curtipes*	48	18	**38**	99120	14652	**15**
14		*S. retroflexum*	21	9	**43**	42021	4284	**10**
15	72	*S. nigrum*	60	7	**12**	62760	5929	**9**
16		*S. nig.* v. *chlorocarpum*	46	8	**17**	129996	7856	**6**
17		*S. nigrum* v. *gracile*	46	2	**4**	77648	1570	**2**
18		*S. nigrum* v. *humile*	44	5	**11**	74008	1145	**2**
19		*S. nigrum* v. *memphiticum*	44	+	**0**	71148	+	**0**
20		*S. Roberti-Eliae*	56	8	**14**	84616	3472	**4**
21		*S. Guineense*	84	+	**0**	?	+	**0**

much lower than in the diploid parents. In 6 cases, however, (nos. 27, 35, 40, 41, 42, 46) the berry production of the hybrid is higher than in one of the parental species; in 4 of these cases *S. Insulae-pascalis* was one of the parents. In one case (no. 33) the amphidiploid produced more berries than any of the parents. The seed number per berry (Table 2 *b*) is also generally much lower in the amphidiploids than in the parents, but in two cases (nos. 35 and 41) the berries of the hybrid had more seeds than one of the parental species, viz. *S. retroflexum*. The seed production per plant is also much lower in the amphidiploid than in the diploid parental species except in 4 cases (nos. 35, 40, 41, 42, all tribasic amphidiploids), where the experimentally produced

Table 2 b. Number of Seeds per Plant, Allopolyploids.

Case no.	2 n	Cross ♀ × ♂	Seeds per Berry			F_1 in p.c. of		Seeds per Plant			4 n, F_1 in p. c. of	
			2 n ♀	2 n ♂	4 n, F_1	2 n ♀	2 n ♂	2 n ♀	2 n ♂	4 n, F_1	2 n ♀	2 n ♂
22	48	*S. nodiflorum* × *S. nod.* v. *dentatum*	59	88	41	69	47	..	..	..	..	..
23		*S. nodiflorum* × *S. gracile*	59	45	25	42	56	157412	61560	6675	4	11
24		*S. nodiflcrum* × *S. Dillenianum*	59	73	25	42	34	157412	71608	6850	4	32
25		*S. gracile* × *S. nod.* v. *dentatum*	45	88	27	60	31	61560	128656	7290	12	6
26		*S. Insulae-pascalis* × *S. nodiflorum*	52	59	14	27	24	..	..	..	..	..
27		*S. Insulae-pasc.* × *S. nod.* v. *dentatum*	52	88	25	48	28	17732	128656	13750	78	11
28		*S. Insulae-pascalis* × *S. gracile*	52	45	27	52	60	..	..	..	..	..
29	72	*S. nodiflorum* × *S. villosum*	59	39	0	0	0	157412	46817	0	0	0
30		*S. nodiflorum* × *S. bengalensis*	59	45	19	32	42	157412	38025	33193	21	87
31		*S. nodiflorum* × *S. curtipes*	59	48	16	27	33	157412	99120	12272	8	12
32		*S. nodiflorum* × *S. retroflexum*	59	21	6	10	29	157412	42021	636	0.4	2
33		*S. nod.* v. *dent.* × *S. bengalensis*	88	45	13	15	29	128656	38025	28522	22	75
34		*S. nod.* v. *dent.* × *S. curtipes*	88	48	23	26	48	128656	99120	25668	20	26
35		*S. nod.* v. *dent.* × *S. retroflexum*	88	21	26	30	124	128656	42021	44772	35	107
36		*S. gracile* × *S. villosum*	45	39	+	0	0	61560	46917	0	0	0
37		*S. gracile* × *S. bengalensis*	45	45	9	20	20	61560	38025	+	0	0
38		*S. gracile* × *S. curtipes*	45	48	+	0	0	61560	99120	+	0	0
39		*S. gracile* × *S. retroflexum*	45	21	+	0	0	61560	42021	+	0	0
40		*S. Insulae-pascalis* × *S. curtipes*	52	48	26	50	54	17732	99120	33046	186	33
41		*S. Insulae-pascalis* × *S. retroflexum*	52	21	30	58	143	17732	42021	28560	161	68
42		*S. Dillenianum* × *S. curtipes*	73	48	35	48	73	21608	99120	26880	124	27
43	96	*S. nigrum* × *S. nodiflorum*	60	59	15	25	25	62760	157412	6885	11	4
44		*S. nigrum* × *S. nod.* v. *dentatum*	60	88	15	25	17	62760	128656	10530	17	8
45		*S. nigrum* × *S. gracile*	60	45	23	38	51	62760	61560	18952	30	31
46		*S. nigrum* × *S. Insulae-pascalis*	60	52	10	17	19	62760	17732	6160	10	35
47		*S. nigrum* × *S. nitidibaccatum*	60	23	22	37	96	62760	31165	20636	33	66
48		*S. nig.* v. *chlorocarp.* × *S. nitidibac.*	46	23	21	46	91	129996	31165	26082	20	84
49	120	*S. nigrum* × *S. villosum*	60	39	8	13	21	62760	46917	6560	10	14
50		*S. nig.* v. *chlorocarp.* × *S. villosum*	46	39	7	15	18	129996	46917	2968	2	6

plants are more fertile than one of the parents. In one case, no. 35, this is due to the hybrid producing more seeds per berry than the parent, in the three remaining cases an increased berry production per plant is responsible for the increased fertility.

If the seed production of the amphidiploids is compared with the average production of the two parental species ((♀ + ♂): 2), the 4 dibasic hybrids (nos. 23, 24, 25, 27) on an average produce 9 per cent of the parents. If the sterile amphidiploids are omitted from the tribasic group, the synthetic amphidiploids on an average produce 31 per cent as compared with the parents. In the tetrabasic group 20 per cent of the fertility is maintained, and in the two pentabasic hybrids 7 per cent only.

Comparison between autotetraploids and amphidiploids. The present material offers a very good opportunity of comparing the effect of autopolyploidy versus allopolyploidy on fertility, because in a number of cases the seed production of the amphidiploid can be compared with that of the autotetraploids of both parental species. These cases are grouped in Table 3. In 5 cases (nos. 23, 25, 31, 32, 50) the amphidiploid produces less seeds than any of the two autotetraploids. To this group should be added the sterile amphidiploids between *S. nodiflorum* or *S. gracile* and the dibasic *S. villosum* types, these sterile amphidiploids not being included in Table 3. In 6 cases the seed production of the amphidiploid is intermediate between the two autotetraploids (nos. 24, 27, 34, 43, 44, 49) and in the remaining 10 hybrids (nos. 30, 33, 35, 40, 41, 42, 45, 46, 47, 48) the fertility of the amphidiploid is higher than in any of the autotetraploids, in some cases (especially nos. 35, 40, 41, 42, 45, 47, 48) even very much higher.

Seed weight per plant (Tables 4*a* and 4*b*). Chromosome doubling causes a considerable increase in the weight of the seeds in all cases, and the increase is especially pronounced in some of the amphidiploids. However, in the autotetraploids the increased seed weight cannot compensate for the reduction in seed number, and the seed production of the tetraploids, even when measured by weight, is much inferior to the diploid species; in two cases only, it amounts to more than 50 per cent of the diploids (nos. 6 and 11). In the amphidiploids on the other hand, one of the hybrids yields a higher seed weight than any

Table 3.
Comparison between Seed Production of Autopolyploids and Allopolyploids.

Case no.	2 n	Cross ♀ × ♂	4 n ♀	4 n in p.c. of 2 n ♀	4 n ♂	4 n in p.c. of 2 n ♂	4 n, F_1	4 n, F_1 in p.c. of	
								2 n ♀	2 n ♂
1-3-23	48	*S. nodiflorum* × *S. gracile*	28782	18	10452	17	6675	4	11
1-5-24		*S. nodiflorum* × *S. Dillenianum*	28782	18	384	2	6850	4	32
3-2-25		*S. gracile* × *S. nod.* v. *dentatum*	10452	17	26554	21	7209	12	6
4-2-27		*S. Insulae-pasc.* × *S. nod.* v. *dent.*	3250	18	26554	21	13750	78	11
1-12-30	72	*S. nodiflorum* × *S. bengalensis*	28782	18	8925	23	33193	21	87
1-13-31		*S. nodiflorum* × *S. curtipes*	28782	18	14652	15	12272	8	12
1-14-32		*S. nodiflorum* × *S. retroflexum*	28782	18	4284	10	636	0.4	2
2-12-33		*S. nod.* v. *dent.* × *S. bengalensis*	26554	21	8925	23	28522	22	75
2-13-34		*S. nod.* v. *dent.* × *S. curtipes*	26554	21	14652	15	25668	20	26
2-14-35		*S. nod.* v. *dent.* × *S. retroflexum*	26554	21	4284	10	44772	35	107
4-13-40		*S. Insulae-pasc.* × *S. curtipes*	3250	18	14652	15	33046	186	33
4-14-41		*S. Insulae-pasc.* × *S. retroflexum*	3250	18	4284	10	28560	161	68
5-13-42		*S. Dillenianum* × *S. curtipes*	384	2	14652	15	26880	124	27
15-1-43	96	*S. nigrum* × *S. bengalensis*	5929	9	28782	18	6885	11	4
15-2-44		*S. nigrum* × *S. nod.* v. *dentatum*	5929	9	26554	21	10530	17	8
15-3-45		*S. nigrum* × *S. gracile*	5929	9	10452	17	18952	30	31
15-4-46		*S. nigrum* × *S. Insulae-pascalis*	5929	9	3250	18	6160	10	35
15-7-47		*S. nigrum* × *S. nitidibaccatum*	5929	9	3108	10	20636	33	66
16-7-48		*S. nig.* v. *chlorocarp.* × *S. nitidibac.*	7856	6	3108	10	26082	20	84
15-8-49	120	*S. nigrum* × *S. villosum*	5929	9	6936	15	6560	10	12
16-8-50		*S. nig.* v. *chlorocarpum* × *S. villos.*	7856	6	6936	15	2968	2	6

Table 4 a.
Seed Weight per Plant, Autopolyploids.

Case no.	2 n	Species	Weight of 1000 Seeds 2 n gms.	Weight of 1000 Seeds 4 n gms.	4 n in p.c. of 2 n	Seed Weight per Plant 2 n gms.	Seed Weight per Plant 4 n gms.	4 n in p.c. of 2 n
1	24	*S. nodiflorum*	0.23	0.31	**135**	36.2	8.9	**25**
2		*S. nodiflorum* v. *dent.*	0.35	0.57	**163**	45.0	15.1	**34**
3		*S. gracile*	0.45	0.67	**149**	27.7	7.0	**25**
4		*S. Insulae-pascalis*	0.37	0.47	**127**	6.6	1.5	**23**
5		*S. Dillenianum*	0.47	0.69	**147**	10.2	0.3	**3**
6		*S. adventitium*	0.47	0.63	**134**	17.8	9.4	**53**
7		*S. nitidibaccatum*	1.23	1.68	**137**	38.3	5.2	**14**
8	48	*S. villosum*	1.25	1.70	**136**	58.6	11.8	**20**
10		*S. miniatum*	1.24	1.74	**140**	45.5	12.0	**26**
11		*S. alatum*	1.12	1.46	**130**	47.7	27.1	**57**
12		*S. bengalensis*	0.83	1.10	**133**	31.6	9.8	**31**
13		*S. curtipes*	0.81	0.91	**112**	80.3	13.3	**17**
14		*S. retroflexum*	1.06	1.60	**151**	44.5	6.9	**16**
15	72	*S. nigrum*	0.88	1.28	**145**	55.2	7.5	**14**
17		*S. nigrum* v. *gracile*	1.23	1.70	**138**	95.5	2.7	**3**
18		*S. nigrum* v. *humile*	1.14	1.82	**160**	84.4	2.1	**2**
20		*S. Roberti-Eliae*	0.90	1.13	**141**	76.2	3.9	**5**

of the diploid parents (no. 35), and in 6 cases the yield of the amphidiploid is higher than in one of the parents (nos. 27, 30, 40, 41, 42, 46). In one case the seed weight is almost 6 times as high in the hybrid as in the parent (no. 40, where the amphidiploid gives 38.8 gms. per plant as against 6.6 gms. in the parental species *S. Insulae-pascalis*).

In Table 5 the seed weight of the amphidiploids is compared with that of the experimentally raised tetraploids of the two parental species (cf. Table 3). In three cases the yield is lower in the hybrid than in both tetraploids (nos. 23, 25, 32), in 6 cases it is between the tetraploids (nos. 24, 27, 31, 43, 44, 49), and the 10 remaining hybrids give a higher yield than any of the two tetraploids. In most of these cases the yield is very much higher—about three times as high—as in the tetraploids.

Table 4 b.

Seed Weight per Plant, Allopolyploids.

Case no.	2 n	Cross ♀ × ♂	Weight of 1000 Seeds			F_1 in p.c. of		Weight per Plant			4 n, F_1 in p.c. of	
			2 n ♀ gms.	2 n ♂ gms.	4 n, F_1 gms.	2 n ♀	2 n ♂	2 n ♀ gms.	2 n ♂ gms.	4 n, F_1 gms.	2 n ♀	2 n ♂
22		*S. nodiflorum* × *S. nod.* v. *dentatum*	0.23	0.35	0.52	**183**	**149**	..	..	..	..	..
23		*S. nodiflorum* × *S. gracile*	0.23	0.45	0.69	**300**	**153**	36.2	27.7	4.6	**13**	**17**
24		*S. nodiflorum* × *S. Dillenianum*	0.23	0.47	0.69	**300**	**147**	36.2	10.2	4.7	**13**	**46**
25	48	*S. gracile* × *S. nod.* v. *dentatum*	0.45	0.35	0.60	**133**	**171**	27.7	45.0	4.3	**16**	**10**
26		*S. Insulae-pascalis* × *S. nodiflorum*	0.37	0.23	0.53	**143**	**230**	..	..	..	..	..
27		*S. Insulae-pasc.* × *S. nod.* v. *dentatum*	0.37	0.35	0.55	**149**	**157**	6.6	45.0	7.6	**115**	**17**
28		*S. Insulae-pascalis* × *S. gracile*	0.37	0.45	0.68	**184**	**151**	..	..	..	..	..
30		*S. nodiflorum* × *S. bengalensis*	0.23	0.83	0.96	**417**	**116**	36.2	31.6	31.9	**88**	**101**
31		*S. nodiflorum* × *S. curtipes*	0.23	0.81	0.96	**417**	**119**	36.2	80.3	11.8	**33**	**15**
32		*S. nodiflorum* × *S. retroflexum*	0.23	1.06	1.02	**443**	**96**	36.2	44.5	0.6	**2**	**1**
33		*S. nod.* v. *dent.* × *bengalensis*	0.35	0.83	1.03	**294**	**124**	45.0	31.6	29.4	**65**	**93**
34	72	*S. nod.* v. *dentatum* × *S. curtipes*	0.35	0.81	0.95	**271**	**117**	45.0	80.3	24.4	**54**	**30**
35		*S. nod.* v. *dent.* × *S. retroflexum*	0.35	1.06	1.20	**343**	**113**	45.0	44.5	53.7	**119**	**121**
40		*S. Insulae-pascalis* × *S. curtipes*	0.37	0.81	1.16	**314**	**143**	6.6	80.3	38.3	**580**	**48**
41		*S. Insulae-pasc.* × *S. retroflexum*	0.37	1.06	1.21	**327**	**114**	6.6	44.5	34.6	**524**	**78**
42		*S. Dillenianum* × *S. curtipes*	0.47	0.81	1.31	**279**	**162**	10.2	80.3	35.2	**345**	**44**
43		*S. nigrum* × *S. nodiflorum*	0.88	0.23	1.06	**120**	**461**	55.2	36.2	7.3	**13**	**20**
44		*S. nigrum* × *S. nod.* v. *dentatum*	0.88	0.35	1.14	**130**	**326**	55.2	45.0	12.0	**22**	**27**
45	96	*S. nigrum* × *S. gracile*	0.88	0.45	1.27	**144**	**282**	55.2	27.7	24.1	**44**	**87**
46		*S. nigrum* × *S. Insulae-pascalis*	0.88	0.37	1.25	**142**	**338**	55.2	6.6	7.7	**14**	**117**
47		*S. nigrum* × *S. nitidibaccatum*	0.88	1.23	1.64	**209**	**133**	55.2	38.3	33.8	**61**	**88**
49	120	*S. nigrum* × *S. villosum*	0.88	1.25	1.70	**173**	**124**	55.2	58.6	11.2	**20**	**19**

Table 5.

Comparison between Seed Weight of Autopolyploids and Allopolyploids.

Case no.	2 n	Cross ♀ × ♂	4 n ♀ gms.	4 n ♀ in p.c. of 2 n ♀	4 n ♂ gms.	4 n ♂ in p.c. of 2 n ♂	4 n, F_1 gms.	4 n, F_1 in p.c. of 2 n ♀	4 n, F_1 in p.c. of 2 n ♂
1-3-23	48	*S. nodiflorum* × *S. gracile*	8.9	25	7.0	25	4.6	13	17
1-5-24		*S. nodiflorum* × *S. Dillenianum*	8.9	25	0.3	3	4.7	13	46
3-2-25		*S. gracile* × *S. nod.* v. *dentatum*	7.0	25	15·1	34	4.3	16	10
4-2-27		*S. Insulae-pascalis* × *S. nod.* v. *dentatum*	1.5	23	15.1	34	7.6	115	17
1-12-30	72	*S. nodiflorum* × *S. bengalensis*	8.9	25	9.8	31	31.9	88	101
1-13-31		*S. nodiflorum* × *S. curtipes*	8.9	25	13.3	17	11.8	33	15
1-14-32		*S. nodiflorum* × *S. retroflexum*	8.9	25	6.9	16	0.6	2	1
2-12-33		*S. nod.* v. *dentatum* × *S. bengalensis*	15.1	34	9.8	31	29.4	65	93
2-13-34		*S. nod.* v. *dentatum* × *S. curtipes*	15.1	34	13.3	17	24.4	54	30
2-14-35		*S. nod.* v. *dentatum* × *S. retroflexum*	15.1	34	6.9	16	53.7	119	121
4-13-40		*S. Insulae-pascalis* × *S. curtipes*	1.5	23	13.3	17	38.3	580	48
4-14-41		*S. Insulae-pascalis* × *S. retroflexum*	1.5	23	6.9	16	34.6	524	78
5-13-42		*S. Dillenianum* × *S. curtipes*	0.3	3	13.3	17	35.2	345	44
15-1-43	96	*S. nigrum* × *S. nodiflorum*	7.5	14	8.9	25	7.3	13	20
15-2-44		*S. nigrum* × *S. nod.* v. *dentatum*	7.5	14	15.1	34	12.0	22	27
15-3-45		*S. nigrum* × *S. gracile*	7.5	14	7.0	25	24.1	44	87
15-4-46		*S. nigrum* × *S. Insulae-pascalis*	7.5	14	1.5	23	7.7	14	117
15-7-47		*S. nigrum* × *S. nitidibaccatum*	7.5	14	5.2	14	33.8	61	88
15-8-49	120	*S. nigrum* × *S. villosum*	7.5	14	11.8	20	11.2	20	19

III. Discussion.

A more thorough discussion of these data will be postponed until the final paper in this series of publications, when all the cytological and experimental data are available, because one of the most interesting problems, *viz.* the cause of the reduced fertility of the polyploids, must be discussed in relation to meiotic behaviour and pollen formation of the plants.

However, the following general conclusions from the above data may be briefly commented on: The reduction in the fertility of the experimentally produced autotetraploids (Table 2 *a*) is due to a reduction in the berry production as well as to a decreased number of seeds per berry. In the tribasic group only, this reduction is strongly correlated with the chromosome number of the diploid species, whereas in the monobasic and dibasic groups there is a great variation in seed reduction not correlated with chromosome number. The two monobasic species *S. adventitium* and *S. nitidibaccatum* are less fertile than any of the other monobasic or dibasic species. In the first type the reduction is due to a decreased number of berries per plant, whereas in *S. nitidibaccatum* a low number of seeds per berry is the cause. It can be said already that this difference cannot be explained as due to visible meiotic differences between the different types. Hence the effect of chromosome doubling on the fertility of the tetraploids depends upon the genotypic constitution of the diploid more than upon the chromosome number, at least when this is not too high.

In the amphidiploids the fact that some of the artificial, constant hybrids are more fertile than one of the parental species is very important. In all these cases the hybrid has resulted from a cross between two diploid species which show a great difference in seed production. Unfortunately, due to the sterility of the F_1 hybrids, the genetic background of this difference cannot be analysed, but there is good reason to assume that it is under control of polygenes. On the other hand, not all crosses between high and low diploid seed producers resulted in superior amphidiploids, the most striking examples being the sterile amphidiploids in which the very high seed producers *S. nodiflorum* or *S. gracile* are involved. Hence the result again first and foremost depends upon the general genotypic constitution of the diploid parents and upon how far the two genomes can harmonize in the hybrid, whereas the meiotic behaviour of the amphidiploids is of secondary importance only. Fertility and sterility are to be explained in genetic terms rather than on a cytological basis, as emphasised by MÜNTZING (1943).

On the basis of this assumption it is not difficult to explain that the amphidiploids are not always more fertile than the autotetraploids (Table 3). In the latter case only one step is involved in the production of the new type, and we are dealing with the same genes as were present in the diploid species. Amphidiploidy on the other hand involves two steps, crossing and chromosome doubling, and the result is therefore likely to be more uncertain.

The problems of the fertility of the artificial polyploids is of great importance for the practical plant breeder, who in recent years on an increasing scale has devoted his attention to experimental polyploids in his breeding work. The fact that it is possible to produce amphidiploids which give a higher yield than one of the diploid parents, and in one case even a higher seed weight than any of the diploid parents, is indeed very encouraging and points towards amphidiploids rather than autopolyploids as material for producing superior plants. However, the utilisation of the autopolyploids and of most amphidiploids will depend upon the extent and speed with which it will be possible to improve their fertility by selection. That such an improvement is possible, and actually has taken place, under the influence of natural selection, is obvious from the fact that the polybasic natural *Solanum* species as well as many other polybasic plant species are as good or even superior seed producers as the monobasic species. However, we do not know whether this process takes thousands of generations or only a few, or how much it can be speeded up by artificial selection. In this laboratory some of the *Solanum* polyploids have been under cultivation for at least 15 generations. No attempts have been made to improve the fertility by selection and there is no indication that the seed production has actually increased. For instance, JØRGENSEN (1928) counted 40—50 seeds per berry in the diploid *S. nigrum* and 10—15 in the tetraploid. The corresponding figures in my investigations are 60 seeds in 2 n and 8 in 4 n *S. nigrum*. The amphidiploid *S. nigrum* × *S. villosum* (*S. luteum* in JØRGENSEN's paper) had 8—11 seeds per berry in 1927 as against 8 in the present investigations. On the other hand other authors have obtained encouraging results in improving the fertility of both autotetraploids (*Zea mays*, RANDOLPH 1941, *Galeopsis*, MÜNTZING 1943, *Secale*, MÜNTZING 1948) as well as amphidiploids (for instance *Triticale*, MÜNTZING 1948) by selection.

IV. Summary.

The seed number and the seed weight per plant have been investigated in a number of *Solanum* species and their artificially produced polyploid derivatives (21 autopolyploids and 39 amphidiploids).

All the autotetraploids produce less than 50 per cent of the seeds of the diploid species. Most of the amphidiploids produce less seeds than any of the diploid parental species, but a few produce more seeds than one of the parents. In one case an amphidiploid yielded a higher seed weight than any of the diploid parents. A group of amphidiploids are completely male-sterile.

A comparison between the seed production of an amphidiploid and that of the autotetraploids of the two parental species shows (Tables 3 and 5) that in some cases the allopolyploid is inferior to the autotetraploids, in others, the fertility of the hybrid is intermediate between that of the two tetraploids, and in others again, the amphidiploid produces more seeds than any of the two related autopolyploids.

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Indleveret til Selskabet den 12. Februar 1948.
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