

DET KGL. DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE MEDDELELSER, BIND XVIII, NR. 2

THE ASPECTS OF POLYPLOIDY IN THE GENUS SOLANUM

II.

PRODUCTION OF DRY MATTER, RATE
OF PHOTOSYNTHESIS AND RESPIRATION, AND
DEVELOPMENT OF LEAF AREA IN SOME DIPLOID,
AUTOTETRAPLOID AND AMPHIDIPLOID
SOLANUMS

BY

POUL LARSEN



KØBENHAVN

I KOMMISSION HOS EJNAR MUNKSGAARD

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A. Introduction.

A feature, generally much emphasized in the description of polyploid plants, is their so-called "gigas" character. This expression refers to the fact that these plants, like the tetraploid "gigas" form of *Oenothera Lamarckiana* arisen in 1895 in the cultures of DE VRIES, have a more vigorous growth and larger organs than the diploid forms from which they descend. Even though exceptions are known, this feature is characteristic of the majority of polyploid plants. The idea to utilize the luxuriance in plant breeding is quite natural; however, not until recent years methods were developed which permit an experimental formation of polyploid plants to an extent required for an application to plant breeding practice. Since such methods are now at our disposal, these problems were resumed. When investigating the cultural value of a given polyploid plant, primarily its productivity should be compared with that of the corresponding diploid plant; this means a quantitative determination of the "gigas" character. A few such comparisons are available; however, just as previous rough estimates, they seem to refer to individual plants, only, while in agricultural practice, the size of the crop in a stock of plants in the field is the essential point.

A brief report of the main points of the investigations on the production of matter in polyploid plants so far published is given below.

FABERGÉ (1936) found that the tetraploid strains of tomato examined by him showed no greater production of dry matter than the corresponding diploid ones. In the tetraploid strains of tomato examined by SCHLÖSSER (1937), an excess of dry matter of 20—25 per cent as compared with the diploids could be demonstrated in 4 weeks old plants, (in "old" plants the excess was even 74 per cent). When these experiments were repeated (SCHLÖSSER 1940), the maximum excess,

however, in plants somewhat older than 6 weeks was no more than 8 per cent. In another tetraploid strain of tomato, almost 8 weeks old plants showed a deficiency of 18—27 per cent, in proportion to the diploids. It could, however, be stated that the tetraploids were on the point of overtaking the diploids, the *intensity* of their production at the time of investigation being greater than that of the diploids.—Examinations by the same author on tri- and tetraploid sugar beets showed that the production of dry matter in these plants was 12—15 per cent less than in the corresponding diploids. Similarly, the tetraploid *Petunias* examined by HESSE (1938) produced less dry matter than the diploids. This result has been confirmed by PIRSCHLE (1940) through investigations of the same strain as that used by HESSE.—According to GREIS (1940), the yield of straw of tetraploid Kobai barley, at the beginning of the flowering period, was about 50 per cent greater than that of the diploid plants; the formation of grains, on the other hand, was very bad.—The works mentioned have partly been reviewed more thoroughly by PIRSCHLE (1940).

In experiments performed by GYÖRFFY (1941) various autotetraploids were investigated. The majority of these experiments was carried out in greenhouse; unfortunately, no details as to the cultivation method are given, at least not in the English summary. The main results of GYÖRFFY'S determinations of the production of dry matter are as follows. In different strains of *Capsicum annuum*, the tetraploids yielded an excess of total dry matter varying from 11 to 79 per cent as compared with the diploids.—In two strains of *Epilobium*, an excess of 8 per cent and of 66 per cent, respectively, was produced by the tetraploids.—With *Hyoscyamus albus* and *H. niger*, converse results were obtained. In the former the tetraploids yielded 7 per cent less, while in the latter the tetraploids yielded 33 per cent more than did the corresponding diploids.—With *Petunia nyctaginiiflora* rather inconsistent results were attained, the main point being that a possible excess in the tetraploid was decreasing with age, at last turning into a marked deficiency.

Recently, LEVAN (1942 *a* and *b*) reported some preliminary investigations on the productivity of field-grown polyploid strains of clover and flax. In clover, the tetraploids consistently yielded more green matter than did the diploids, the excess varying from 31 to 40 per cent, and in one case amounting even to 128 per cent. These values correspond with a somewhat smaller excess of dry matter in the tetraploids, since it is stated that their content of dry matter is lowered on an average by 2.1 per cent. The yield of seed in the tetraploids is stated to be "inferior".—In flax, the general viability as well as the fertility was lower in the tetraploids throughout all experiments. The relative dry weight of the tetraploids varied from 42 to 74, the values for diploids being put equal to 100.

Obviously, part of the investigations reviewed above give contradictory information on the productivity of polyploid plants



Fig. 1. *Solanum nodiflorum*. To the left the diploid ($n = 12$), to the right the tetraploid ($n = 24$). ($\times 1/16$).

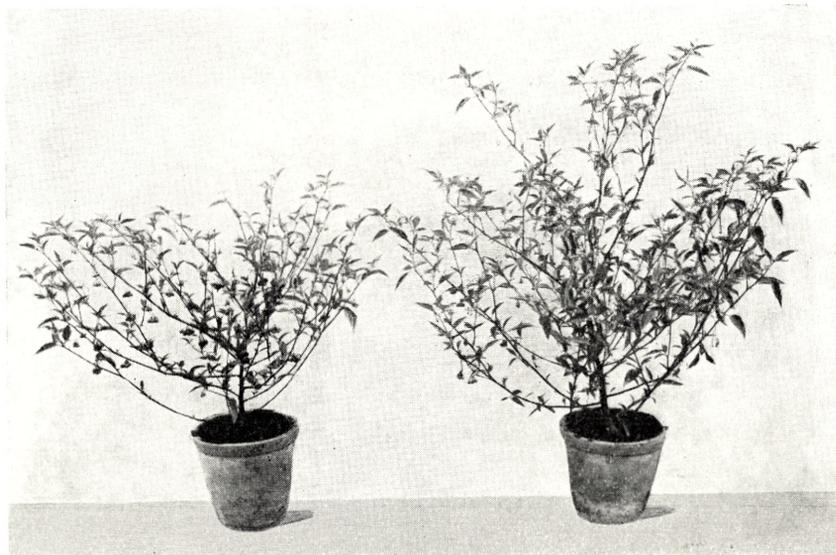


Fig. 2. *Solanum gracile*. To the left the diploid ($n = 12$), to the right the tetraploid ($n = 24$). The small number of berries in the tetraploid should be noticed. ($\times 1/15$).

relative to that of the diploids, although it is the chief impression that the "gigas" character generally does not seem to stand a quantitative examination. Hence, there may be reasons for examining the production of matter of an additional number of species and, particularly, for comparing the yield of diploid and tetraploid plants grown under field conditions; it cannot be taken for granted that the more vigorous development of the individual, solitarily growing plant involves a larger production of leaves, seeds etc., when a multitude of such plants are growing in a stock.

In order to elucidate the problems outlined above the investigations reported on the following pages were carried out. Material of *Solanum* from the cultures of Professor C. A. JØRGENSEN Ph. D. was used. The cultivation of the plants took place in Lyngby, near Copenhagen, in the experimental field of the Laboratory of Genetics of the Royal Veterinary and Agricultural College. The polyploid strains were raised either by the callus method or by a combination of the callus and the colchicine method, as described in detail in the previous paper of this series (JØRGENSEN 1943).

The present investigation was carried out partly on auto-tetraploid strains of *Solanum*, i. e. pure species in which the chromosome number has been doubled, partly on amphidiploids (allotetraploids), i. e. species hybrids the chromosome number of which has been doubled.

The first group included:

	Haploid chromosome number in	
	diploids	tetraploids
<i>Solanum nodiflorum</i> JACQ.	12	24
<i>Solanum gracile</i> OTTO	12	24
<i>Solanum alatum</i> MOENCH	24	48
<i>Solanum nigrum</i> L.	36	72

The habit of these plants appears from figures 1—4. The plants were photographed on September 7th, 1940, towards the end of their vegetation period. They have been dug out of the field and potted immediately before being photographed.

The diploid and the tetraploid *Solanum nodiflorum* (fig. 1) look very much alike. The tetraploid is not so profusely branched as the diploid. On the other hand, the branches are



Fig. 3. *Solanum alatum*. To the left the diploid ($n = 24$), to the right the tetraploid ($n = 48$). ($\times \frac{1}{17}$).

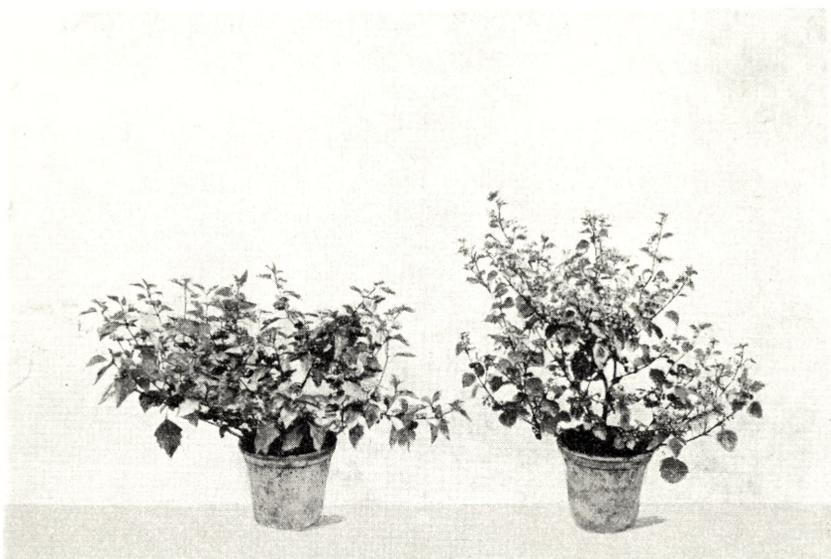


Fig. 4. *Solanum nigrum*. To the left the diploid ($n = 36$), to the right the tetraploid ($n = 72$). ($\times \frac{1}{16}$).

generally somewhat longer. The number of berries is not very different in the two forms. From the habit of the $2n$ and $4n$ strains of this species, only a slight excess of dry matter could be expected in the tetraploid.

The vegetative development of the tetraploid *Solanum gracile* (fig. 2) is much more vigorous than that of the diploid plant, the number of berries, however, is markedly decreased. Nevertheless, according to the appearance of the habit of the plant, a considerable excess of dry matter was to be expected in the tetraploid.

In *Solanum alatum* (fig. 3), the diploid plant is more vigorous both with respect to vegetative growth and to production of berries. In this case, one would expect a pronounced deficiency of dry matter in the tetraploid as compared with the diploid.

Finally, the ratio between the diploid and the tetraploid *Solanum nigrum* (fig. 4) is about the same as in *Solanum gracile*, the tetraploid having the more vigorous vegetative growth and the diploid, in return, the larger amount of berries. (Unfortunately, the latter feature is not so clearly shown in the photo.) The tetraploid, however, is not quite so infertile as the tetraploid *Solanum gracile*. The expectation of a considerable excess in the yield of dry matter in the tetraploid seemed to be justifiable.

About 2500 individuals of each of the two chromosome races of *S. nodiflorum* were used in the experiments; the number of individuals used in the case of *S. gracile* was 1100 of each of the two strains. Of each of the other plants concerned about 600 individuals were grown.

The second group of plants used for the experiments included:

	Haploid chromosome number in	
	parents	amphidiploid hybrids
<i>S. gracile</i> OTTO	12	..
<i>S. insulae-pascalii</i> BITT.	12	..
<i>S. gracile</i> × <i>S. insulae-pascalii</i> , amphidiploid	24
<i>S. nigrum</i> L.	36	..
<i>S. nitidibaccatum</i> BITT.	12	..
<i>S. nigrum</i> × <i>S. nitidibaccatum</i> , amphidiploid	48

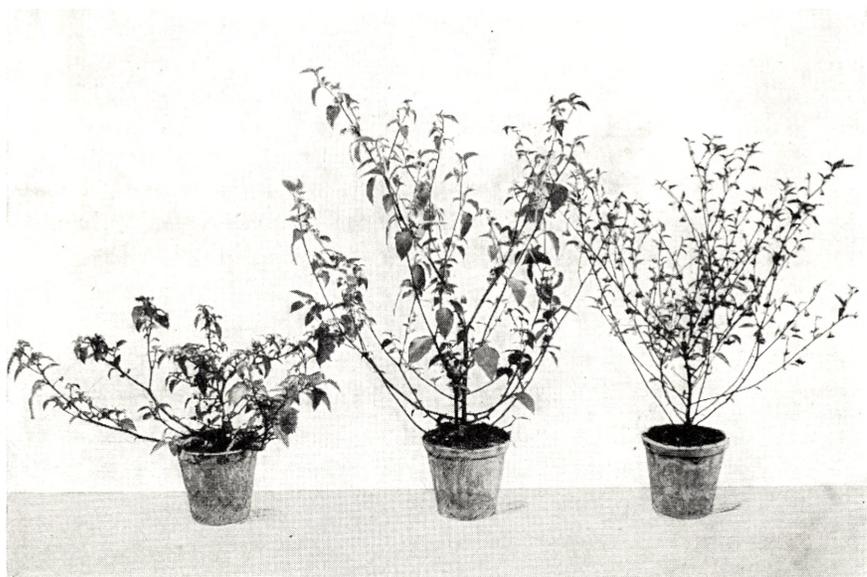


Fig. 5. To the left *Solanum insulae-pascalis*, ($n = 12$), in the middle *S. gracile* \times *S. insulae-pascalis*, amphidiploid ($n = 24$), and to the right *S. gracile* ($n = 12$). ($\times 1/19$).



Fig. 6. To the left *S. nitidibaccatum* ($n = 12$), in the middle *S. nigrum* \times *S. nitidibaccatum*, amphidiploid ($n = 48$), and to the right *S. nigrum* ($n = 36$). ($\times 1/19$).

Figs. 5 and 6 show the habit of these plants. Both of the amphidiploid hybrids look coarser, more vigorous, and therefore more productive than do the initial forms. About 500 individuals of each of these plants were employed.

The aim of the investigations was, first and foremost, to measure and to compare the production of dry matter in the diploid and tetraploid plants; moreover, it was attempted, through a detailed analysis, to elucidate the causes of the differences expected. However, a thorough analysis of all species examined could not be carried out. For this purpose one species, only, was chosen, viz. *Solanum nodiflorum*, since most material of this species could be supplied. Unfortunately, the course of the production of matter in diploids and tetraploids of this very species proved to be very much alike, practically speaking, no difference being present. For this reason, it might have been better if f. inst. *S. gracile* had been chosen instead. The analysis in itself, however, aimed at a further special achievement, viz. to elucidate whether it is possible to calculate the production of matter in a stock of annual plants on the basis of measurements concerning the rate of photosynthesis and of respiration of the plants, supposed the external factors during the development are known. The latter investigation has already been reported (LARSEN 1941). Only the data concerning the production of matter, i. e. the rate of photosynthesis and of respiration, and furthermore the size of the leaf area will be given here. These quantities were determined in *Solanum nodiflorum* and in some of the other experimental plants. The physiological investigations were carried out at the Laboratory of Plant Physiology of the University of Copenhagen. The present work was supported by a grant from the Carlsberg Foundation to which my best thanks are due.

B. Production of Dry Matter.

I. Methods.

In most investigations mentioned in the introduction the plants were grown either in water culture, in flower pots, or in flat boxes, generally in greenhouse. It was the aim of the present series of experiments to determine the production of dry matter under conditions as similar as possible to practical cultivation. Hence, the plants were grown in stocks under field conditions. This enables us to calculate the results per hectare.

The experiments on autotetraploids were carried out in 1939 and those on amphidiploids in 1940. Three or four weeks before the transplantation to the field, the seeds were sown into earthenware dishes in sifted soil, sterilized previously at 100° C. The dishes were kept in greenhouse during germination. About ten days later, the seedlings were pricked off to flat boxes which were kept in frames under glass for two or three weeks; subsequently, the transplantation took place.

In both years, the field consisting of good, loamy soil was fertilized in the spring with 150 kg. per hectare of superphosphate and 250 kg. of a potash manure containing 40 per cent of K₂O (or 33.2 per cent of potassium). Shortly before transplantation, 200 kg. per hectare of calcium nitrate were sown. (In 1939, on August 4th and 12th, 135 kg. per hectare of calcium nitrate were given in addition.)

The area under experiment was divided into strips, each of which, except the outer ones, was 2.88 m. wide and 25 m. long. Each strip was planted up with plants of the same kind. They were planted by rows at a distance of 32.0 cm. on an average, the interval between two consecutive rows being the same. When one strip was planted up with diploid plants, the next one contained tetraploids of the same species. The strips were subdivided into plots. In the main experiment with *Solanum nodiflorum* and in the majority of the other experiments, the size of each plot was 2.153 sq. m., including $3 \times 7 = 21$ plants. On all sides they were surrounded by protective belts consisting of 2 rows of plants. The external belts, however, included 3—10 rows of plants. In the experiments on autotetraploid *S. gracile*, *S. alatum*, and *S. nigrum*, the size of each plot was 1.536 sq. m., the plot containing 15 plants, only.

The increase in dry weight of the experimental plants was determined at shorter intervals during the whole period of vegetation. Each time 2 replicate plots were reaped. The fresh weight and the dry weight of the roots, the stems, the leaves, and the reproductive organs were determined and the leaf area was measured. "Stems" embraces leaf stalks, too. After having been weighed in fresh state, the plants were transferred to paper bags, previously dried and weighed. Next, they were killed in an oven at 90—100° C, and finally dried to constant weight at 100° C. In this way, the dry weight of the plants and

of their constituent parts was found in grams per 4.305 sq. m., which is the total area of two plots. This value was converted into hectokilograms per hectare by multiplication by the factor 0.02323. For the 1.536 sq. m. plots the corresponding factor is 0.03254.

The soil of the field proved to be not quite uniform. One part of the field in which the plants, diploids as well as tetraploids, developed extraordinarily well was not taken into account at all. Moreover, each time samples were taken, the two plots were chosen as different as possible in order to obtain the most probable average. The difference between such replicate plots appears from tables 1 and 2. As is seen from table 1, the variation of the two replicates in the main experiment in a single case amounted to nearly 30 per cent of the mean. In the experiments represented in table 2 the variation in one case is almost 37 per cent. However, these figures are the maxima, and in most cases, especially towards the end of the experiment, when the most important harvests are taken, the variation is less than 10 per cent. In the main experiment with *S. nodiflorum*, the dry weight in the 6 first harvests was determined directly through drying of the total quantity of roots, of stems, etc. In the next 3 harvests, the roots of the 21 plants from each plot have been desiccated, while the green parts of 11 to 6 plants only have been completely analyzed. The green parts of the rest of the plants have been dried without being specified in stems, leaves, and reproductive organs. The contribution of their individual organs to the total weight could be calculated on the basis of the composition found in the analyzed plants. In the 8 last harvests, only 5 or 4 plants per plot have been completely analyzed and desiccated. The various fresh weights, of course, were determined immediately after the plants had been lifted out of the soil, so that the water content of those analyzed and of those not analyzed was as uniform as possible.

The determination of the weight of the roots took place after the roots had been washed repeatedly with water and wiped with filter-paper. When the plants are dug out, part of the roots is generally left in the soil. In order to determine this fraction some plants with a big rootball were carefully taken out. The soil was removed, the loosened soil being sifted in order to pick up all the torn-off parts of the roots. The dry weight of the roots dug out in this way was found to be on an average 64 per cent higher than that of the roots dug out in the usual way. As an estimation of this kind cannot, of course, be done very accurately, the correction was assumed to be 50 per cent and therefore, all weights of roots have been multiplied by 1.5.

Towards the end of the growth season, some of the species are more or less markedly inclined to shed leaves or fruits, so that a given yield may be less than the preceding one. In such cases, when comparing the yields of the various strains, the highest measurement has been reckoned with. Consequently, some disagreement may be found between the amounts of dry matter evaluated directly, as given

in the tables representing the raw material, and the corresponding amounts in those tables and diagrams which serve for a comparison of the maximum productivity of the strains.

II. Production of Dry Matter in Autotetraploids.

a. The Course of Production of Dry Matter.

As mentioned previously, the main experiment was carried out on *Solanum nodiflorum*. The transplanting to the field took place on May 20th, 1939. The dry weight was determined during the vegetation period at approximately one week intervals. From harvest No. 7 it was no longer possible, due to the increasing amount of work, to reap on the same day the diploid and the tetraploid plots to be compared.—The results of the determinations of dry matter are given in table 1. The yields, calculated

Table 1.

Main experiment. *Solanum nodiflorum*, diploid and autotetraploid. Yield of each of the two replicate plots. Shed parts not included.

Harvest No.	Diploid					Tetraploid				
	Date 1939	Amount of dry matter of the two replicate plots, g.		Average amount of dry matter per plot, g.	Variation, percent of the mean	Date 1939	Amount of dry matter of the two replicate plots, g.		Average amount of dry matter per plot, g.	Variation, percent of the mean
1	May 20	2.99	..	May 20	2.84	..
2	May 30	2.82	4.20	3.51	±19.8	May 30	3.87	3.87	3.87	± 0.0
3	June 6	4.75	5.17	4.96	4.2	June 6	3.54	5.46	4.50	21.3
4	June 12	4.81	7.89	6.35	24.2	June 12	5.66	6.42	6.04	6.3
5	June 19	9.54	11.66	10.60	10.0	June 19	10.06	11.06	10.56	4.7
6	June 26	21.4	39.2	30.3	29.4	June 26	19.0	31.4	25.2	24.7
7	July 4	65.1	72.2	68.6	5.1	July 3	50.3	51.5	50.9	1.1
8	July 10	92.9	98.9	95.9	3.1	July 11	67.2	97.0	82.1	18.1
9	July 17	110.7	160.9	135.8	18.5	July 18	127.8	168.8	148.3	13.8
10	July 24	262	268	265	1.0	July 25	245	329	287	14.6
11	July 31	344	456	400	14.0	Aug. 1	467	553	510	8.4
12	Aug. 7	597	705	651	8.3	Aug. 8	489	623	556	12.1
13	Aug. 14	727	813	770	5.6	Aug. 15	632	656	644	1.8
14	Aug. 21	772	820	796	0.3	Aug. 22	800	898	849	5.8
15	Aug. 28	802	854	828	3.2	Aug. 29	766	932	849	9.8
16	Sept. 4	824	848	836	1.4	Sept. 5	798	894	846	5.7
17	Sept. 11	964	990	977	1.3	Sept. 12	905	1031	968	6.5
18	Sept. 18	939	949	944	0.5	Sept. 19	905	1037	971	6.8

per hectare, are rendered in fig. 7, curve *a*. From the 11th harvest and further on, the values of this curve have been gained by summing up the values of the smoothed curves of fig. 13, representing the distribution over the various organs of the dry matter produced. It appears that the course of production of dry matter in the diploid and the tetraploid plants is very much the same. If the relative production of dry matter of the tetraploids is calculated, setting the production of the diploids equal to 100, the result will be the following.

Harvest No.

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18

Relative weight
of the tetraploids
(Diploids = 100):

95 107 92 94 98 84 80 80 100 100 106 87 87 92 96 99 99 99.

The amount of dry matter of the tetraploids, on the day when the diploids were reaped, was read from a curve drawn on a large scale. Only in the second and the 11th harvest the dry weight of tetraploids showed a larger value than did the diploids. In the 9th and 10th harvests, identical figures were found for diploids and tetraploids. Otherwise the tetraploids were always inferior, though the differences on the whole are very small. Hence, the question, whether the tetraploids show a larger production than the diploids, must presumably be answered negatively for this species.

The slope of the drawn curves is an expression of the production intensity at every given moment. During the first 10 periods, both types of plants produce almost equal amounts of dry matter per unit of time. In the beginning of August, the daily production of the diploids reaches the maximum. The intensity of production of the tetraploids, during this period, is less than that of the diploids. The difference, however, will be counterbalanced, during the last half of August, through the increase in production intensity of the tetraploids, the final result in diploids and tetraploids becoming the same.

The results obtained with other species of *Solanum* are given below. The plants were transplanted to the field on May 22nd, 1939. The dry weight was determined only three or four times during the season.

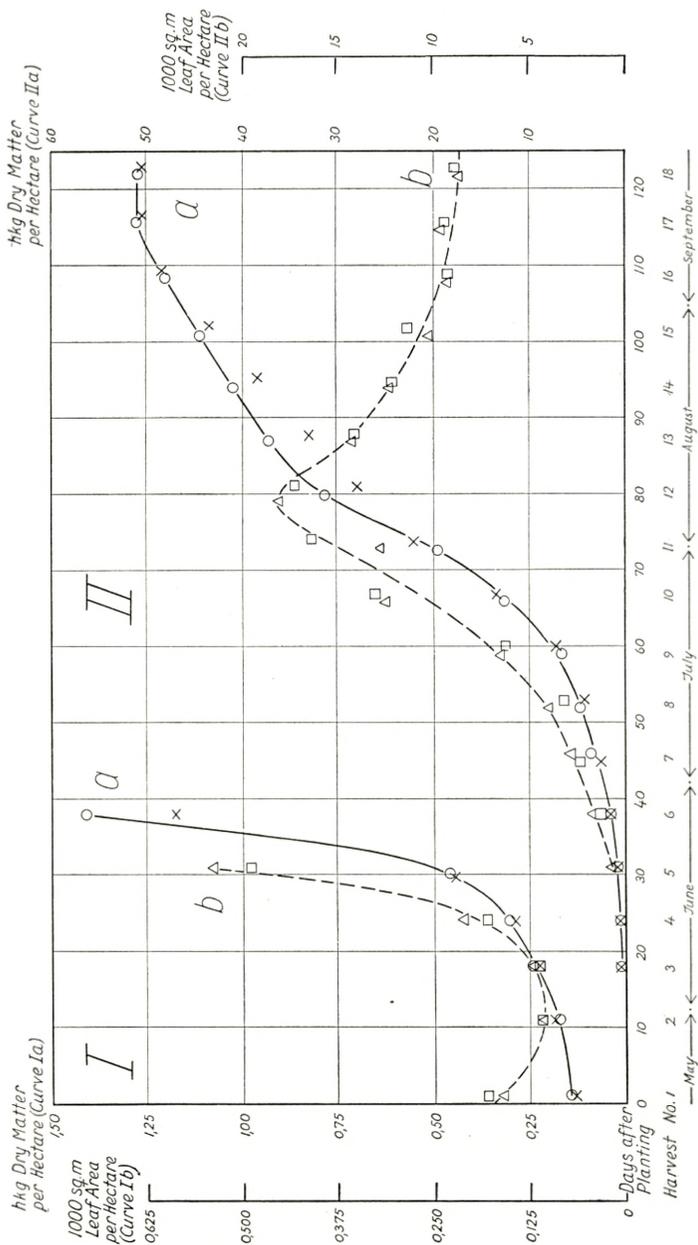


Fig. 7. *Solanum nodiflorum*, diploid and autotetraploid, grown in 1939. The curves I (ordinate to the left) represent the first part of the curves II (ordinate to the right) drawn on a larger scale. The points representing the diploids, only, are connected by a line. a total production of dry matter, hkg. per hectare. O—O diploid, x x tetraploid. b leaf area, 1000 sq. m. per hectare; Δ — Δ diploid, \square tetraploid.

Table 2.

Yield of each of the two replicate plots in *Solanum gracile*, *S. alatum*, and *S. nigrum*, diploid and autotetraploid.

	Date 1939	Diploid				Tetraploid			
		Amount of dry matter of the two replicate plots, g.		Average amount of dry matter per plot, g.	Vari- ation, per cent of the mean	Amount of dry matter of the two replicate plots, g.		Average amount of dry matter per plot, g.	Vari- ation, per cent of the mean
<i>Solanum gracile</i>	May 22	1.53	1.71	1.62	± 5.5	1.02	1.34	1.18	± 13.8
	June 28	34.3	49.2	41.8	17.9	21.6	23.2	22.4	3.5
	Aug. 31	696	716	706	1.3	754	772	763	1.2
<i>Solanum alatum</i>	May 22	1.97	1.99	1.98	0.5	1.15	1.49	1.32	13.1
	June 28	31.3	38.3	34.8	10.0	8.2	17.6	12.9	36.7
	Aug. 31	714	868	791	9.7	590	636	613	3.7
<i>Solanum nigrum</i>	May 22	5.56	6.58	6.07	8.5	2.67	2.69	2.68	0.5
	June 28	44.0	83.2	63.6	30.8	20.5	25.2	22.9	10.2
	Aug. 31	936	968	952	1.7	770	873	822	6.3
	Sept. 29	946	1021	984	3.8	533	990	762	30.0

The behaviour of *Solanum gracile* appears from table 2 and fig. 8. In the beginning, the amount of dry matter is less in the tetraploids than in the diploids. On the 102nd day, however, an amount of dry matter was gained, larger by 8 per cent in the tetraploids than in the diploids (cf. table 3). In both cases, the variation of the two replicate plots was slight, only 1.2 and 1.3 per cent of the mean, and the difference may thus be a real one.

In *Solanum alatum* and *Solanum nigrum*, on the other hand, the tetraploids were markedly inferior, never reaching the weight of the diploids (cf. tables 2 and 3, and figs. 9 and 10).

A summary of the relation between the productivity of the diploid and the autotetraploid plants examined is given in table 3. A common feature of the four species of *Solanum* examined is that in the beginning the rate of development is slower in the tetraploids than in the diploids, a fact which is also

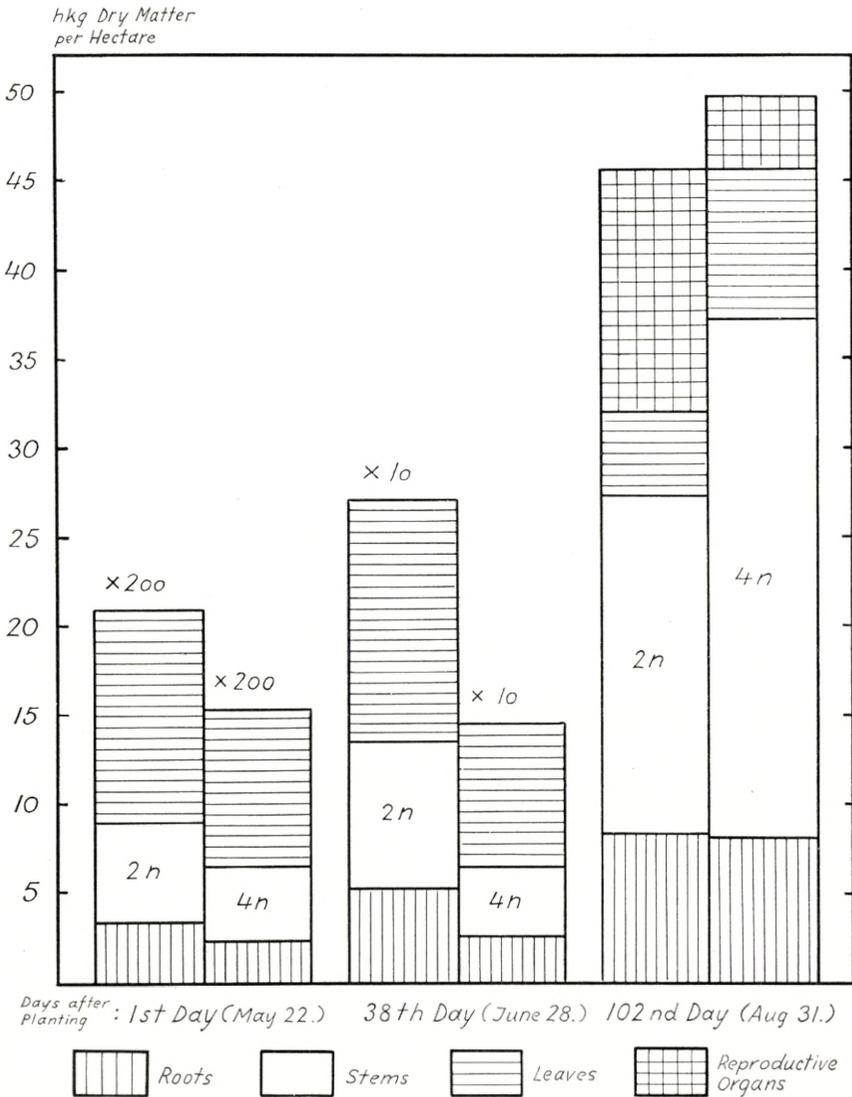


Fig. 8. *Solanum gracile*, diploid and autotetraploid, grown in 1939. Total production of dry matter and distribution of dry matter over the various organs, hkg. per hectare. NB. different scale. In the case of the first and the second pair of columns the readings on the ordinate should be divided by 200 and by 10, respectively.

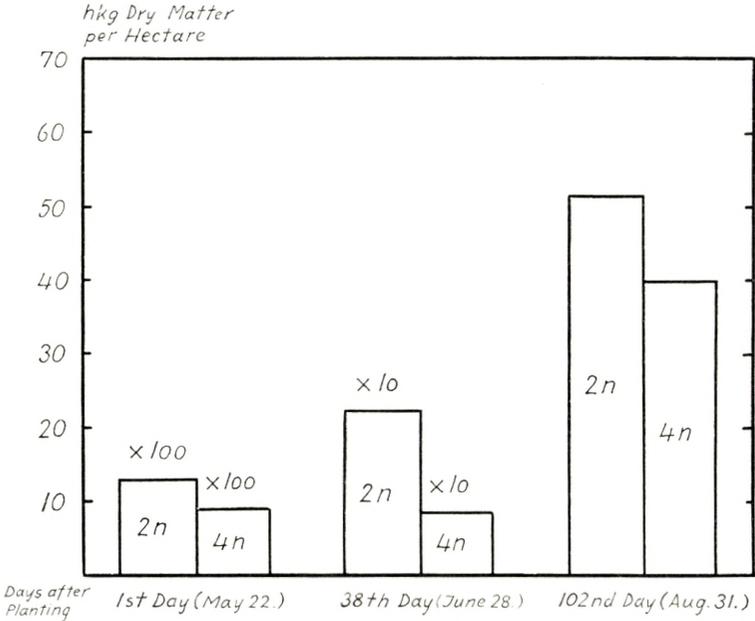


Fig. 9. *Solanum alatum*, diploid and autotetraploid, grown in 1939. Total production of dry matter, hkg. per hectare. NB. different scale. In the case of the first and the second pair of columns the readings on the ordinate should be divided by 100 and by 10, respectively.

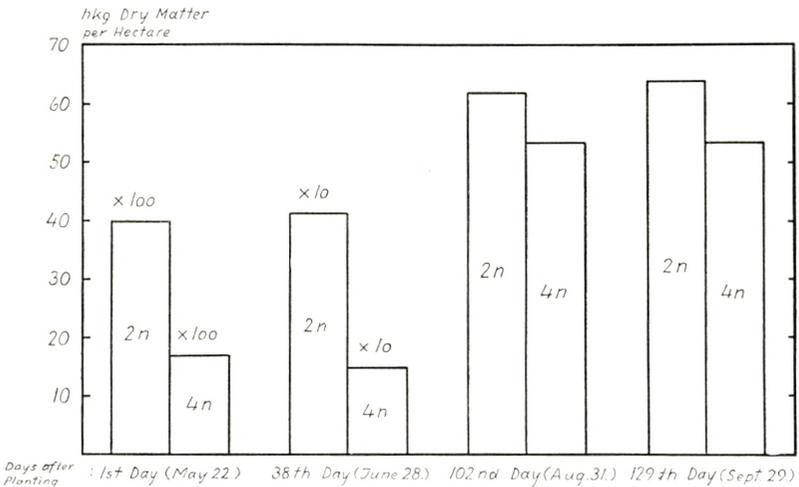


Fig. 10. *Solanum nigrum*, diploid and autotetraploid, grown in 1939. Total production of dry matter, hkg. per hectare. NB. different scale. In the case of the first and the second pair of columns the readings on the ordinate should be divided by 100 and by 10, respectively.

Table 3.

Dry weight of tetraploids, the dry weight of diploids
being = 100.

Number of days after transplantation to the field	<i>Solanum nodiflorum</i>	<i>Solanum gracile</i>	<i>Solanum alatum</i>	<i>Solanum nigrum</i>
1	95	89	69	44
38	84	54	37	36
102	96	108	78	86
131	—	—	—	84

recognizable directly from the appearance of the plants. From a mere inspection of the field, the following impression of the further development may be gained (comp. also the photographs figs. 1—4): In *S. nodiflorum*, the diploids seem to be reached by the tetraploids. In *S. gracile*, they seem to be overtaken, the tetraploids looking twice as big as the diploids. In *S. alatum*, the tetraploids do not seem to attain the size of the diploids, and finally, in *S. nigrum*, the tetraploids look considerably larger. In the case of *S. nodiflorum* and of *S. alatum*, only, the impression gained in this way is confirmed by the determinations of dry matter. In *S. gracile*, on the other hand, the actual excess of dry matter in the tetraploids was only 8 per cent, and in the tetraploid *S. nigrum* even a deficiency of 14—16 per cent was found. The wrong presumption of a much higher production in the tetraploid *S. gracile* and *S. nigrum* is caused by a change in the distribution of the matter produced, i. e. an alteration of the form of the plant which is to be analyzed in detail in the next section.—An evident change of the luxuriance during the development was shown still more markedly by the tetraploid Kobai barley examined by GREIS (1940).

The growth of plants depends on several external conditions; a change in one or more of them may greatly influence the development of a given plant. From agricultural practice it is well-known that varieties of the same plant species, no more different than diploids and tetraploids, often respond in different ways to a change in external conditions. It might therefore be possible, too, that the proportion between diploids and tetraploids found in the previous experiments would be

different under changed conditions. From this point of view, a few preliminary experiments were carried out in which the plants were grown under conditions different from those in the experiments hitherto described. The effect of the variation of two factors, only, was examined, viz. the planting distance and the supply of nitrogen, both of which are known to be of great importance to the size of the crop.

Experiments on the effect of varying distance between the plants were carried out with diploid and tetraploid *Solanum nodiflorum*.

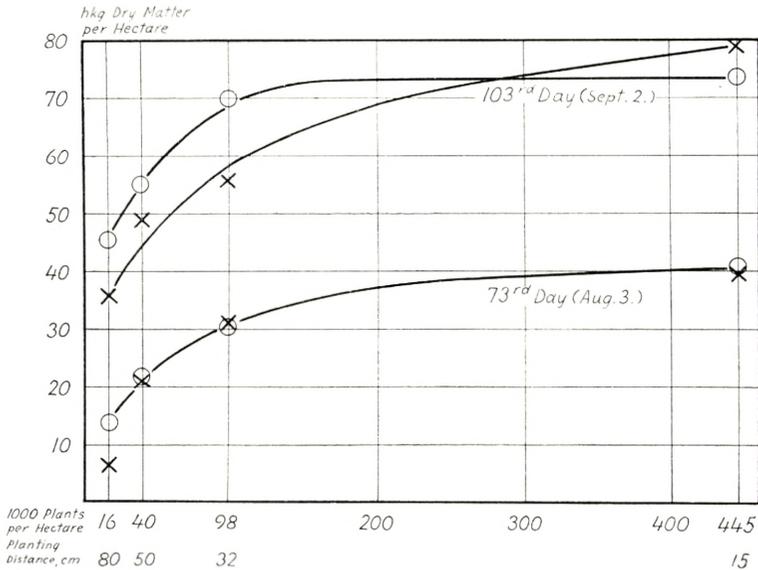


Fig. 11. *Solanum nodiflorum*, 2n and 4n, grown in 1939. Effect of various planting distances on production of matter. ○○ diploid; ×× tetraploid.

The intervals used were 15, 32, 50 and 80 cm., the size of each plot being 0.876, 1.54, 3.00 and 6.40 sq. m. and the plots including 39, 15, 12 and 10 plants, respectively. One plot, only, of each of the types of plant was reaped on the 73rd and 103rd day of vegetation. The results are represented in fig. 11. As is generally the case, the production increases according to the number of plants per hectare. The tetraploids yielded a small excess (7 per cent) in case of the greatest density of plants. This result is, however, encumbered with great uncertainty.

The influence of varying amounts of nitrogen on the production of dry matter was determined in experiments on *Solanum gracile*, 200, 300, and 500 kg. of calcium nitrate being given per hectare. Before the transplantation of the plants took place, all three experimental areas got 200 kg. per hectare; on the 23rd day of vegetation, two of them got 100 and 300 kg. respectively, per hectare. On the 77th and 103rd day, two plots

of each type of plant were reaped; on the 130th day, however, only one diploid and one tetraploid plot have been harvested. The result is illustrated in fig. 12. The increased supply of nitrogen had a furthering effect on the productive capacity of both types of plants. At a large supply of nitrogen and a prolonged duration of vegetation, the tetraploid *Solanum gracile* will possibly produce a little more than the diploid; analogously, in the last harvest of the previous experiment on this species (p. 16 and fig. 8), the production in the tetraploids was somewhat larger than in the diploids.

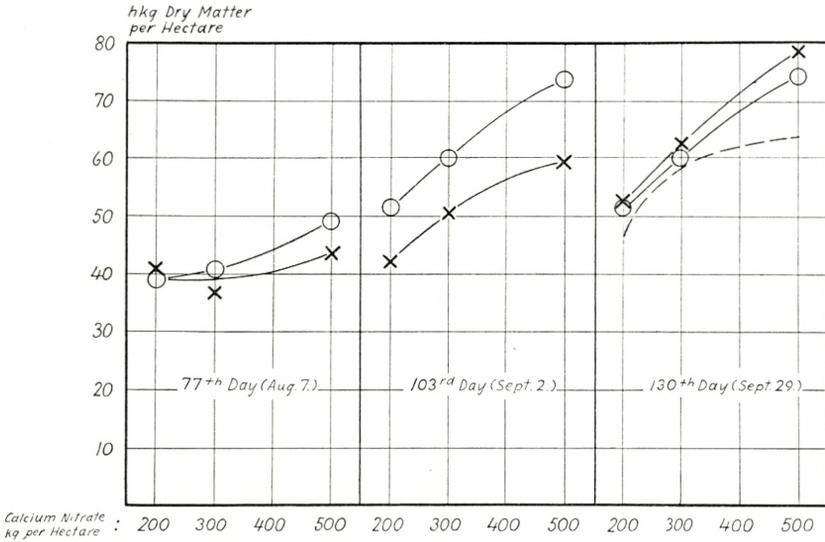


Fig. 12. *Solanum gracile*, 2n and 4n, grown in 1939. Effect of increasing amounts of nitrogen on the production of dry matter. ○—○ diploid; ×—× tetraploid; --- diploid, shed parts not included.

b. Distribution of the Dry Matter Produced.

In the previous section, only the total amount of dry matter was considered. By now, the distribution of the organic substance produced is to be studied. The proportion between the quantity of roots, stems, leaves, and reproductive bodies is of interest for two reasons. First it is determinative for the production of matter itself (the more leaves, the more of photosynthates). It would further be of genetical interest to know whether the chromosome doubling has any effect on this proportion, i. e. whether it is capable of modifying the form of plants.

Solanum nodiflorum: The amount of roots, stems, leaves and reproductive organs reaped directly at every second harvest is

Table

Solanum nodiflorum, 2*n* and 4*n*. Dry weight of the individual organs represented. g. per

Harvest No.....	1		3		5		7	
	May 20	May 20	June 6	June 6	June 19	June 19	July 4	July 3
	2 <i>n</i>	4 <i>n</i>						
Roots	2.02	1.68	5.32	4.69	9.12	10.06	34.8	29.8
Stems	1.29	1.33	1.98	1.72	4.81	4.21	43.9	29.1
Leaves	2.66	2.66	2.62	2.58	7.26	6.84	56.4	41.9
Reproductive organs .	—	—	—	—	—	—	2.0	0.9
Total ...	5.97	5.67	9.92	8.99	21.19	21.11	137.1	101.7

given in table 4. In fig. 13, the production of the individual plant organs is graphically represented by the results of each harvest, calculated per hectare. The points correspond to the values actually found, while the curves plotted have been smoothed. When smoothing the growth curves of the roots, the average of the two highest values was used as a maximum value. The lower values found after the 13th harvest were not taken into account, since they probably result from the ever increasing difficulty of getting the roots out of the soil, owing to their increasing size. Regarding the leaves, two curves were plotted. One, fig. 13 *a*, represents the amount of the living, the other (*b*) that of the living + dead leaves. Both types of plant, the diploid and the tetraploid, on the whole behave in the same way, particularly during the first part of the vegetation period. Afterwards certain deviations occur which, however, are partly accompanied by incidental fluctuations of the yield, hence being less reliable. Nevertheless, it may be concluded that the tetraploids produce a somewhat larger amount of stems and leaves than the diploids, since in each of the last 5 harvests larger amounts of tetraploid stems were reaped, and the same holds for tetraploid leaves in the harvests 10 to 15.—Until the 70th day, the slope of the curve for the production of flowers and fruits, indicating the intensity of production, for instance per day, is approximately the same in both types of plant. During the next two weeks, a great rise in the production of berries appeared

4.

directly reaped. Shed parts not included. Only every second harvest two replicate plots.

9		11		13		15		17	
July 17	July 18	July 31	Aug. 1	Aug. 14	Aug. 15	Aug. 28	Aug. 29	Sept. 11	Sept. 12
2n	4n	2n	4n	2n	4n	2n	4n	2n	4n
74.5	79.5	183	212	360	290	258	261	264	311
95.0	106.6	327	428	565	500	480	574	559	589
91.2	97.6	208	275	208	236	150	168	151	132
10.8	12.9	81	104	407	262	767	694	980	903
271.5	296.6	799	1019	1540	1288	1655	1697	1954	1935

in the diploids, which was only incompletely compensated by a later increase in the production of berries in the tetraploids. The dry weight of the berries in diploids and tetraploids in the harvests Nos. 17 and 18 is as 100 to 92 and 100 to 86, respectively.

Hence, the diploid and tetraploid strains of *S. nodiflorum* being so much alike in total production of dry matter are also found to be very similar as to the distribution of the substance produced.

Quite another picture is seen in *Solanum gracile* which, however, was reaped only three times. In table 5, the amounts

Table 5.

Solanum gracile, diploid and autotetraploid. Dry weight of the individual plant organs directly reaped. Shed organs not included. g. per two replicate plots.

Date 1939	May 22		June 28		August 31	
	2n	4n	2n	4n	2n	4n
Roots	0.52	0.36	16.5	8.2	258	255
Stems	0.86	0.64	25.4	12.4	581	898
Leaves	1.86	1.36	41.5	24.1	143	260
Reproductive Organs..	—	—	—	—	432	113
Total ...	3.24	2.36	83.4	47.7	1414	1526

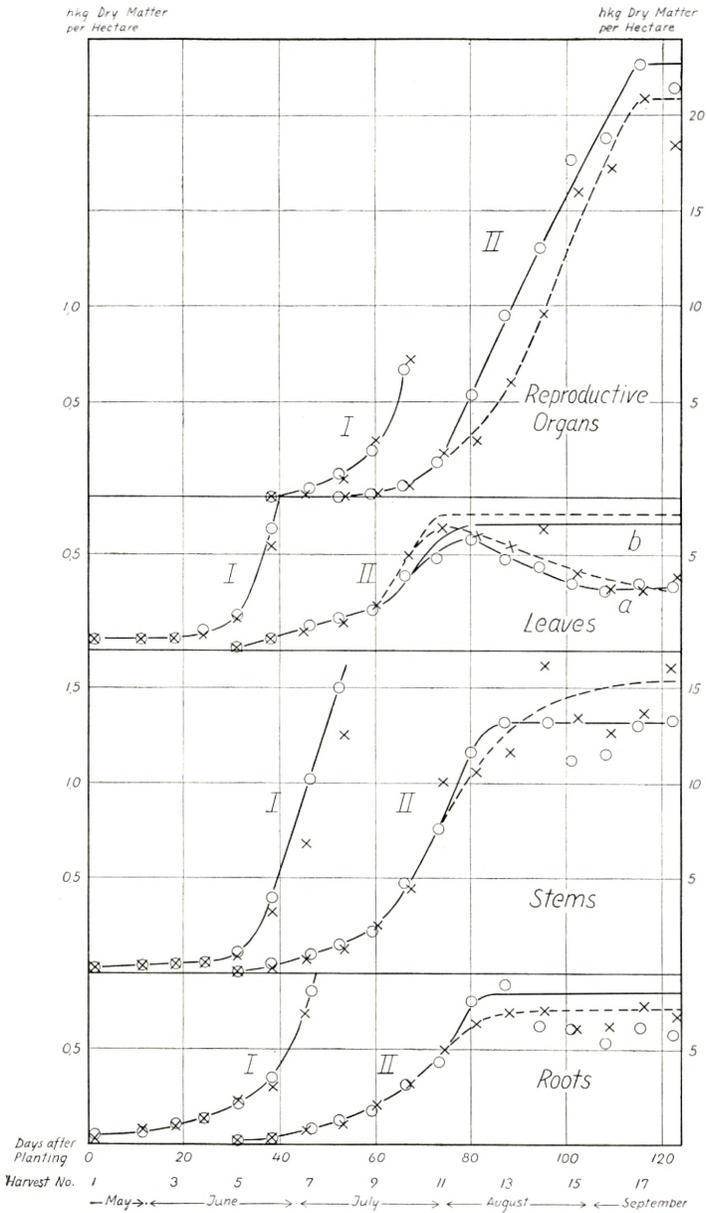


Fig. 13. *Solanum nodiflorum*, $2n$ and $4n$, grown in 1939. Distribution of dry matter produced. The curves I (ordinate to the left) represent the first part of the curves II (ordinate to the right), drawn on a larger scale. $\circ-\circ$ diploid; $\times---\times$ tetraploid. As to the representation of the production of leaves, curve *a* shows the amount of living and curve *b* that of living + dead leaves.

of dry matter actually reaped in each harvest are represented. The production per hectare is shown graphically in fig. 8. In this species, too, until the appearance of the reproductive organs (flower buds) the relative distribution of dry matter is approximately the same in the diploid and the tetraploid plants. At this time, the total weight of the diploids is almost twice that of the tetraploids. Later, when the tetraploids exceed the diploids as to dry weight, the distribution of dry matter in the two types of plant becomes very different. The ratio of dry weight in the fruits of the diploids and of the tetraploids at the end of the experiment is 100 to 27 (cf. also table 19). On the other hand, in the tetraploids the amount of leaves is about twice and that of the stems one and a half times that of the diploids. At a rough estimate in the field, one would judge the total production in the tetraploids considerably higher than that of the diploids. The exact measurement, however, showed but a relatively small superiority in the production of the tetraploids, these plants producing only 8 per cent more than the diploids. The cause of this contradiction has to be sought in the fact that the stems of the tetraploids are stronger and more erect and their leaves are larger and more numerous, which makes the plants look much more bulky. As, however, the diploids simultaneously deposit a large amount of their photosynthates in the berries, the weight of which one is highly inclined to underestimate, their amount of dry matter will be nearly as high as that of the tetraploids.

Solanum nigrum, too, behaves in almost the same way as *Solanum gracile*: in the tetraploids of this species, a considerable excess would be estimated by a mere inspection of the cultures while, on the other hand, the determinations of dry matter showed a deficiency of 14—16 per cent. Unfortunately, determinations of the distribution of matter were not carried out in this plant; but also here the tetraploids produced a by far smaller number of berries than did the diploids.

The change in the form of the plant, which follows the doubling of the chromosome number in species like *S. gracile* (and very likely *S. nigrum*, too), thus involves a more luxuriant development of the vegetative parts, but at the same time a marked

decrease in the amount of fruit produced. In tobacco, cabbage, grass, clover, and other plants, the vegetative parts of which are the aim of cultivation, the possibility of an increased production induced by polyploidy is thus at hand. As far as reproductive organs are concerned, however, the prospects seem rather unpromising.

Table 6.

Diploid and corresponding amphidiploid *Solanums*. Total yield of dry matter and its distribution throughout the individual plant organs.
g. per two replicate plots.

Date 1939.....	<i>S. gracile</i>				<i>S. gracile</i> × <i>S. insulae-pascalis</i> ; amphidiploid				<i>S. insulae-pascalis</i>			
	June 24	Aug. 1-2	Aug. 26-28	Sept. 16-18	June 24	Aug. 1-2	Aug. 26-28	Sept. 16-18	June 24	Aug. 1-2	Aug. 26-28	Sept. 16-18
Days after planting	25	63	88	109	25	63	88	109	25	63	88	109
Roots	13.3	278	580	513	7.1	223	551	704	4.1	112	311	495
Stems	13.6	769	1347	1390	5.3	480	1311	1748	5.6	262	806	977
Leaves	24.6	460	362	107	13.1	474	533	538	13.5	464	406	237
Reproductive organs	0.3	85	486	865	—	24	151	250	—	13	154	232
Total ...	51.8	1592	2775	2875	25.5	1201	2546	3240	23.2	851	1677	1941

Date 1939.....	<i>S. nigrum</i>				<i>S. nigrum</i> × <i>S. nitidibaccatum</i> amphidiploid				<i>S. nitidibaccatum</i>		
	June 25	Aug. 5-6	Aug. 27-29	Sept. 17-19	June 25	Aug. 5-6	Aug. 27-29	Sept. 17-19	June 25	Aug. 5-6	Aug. 27-29
Days after planting	25	67	89	110	25	67	89	110	25	67	89
Roots	18.2	210	306	304	20.7	297	443	511	11.1	139	158
Stems	11.7	382	502	408	15.5	736	948	922	17.2	914	670
Leaves	20.0	316	397	204	30.0	504	482	284	29.7	472	136
Reproductive organs	5.1	688	1283	1480	2.3	483	1426	1198	7.6	691	566
Total ...	55.0	1596	2488	2396	68.5	2020	3299	2915	65.6	2216	1530

hKg Dry Matter
per Hectare

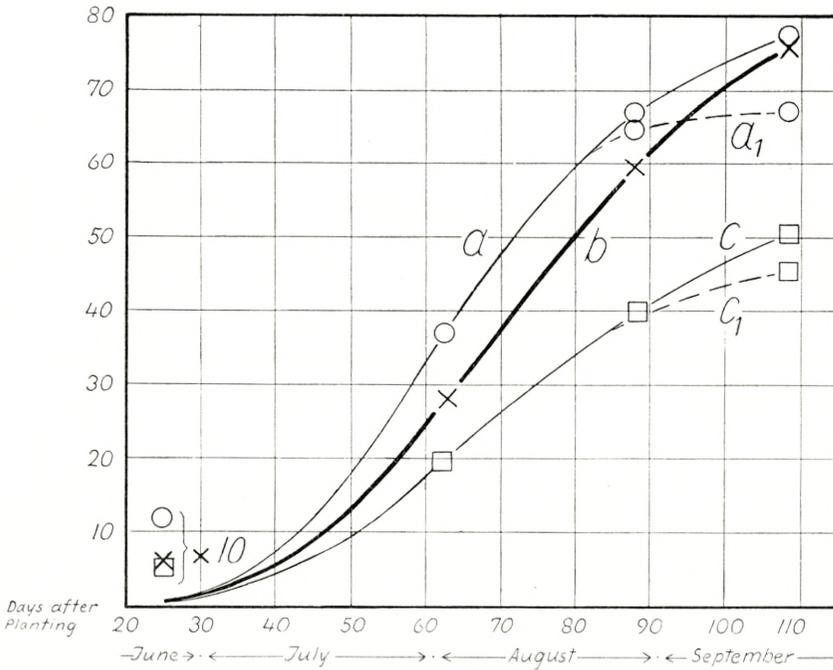


Fig. 14. Diploid and amphidiploid *Solanums*, grown in 1940. Total production of dry matter; hkg. per hectare.

- a *Solanum gracile*; shed organs included (a₁ shed organs not included).
- b *S. gracile* × *S. insulae-pascalis*, amphidiploid.
- c *S. insulae-pascalis*; shed organs included (c₁ shed organs not included).

III. Production of Dry Matter in Amphidiploids.

a. The Course of Production of Dry Matter.

The amphidiploid plants and their parent species were cultivated in 1940. The transplanting to the field took place on June 1st. The amounts of dry matter directly reaped are given in table 6.

The table shows but the sum of the amounts of dry matter reaped in two replicate plots, because the harvest was carried out in the way that one plot, only, of each of the three types of plant to be compared was reaped on the same day; the second of the replicates was reaped one or two days later. Consequently, the difference between the yields of the individual

replicate plots does not give any information as to the variation between the two plots. On the other hand, the figures representing the yield of each of the three types of plant, the parent species, and their amphidiploid hybrid, are fully comparable.

The total production of dry matter per hectare in *Solanum gracile*, *S. insulae-pascalis* and their amphidiploid hybrid is shown graphically in fig. 14. The amount of dry matter of the hybrid, at the beginning, is the same as in *S. insulae-pascalis*, the smaller of the two parent species. The course of its production during the development is intermediate as compared with the parents, its weight in the end being almost the same as the weight of *Solanum gracile*, the more productive of the parent species. The same appears from table 7 which gives the relative weight of the three types of plant.

Table 6 and fig. 15 show the course of the production in *Solanum nitidibaccatum*, *S. nigrum* and the amphidiploid hybrid of these species. *S. nitidibaccatum* develops most quickly, but very early the production is slowed down, and the plant begins to shed berries and leaves. Meanwhile, *S. nigrum* and the amphidiploid hybrid continue to grow, the weight of the hybrid being

Table 7.

Relative dry weight of diploid and corresponding amphidiploid *Solanums*.

Number of days after transplantation to the field	<i>Solanum gracile</i>	<i>S. gracile</i> × <i>S. insulae-pascalis</i> ; amphidiploid	<i>S. insulae-pascalis</i>
25	224	110	100
63	187	141	100
88	166	147	100
109	153	150	100
	<i>Solanum nitidibaccatum</i>	<i>S. nigrum</i> × <i>S. nitidibaccatum</i> ; amphidiploid	<i>S. nigrum</i>
25	119	124	100
67	139	127	100
89	90	134	100
110	—	126	100

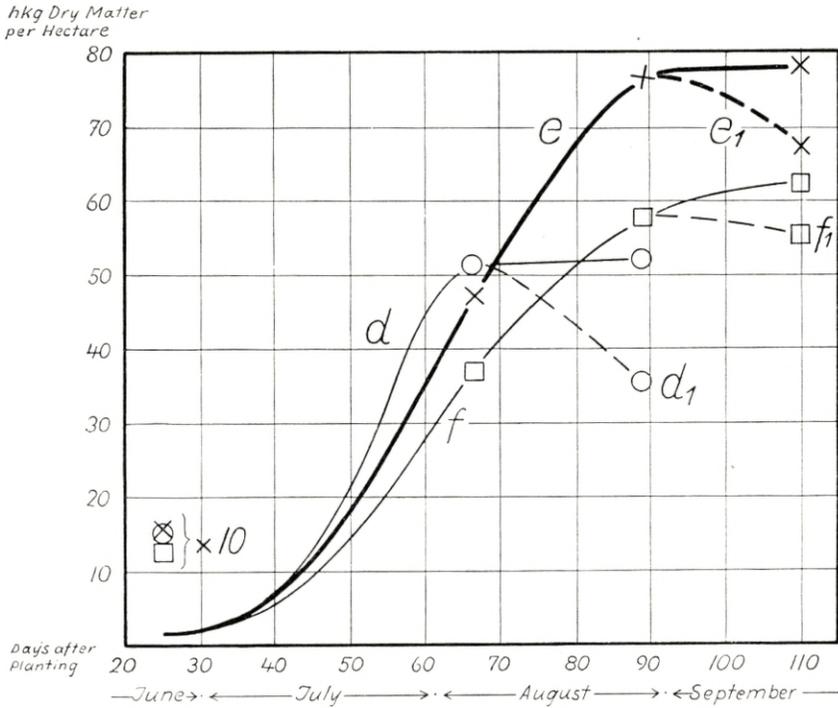


Fig. 15. Diploid and amphidiploid *Solanums*, grown in 1940. Total production of dry matter; hkg. per hectare.
d *Solanum nitidibaccatum*; shed organs included (*d*₁ shed organs not included).
e *S. nigrum* × *S. nitidibaccatum*, amphidiploid; shed organs included (*e*₁ shed organs not included).
f *S. nigrum*; shed organs included (*f*₁ shed organs not included).

the higher one. The proportion of the dry weights of the three types of plant is given in table 7. On the 89th day of vegetation, at any rate, a considerable superiority is found in the amphidiploid hybrid as compared with both initial forms.

b. Distribution of the Dry Matter Produced.

The distribution over the various organs of the matter produced in the amphidiploid plants and the parent species appears from table 6 which shows the amounts of dry matter actually reaped. The values calculated per hectare and corrected for shed organs are represented graphically in figs. 16 and 17.

It is seen that the amphidiploid hybrid between *S. gracile* and *S. insulae-pascalis* produces about the same quantity of roots

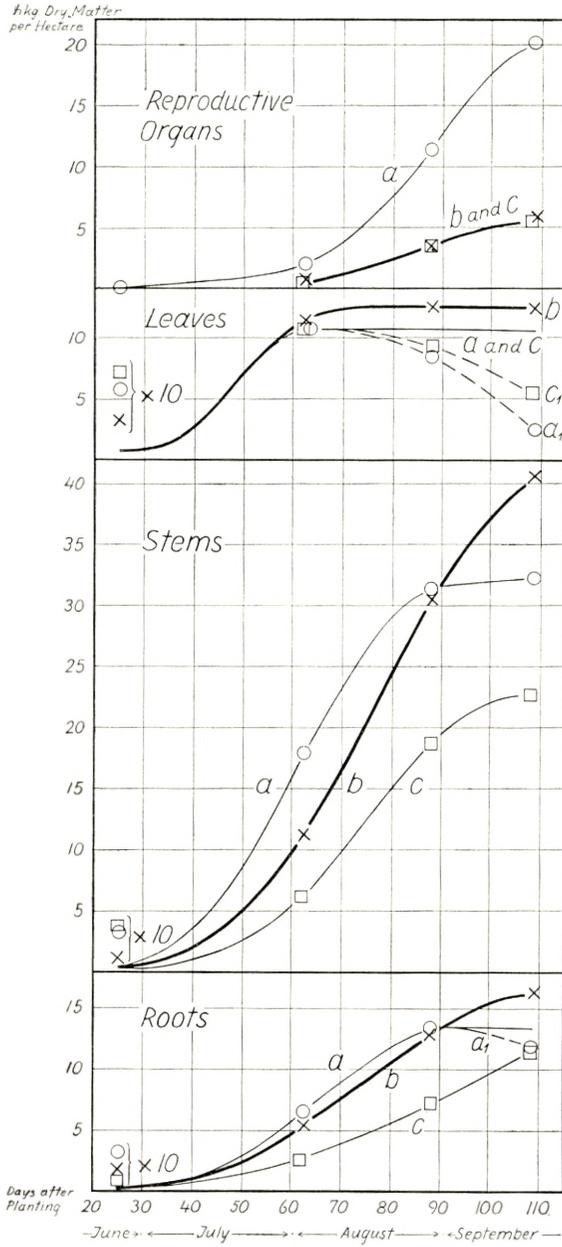


Fig. 16. Diploid and amphidiploid *Solanums*, grown in 1940. Distribution of the dry matter produced.

a *Solanum gracile*; shed organs included (a₁ shed organs not included).

b *S. gracile* × *S. insulae-pascalii*, amphidiploid.

c *S. insulae-pascalii*; shed organs included (c₁ shed organs not included).

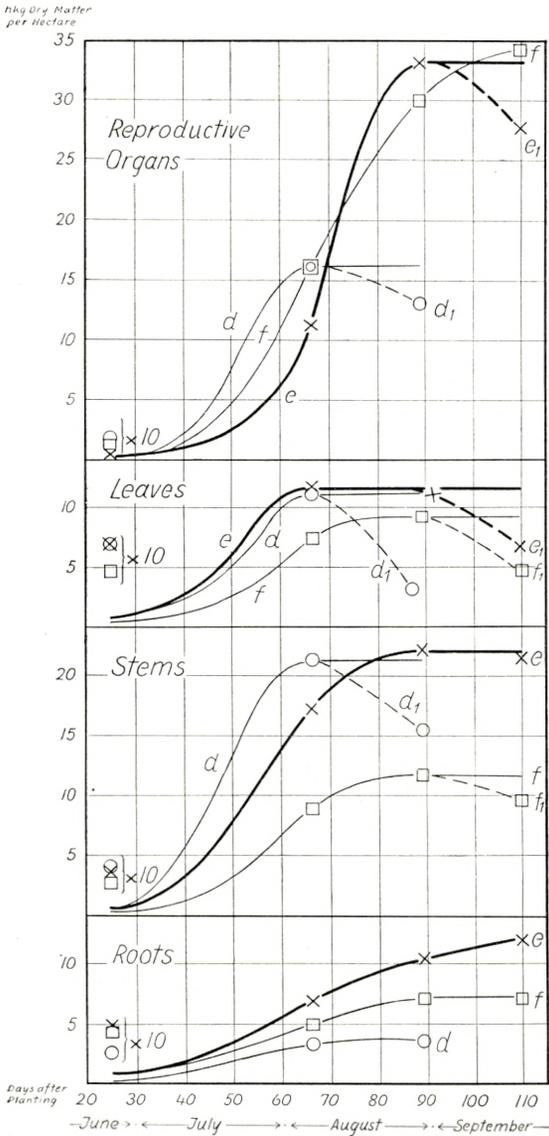


Fig. 17. Diploid and amphidiploid *Solanums*, grown in 1940. Distribution of the dry matter produced.

d *Solanum nitidibaccatum*; shed organs included (*d*₁ shed organs not included).
e *S. nigrum* × *S. nitidibaccatum*, amphidiploid; shed organs included (*e*₁ shed organs not included).

f *S. nigrum*; shed organs included (*f*₁ shed organs not included).

as *S. gracile*, which is considerably more than in *S. insulae-pascalis*. The hybrid further produces a larger amount of stems and, in contradistinction to both parent species, it keeps its leaves until the 110th day at least. At this time, only 50 per cent of the leaves are left in *S. insulae-pascalis* and only 20 per cent in *S. gracile*. The production of berries of the hybrid is exactly consistent with that of *S. insulae-pascalis*, i. e. only about one fourth of that of *S. gracile*.

The production of roots, stems, and leaves in the amphidiploid hybrid between *S. nigrum* and *S. nitidibaccatum* is larger than in *S. nigrum*, while the production of berries is the same. Compared with *S. nitidibaccatum*, the hybrid has twice the production of roots and berries, while the production of stems and leaves is equally large in both forms. As early as after the 66th day *S. nitidibaccatum* begins to shed the older leaves. The hybrid and *S. nigrum*, on the other hand, keep their leaves three weeks longer. *S. nitidibaccatum* is markedly inclined to drop its fruits. In the amphidiploid, too, this inconvenient character is present, though to a less extent, the shedding occurring not until three weeks later.

Of the two amphidiploids investigated the first one represents a case in which the productivity of the hybrid does not exceed that of the parent species. In the last mentioned amphidiploid, *S. nigrum* \times *S. nitidibaccatum*, however, an absolute excess of dry matter is produced, which is combined with a remarkable fertility (cf. also table 19). The expectations of many geneticists and plant breeders, that amphidiploids would prove more favourable than their parent species, have thus been realized in this case.

The formation of the amphidiploid plants has been carried out in two steps. First, the two species have been crossed and, next, the chromosome number of their hybrid has been doubled. Which of these steps is responsible for the increased productivity, either hybridization (heterosis) or chromosome doubling ("gigas"-growth), cannot be ascertained, since the productivity of the diploid hybrid itself is unknown. According to the experience with autotetraploid forms of *Solanum*, it is impossible to know *a priori* whether the amphidiploid or the diploid hybrid would have been the superior. From the appearance

of the diploid hybrid, the result is most likely to be taken as an effect mainly of the chromosome doubling and to a minor degree—if at all—of hybrid vigour. As has been demonstrated earlier in this paper, however, the appearance of plants is a rather unsafe basis of estimation of the productivity.—Setting aside whether the diploid or the amphidiploid hybrid is the more productive, the amphidiploid has the indisputable advantage of being fully fertile, while the diploid hybrid is completely sterile.

C. Rate of Photosynthesis.

The determination of the rate of photosynthesis was carried out according to the air current method devised and thoroughly described by BOYSEN JENSEN (1928, 1932, 1933). The most recent alterations of the apparatus have been described by ROMOSE (1940).

Through a control by means of BOYSEN JENSEN'S stomatometer, it was secured that leaves only with stomata widely opened were used for the determinations of carbon dioxide assimilation.

In the method described, the amount of carbon dioxide taken up by the leaves from outside, the so-called apparent assimilation, is determined. Simultaneously, however, the carbon dioxide produced by respiration is assimilated, too; the rate of real assimilation is then gained by summing up the intensity of respiration per 50 sq. cm. leaf area per hour at 20° C. and the rate of apparent assimilation measured directly. The rate of respiration mentioned is given in the tables as a footnote. Each rate of photosynthesis given in the tables is an average of 2 to 5 individual determinations.

I. Autotetraploids. Table 8 shows the maximum rate of photosynthesis of the leaves of *Solanum nodiflorum* which can be obtained under natural conditions, i. e. the rate of photosynthesis at such an illumination that an increasing light intensity does not cause any increase in photosynthetic activity. In the case of the diploids, this quantity is on an average 12.5 mg. CO₂ per 50 sq. cm. per hour. The values of the 4 individual plants used vary from 12.1 to 13.1 mg. In the tetraploids, on the other hand,

Table 8.
Rate of photosynthesis in *Solanum nodiflorum*.

Plant No.	Maximum rate of real assimilation; mg. CO ₂ per 50 sq. cm. leaf area per hour at 20° C. and normal pressure of carbon dioxide. Illumination 17100—23800 BJ-Lux																																			
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¹ Average rate of respiration = 0.87 mg. CO₂ per 50 sq. cm. per hour at 20° C.

² Average rate of respiration = 0.42 mg. CO₂ per 50 sq. cm. per hour at 20° C.

³ Roundish-leaved type of plant.

the variation is much greater. The maximum rate of photosynthesis of the 6 individuals fluctuates from 5.8 to 15.4 mg. CO₂ with an average of 11.0 mg. It is noticeable that two of the plants have a considerably higher rate of photosynthesis than the diploids. On the other hand, individuals showing a very low rate of photosynthesis are also found. Among the tetraploids, a morphological variation, too, could be observed, manifesting itself particularly through the shape of leaf. In addition to the normal plants with ovate-elliptical leaves, some with coarser, broader, more roundish leaves were found. According to a rough estimate, this type amounts to 10 per cent of the tetraploid plants. Although this morphological variation is not quite parallel to the variation of the rate of photosynthesis, yet the lowest maximum rate of 5.8 mg. CO₂ was measured in the type with roundish leaves.

Moreover, for a comparison with the *Solanums*, the rate of photosynthesis of diploid and tetraploid plants of *Sinapis alba* was determined on material which had been cultivated in well manured garden soil in the Botanical Garden of Copenhagen. The maximum rate of real assimilation of tetraploid plants was found to be on an average 85 per cent of that of the diploids

Table 9.
Rate of photosynthesis in *Sinapis alba*.

Plant No.	Maximum rate of real assimilation; mg. CO ₂ per 50 sq. cm. leaf area per hour at 20° C. and normal pressure of carbon dioxide. Illumination 21900 BJ-Lux	
Diploid ¹	{ 1	15.0
	{ 2	14.6
	{ 3	15.2
} mean = 14.9		
Tetraploid ²	{ 1	12.5
	{ 2	12.1
	{ 3	11.6
	{ 4	12.6
	{ 5	14.4
} mean = 12.6		

¹ Average rate of respiration = 0.60 mg. CO₂ per 50 sq. cm. per hour at 20° C.
² Average rate of respiration = 0.91 mg. CO₂ per 50 sq. cm. per hour at 20° C.

(cf. table 9). In this case, all measurements in tetraploids are lower than in diploids.

In connection with the examinations on photosynthesis, E. K. GABRIELSEN, Ph. D., the Royal Veterinary and Agricultural College, kindly determined the content of chlorophyll in the leaves of *Sinapis*. The content of chlorophyll (a + b) of the leaves of 6 diploid and 6 tetraploid plants was 2.8 ± 0.12^1 and 2.9 ± 0.07^1 mg., respectively, per 50 sq. cm. of leaf area (measured on one side). The ratio $\text{diff./m}_{\text{diff.}} = 0.1 : 0.14 = 0.71$. Hence, the difference is not significant. The corresponding figures per g. fresh weight are: diploids 3.2 ± 0.16^1 mg., and tetraploids 2.9 ± 0.08^1 mg. $\text{Diff./m}_{\text{diff.}} = 1.7$. Accordingly, calculated in this way, the tetraploids have the minor amount of chlorophyll. However, also in this case the difference is insignificant.—These results are in accordance with the majority of the determinations of chlorophyll in various diploid and polyploid plants carried out by Dr. GYÖRFFY and published by PIRSCHLE 1941 (here additional literature).

II. Amphidiploids. The results from determinations of the rate of photosynthesis in leaves of diploid and corresponding amphidiploid *Solanums* are collected in table 10. It appears from the table that, in the case of the amphidiploid hybrid between

¹ The mean error has been calculated after the formula $m = \pm \frac{\sigma}{\sqrt{n \div 1}}$, in which σ is the standard deviation and n is the number of experiments.

Table 10.

Maximum rate of real assimilation in the leaves of diploid and corresponding amphidiploid *Solanums*. mg. CO₂ assimilated per 50 sq. cm. of leaf area per hour at 20° C. and normal pressure of carbon dioxide. Illumination 21900 BJ-Lux. (For rate of respiration, cf. Table 12.)

Plant No.	<i>Solanum gracile</i>	<i>S. gracile</i> × <i>S. insulae-pascalii</i> ; amphidiploid	<i>S. insulae-pascalii</i>
1	9.1	8.5	9.4
2	8.9	8.7	8.3
3	6.6	11.2	10.2
4	7.5	5.8	—
5	—	11.2	—
Mean	8.0	9.1	9.3

Plant No.	<i>Solanum nigrum</i>	<i>S. nigrum</i> × <i>S. nitidibaccatum</i> ; amphidiploid	<i>S. nitidibaccatum</i>
1	6.5	5.5	10.8
2	7.9	6.5	7.4
3	8.8	7.7	10.7
4	8.1	6.6	10.2
5	—	7.7	—
Mean	7.8	6.8	9.8

These experiments have been carried out by Dr. V. ROMOSE.

S. nigrum and *S. nitidibaccatum*, the rate of photosynthesis of the amphidiploid was less than that of the parent species. In the case of *S. gracile* × *S. insulae-pascalii*, it was nearly equal to the one of the original species having the highest rate of photosynthesis, viz. *S. insulae-pascalii*.

D. Rate of Respiration.

The rate of respiration of the plant organs was determined by means of the same apparatus as used for the determinations of photosynthesis; the plant material was kept in darkness.

Table 11.

Rate of respiration in various organs of *Solanum nodiflorum*,
2n and 4n.

Plant material	Date 1939	Number of days after transplantation to the field	mg of CO ₂ given off per g. dry matter per hour at 16°C.	Relative rate of respiration (diploids = 100)
Roots ..	2n June 17	29	2.25	100
	4n June 17	29	1.72	69
	» June 19	31	1.39	
			1.56	
Stems ..	2n June 17	29	2.52	100
	» June 28	40	2.84	
	4n June 17	29	3.04	122
	» June 28	40	3.47	
			2.68	
			3.26	
Leaves ..	2n June 22	34	3.06 ¹	100
	4n June 19	31	1.90 ¹	62
	2n Aug. 24	97	2.15	100
	4n Aug. 24	97	1.45	67
Reproductive organs	2n June 22	34	3.21	100
	4n July 3	45	3.38	105
	2n Aug. 24	97	1.79	100
	4n Aug. 25	98	1.91	107

¹ Regarding the rate of respiration per 50 sq. cm. leaf area at 20°C., cf. footnote of table 8.

I. Autotetraploids. The results of the determinations of respiration in *Solanum nodiflorum*, carried out at 16°C., are collected in table 11. It appears that the rate of respiration decreased somewhat during the period of vegetation in the diploids as well as in the tetraploids. Otherwise, it is seen from the table that no uniform relation exists between the rates of respiration of the organs of the diploid and the tetraploid plants. While the tetraploid stem in June is respiring at a rate by 22 per cent higher than that of the diploid, the rate of respiration in the roots and leaves of the tetraploids is only 69 and 62 per cent, respectively, of that of the diploids. In the reproductive organs, the rate of respiration in both cases is almost the same. From the rates of respiration and the weights of the individual organs per hectare, the loss of dry matter by

respiration per hectare may be calculated, the temperature being taken into account (cf. LARSEN 1941). From these figures, moreover, the rate of respiration of a whole plant may be calculated, and from the results, the average rate of respiration of a plant, for instance per g. dry matter, may be deduced. For a tetraploid plant, during the first 7 periods (until the middle of July), this quantity was on an average 79 per cent of that of a diploid. During the next month, when the percentage share of the reproductive organs increases, the tetraploid plants have an average rate of respiration of 87 per cent of that of the diploids; during the last part of the vegetation period, when the distribution of dry matter is still more shifted in favour of flowers and fruits which respire at a high rate in the tetraploids, too, the average rate of respiration is equal in both types of plant, the tetraploids respiring at a rate amounting to 99 per cent of that of the diploids.

In the rest of the experimental plants, the rate of respiration was measured in the leaves only, at a temperature of 20°C.

The rate of respiration in the leaves of *Sinapis alba*, cultivated in the Botanical Garden and used for the above mentioned experiments on photosynthesis, was in the diploids 0.60 and in the tetraploids 0.91 mg. CO₂ per 50 sq. cm. per hour. In this case, in contradistinction to *Solanum nodiflorum*, the tetraploid leaves respire at a higher rate. In order to verify this result, determinations were carried out on material from some unpublished experiments on *Sinapis* grown in glazed stoneware pots. According to these determinations, the rates of respiration in leaves of diploids and tetraploids were 0.50 and 0.62 mg. CO₂, respectively. In this case, too, the tetraploid plants show a higher rate of respiration than the diploids, calculated per unit area of leaf. If the latter values are calculated per g. of dry matter, the following rates of respiration will be reached, viz. 3.73 mg. CO₂ in the diploid and 5.07 mg. in the tetraploid leaves. Hence, the latter respire more intensely by 36 per cent.

Also in the leaves of tetraploid ferns examined by HEILBRONN (1933), a higher rate of respiration was found than in the diploids. Through an air current method according to PETTENKOFER, a difference of about 10 per cent was stated. By means of a manometrical procedure according to BARCROFT, on the other

Table 12.

Rate of respiration in the leaves of diploid and corresponding amphidiploid *Solanums*; mg. CO₂ given off per hour at 20° C.

	<i>Solanum gracile</i>	<i>S. gracile</i> × <i>S. insulae-pascalis</i> ; amphidiploid	<i>S. insulae-pascalis</i>
per 50 sq. cm. leaf area.....	0.60	0.78	0.72
per g. dry matter.....	2.96	3.12	3.55
	<i>Solanum nigrum</i>	<i>S. nigrum</i> × <i>S. nitidibaccatum</i> ; amphidiploid	<i>S. nitidibaccatum</i>
per 50 sq. cm. leaf area.....	0.64	0.53	0.84
per g. dry matter.....	2.83	2.15	4.18

These experiments have been carried out by Dr. V. ROMOSE.

hand, it was determined to be 62 per cent. Now HEILBRONN considers the figures, gained by the PETTENKOFER method, the correct ones, because, the results obtained by the other method might have been disturbed by a traumatic stimulus which he

Table 13.

Ratio of the maximum rate of real assimilation of carbon dioxide to the rate of respiration (both per unit leaf area) in leaves of the amphidiploid plants and their parent species.

<i>Solanum gracile</i>	<i>S. gracile</i> × <i>S. insulae-pascalis</i> ; amphidiploid	<i>Solanum insulae-pascalis</i>
13.3	11.7	12.9
<i>Solanum nigrum</i>	<i>S. nigrum</i> × <i>S. nitidibaccatum</i> ; amphidiploid	<i>Solanum nitidibaccatum</i>
12.2	12.8	11.7

assumed to be the more active in the tetraploids. A detailed analysis of the causes of the deviating experimental results is, however, impossible.

II. Amphidiploids. The rate of respiration in the leaves of the amphidiploid plants and their parent species is given in table 12. The interrelation between these figures nearly corresponds to that of the rates of photosynthesis in the leaves of the same plants (table 10). As is seen from table 13, the ratio: rate of photosynthesis to rate of respiration per unit leaf area in all these plants is an almost constant quantity.

E. Size of Leaf Area.

The size of the leaf area per hectare is highly decisive for the absolute height of production of matter. It was determined on the majority of the experimental plants at each harvest. The procedure was as follows. A sample of leaves was drawn on paper with a known weight of area, the drawings of the leaves were cut out and weighed. When moreover the dry weight of the sample and the weight of living leaves per hectare are known, the total leaf area per hectare may be calculated.

I. Autotetraploids. The leaf area of *Solanum nodiflorum* is drawn in fig. 7. The leaf areas of the diploids and the tetraploids are almost equal during the whole period of vegetation.

In *Solanum gracile*, the proportion between the size of the leaf area of the diploids and the tetraploids changes in the course of the development (table 14). On the 38th day, the

Table 14.
Size of leaf area in *Solanum gracile*, $2n$ and $4n$;
1000 sq. m. per hectare.

Number of days after transplantation to the field	1	38	102
$2n$	0.18	2.37	10.20
$4n$	0.14	1.24	15.16

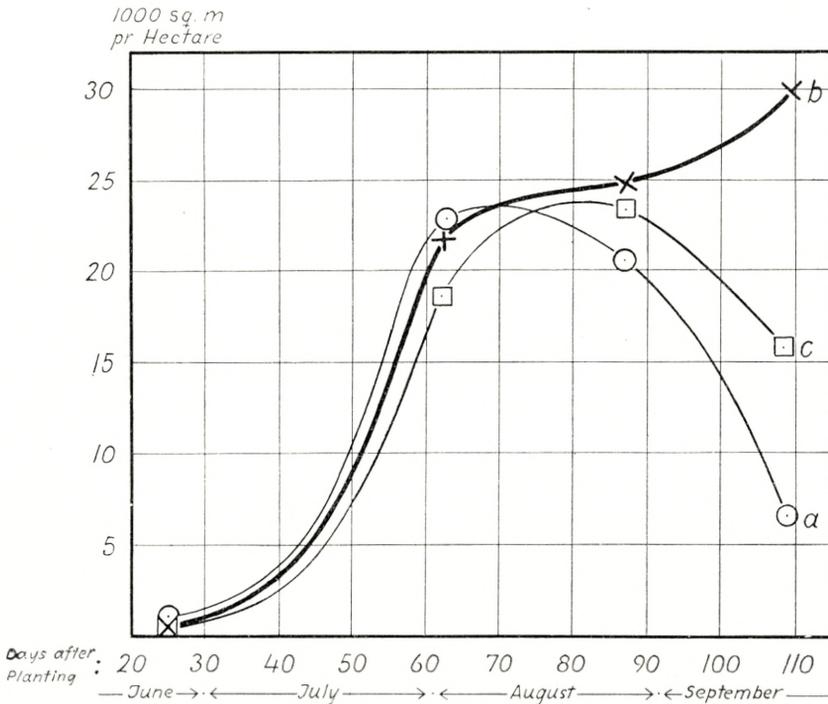


Fig. 18. Diploid and amphidiploid *Solanums*, grown in 1940. Size of leaf area, 1000 sq. m. per hectare.

- a *Solanum gracile*.
- b *S. gracile* × *S. insulae-pascalis*; amphidiploid.
- c *S. insulae-pascalis*.

leaf area in the diploids is twice that of the tetraploids, on the 102nd day, however, the leaf area of the tetraploids is the larger one, viz. one and a half times that of the diploids.

II. Amphidiploids. The leaf areas of the amphidiploid plants and their original species are shown in figs. 18 and 19. It appears from the curves that the amphidiploid hybrid between *Solanum gracile* and *Solanum insulae-pascalis*, in contradistinction to the parent species, at the end of the experiment still possesses a large leaf area which is nearly twice that of *S. insulae-pascalis* and more than four times that of *S. gracile*. This involves the possibility of a longer period of vegetation which, in our lati-

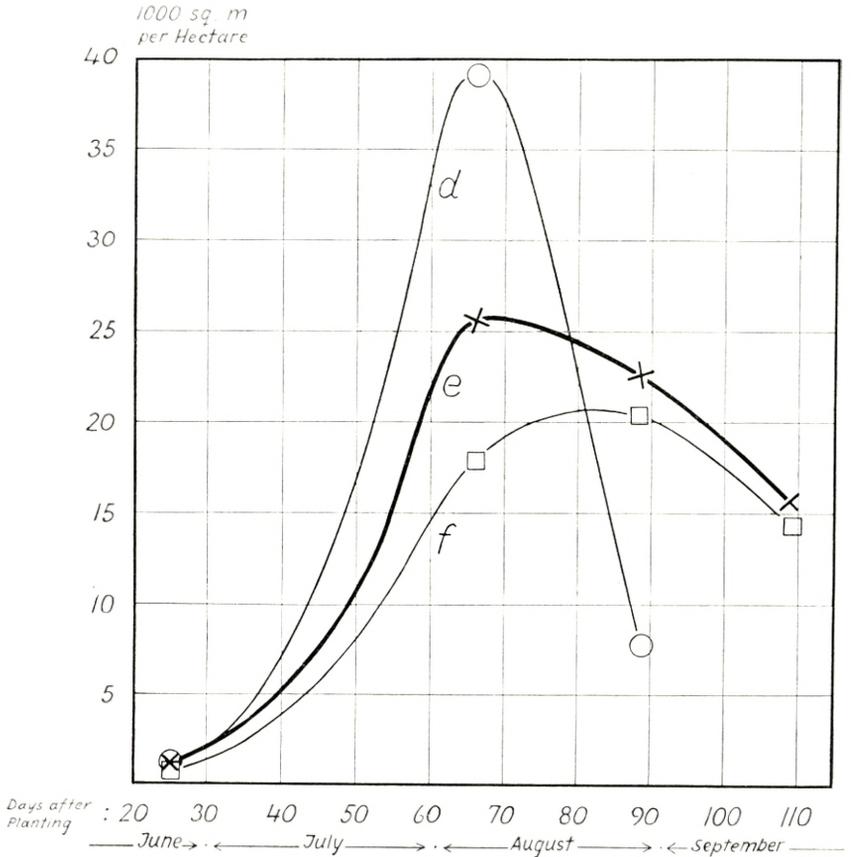


Fig. 19. Diploid and amphidiploid *Solanums*, grown in 1940. Size of leaf area. 1000 sq. m. per hectare.

d *Solanum nitidibaccatum*.

e *S. nigrum* × *S. nitidibaccatum*; amphidiploid.

f *S. nigrum*.

tude, however, soon comes to an end owing to the low temperatures in the autumn.

The leaf area of the other amphidiploid hybrid, *Solanum nigrum* × *Solanum nitidibaccatum*, is intermediate on the 66th day (fig. 19). One of the initial species, *S. nitidibaccatum* after that time sheds the majority of the leaves, while the hybrid and *S. nigrum* do so to a much less extent. At the end of the experiment, the leaf area of the hybrid is only 10 per cent larger than that of *S. nigrum*.

F. Relation between Rate of Photosynthesis and Production of Matter.

As the organic matter of the green plants is produced by photosynthetic assimilation of carbon dioxide, it might perhaps be expected that a proportionality should exist between the rate of photosynthesis and the production of dry matter. As is seen from table 15, this is, however, not the case. The cause hereof will appear from the following.

The yield of a plant stock (the net production) is the difference between the total yield of photosynthesis (the gross production) and the loss by respiration during the period in question:

Net production = gross production \div loss by respiration.

The magnitude of the gross production depends on the size of the leaf area and on the rate of photosynthesis per unit of leaf area. The loss by respiration is proportional to the respiring amount of plant and to the rate of respiration. The absolute magnitude of these quantities is of course dependent on the length of the vegetative period.

Table 15.

Comparison between production of dry matter and rate of photosynthesis in the experimental plants.

Year		Total production of dry matter; hkg. per hectare	Maximum rate of real assimilation; mg. CO ₂ per 50 sq. cm. per hour
1939	<i>Solanum nodiflorum</i> 2n	50.9	12.5
	» » 4n	50.6	11.0
1940	<i>Solanum gracile</i> 2n	76.8	8.0
	» <i>insulae-pascalis</i> ... 2n	50.4	9.3
	<i>S. gracile</i> \times <i>S. insulae-pascalis</i> ; amphidiploid . 4n	75.3	9.1
1940	<i>Solanum nigrum</i> 2n	62.4	7.8
	» <i>nitidibaccatum</i> 2n	52.0	9.8
	<i>S. nigrum</i> \times <i>S. nitidibaccatum</i> ; amphidiploid 4n	78.8	6.8

These facts must be taken into account if we want to compare the productivity of two or more plants, for instance a diploid and a tetraploid one. It is clear that a simple comparison of the rates of photosynthesis is not sufficient to decide, which of the plants concerned is the more capable of production. Even if the leaf area and the duration of vegetation are taken into account, the gross production only, and yet quite roughly, may be compared. Moreover, at an equally large gross production of two plants, very different amounts of dry matter may be stored as net production dependent on the rate of respiration and on the respiring amount of plant, the total loss by respiration during the season being of the same order of magnitude as the net production itself. Nor is the relation between assimilation and respiration decisive for the magnitude of production. HEILBRONN (1933 p. 431) stated: "Wenn also ein Organismus im Vergleich zu einem anderen pro Zeiteinheit vermehrte Trockensubstanz erzeugt, so muss das Verhältnis von Assimilation zur Dissimilation eine Verschiebung zugunsten der ersteren erfahren haben". This is not necessarily the case. If, for instance, assimilation as well as respiration are doubled, the proportion between these quantities will not be changed; the difference between them, which actually is the net production, will nevertheless be doubled. Hence, if the production capability of two types of plant has to be compared, the absolute magnitude of assimilation and of respiration must be calculated on the basis of measurements, at any rate for a short period, of the rate of photosynthesis, rate of respiration, leaf area, amount of plant substance, illumination, and temperature. Subsequently, the net productions gained by subtraction of these quantities may be compared. This method, however, is much more difficult than the simple statement of the production of dry matter, but it may lead to valuable informations as to the causes of possible differences in the production of dry matter in the plants in question. In this way, the production of matter of *Solanum nodiflorum* during the period of vegetation has been analyzed (cf. LARSEN 1941).

The investigations of photosynthesis and leaf area in the amphidiploid plants and the species compared with them permit

no detailed statements as regards the differences in their capability of production of matter; above all, because determinations of the respiration in various organs are lacking. In this series of experiments, the highest rate of photosynthesis is found in *Solanum nitidibaccatum* which, up to a given time, shows the largest total leaf area of all plants in question. In spite of these facts, the production of dry matter of this species is rather small, because the duration of its vegetation period is short.

G. Addendum.

During the present investigations, various results were gained which had no immediate connection with the production of matter. However, these results may be regarded as contributions to the characterization of the experimental plants. Some of these data will be mentioned in the present section.

It has often been stated that polyploid plants contain more water and less dry matter than normal plants. The dry matter content of various organs of autotetraploid *Solanums*, used in this investigation, relative to those of the diploids is given in table 16. The individual values of the absolute content of dry matter show a considerable variation due to the different weather conditions on the days of harvest and due to the state of development. The ratio of the percentage content of dry matter in tetraploids and diploids, however, is fairly constant, and, therefore, this ratio is given in the table. It appears from the figures that the differences in *Solanum nodiflorum* (the average of 36 pairs of determinations), *Solanum gracile*, and *Solanum alatum* (6 pairs of determinations for each species) are quantitatively negligible. In *Solanum nigrum* (8 pairs of determinations), on the other hand, the content of dry matter of the tetraploids is lower, the content of water, consequently, being higher than in the diploids. The differences in the *water content*, however, will be very small. If the ratio of the percentage

Table 16.

Relative content of dry matter in autotetraploid *Solanums*,
the content of the corresponding diploids = 100.

	<i>Solanum nodiflorum</i>	<i>Solanum gracile</i>	<i>Solanum alatum</i>	<i>Solanum nigrum</i>
Roots	96	96	104	86
Stems	101	101	} 101	} 86
Leaves	100	102		
Reproductive organs	98	92		

Table 17.
Relative content of dry matter in diploid and amphidiploid
Solanums.

	<i>Solanum gracile</i>	<i>S. gracile</i> × <i>S. insulae-pascalis</i> ; amphidiploid	<i>Solanum insulae-pascalis</i>	<i>Solanum nitidibaccatum</i>	<i>S. nigrum</i> × <i>S. nitidibaccatum</i> ; amphidiploid	<i>Solanum nigrum</i>
Roots	130	117	100	86	105	100
Stems	124	102	100	66	103	100
Leaves	119	101	100	94	100	100
Reproductive organs	117	107	100	91	98	100

Table 18.
Comparison of the weight of the berries in the various
experimental plants.

	Fresh weight per ripe berry		Dry weight per ripe berry		Number of berries in the sample
	mg.	relative	mg.	relative	
<i>Solanum nodiflorum</i> 2n	232	100	43.6	100	94
» » 4n	235	101	41.2	94	89
<i>Solanum gracile</i> 2n	339	100	73.1	100	91
» » 4n	197	58	34.3	47	56
<i>Solanum gracile</i> 2n	339	90	73.1	134	91
<i>S. gracile</i> × <i>S. insulae-pascalis</i> ; amphidiploid 4n	522	139	87.4	160	67
<i>Solanum insulae-pascalis</i> 2n	375	100	54.6	100	28
<i>Solanum nigrum</i> 2n	459	100	95.8	100	247
<i>S. nigrum</i> × <i>S. nitidibaccatum</i> ; amphidiploid 4n	334	72	68.5	72	73
<i>Solanum nitidibaccatum</i> 2n	257	56	52.9	55	201

of dry matter in two types of plant is, for instance, 100 to 85, this may correspond to a dry matter content of about 20 and 17 per cent of the fresh weight. Hence, the water content is 80 and 83 per cent, respectively, of the fresh weight.

Corresponding proportionals for the diploids and the amphidiploids examined are given in table 17. Each figure is the average of 6–8 pair of determinations. The content of dry matter is considerably higher in *Solanum gracile* than in *Solanum insulae-pascalis*. The dry matter content of the superterranean portions of their amphidiploid hybrid is almost the same as in *S. insulae-pascalis*, while the content of the roots is intermediate. In the other amphidiploid hybrid, the content of dry matter is almost the same as in *Solanum nigrum*, being somewhat higher than in *Solanum nitidibaccatum* especially with respect to stems.

It would also be of interest to compare the size of the fruits of the various diploid and tetraploid strains. Table 18 gives the absolute and the relative average fresh weight and dry weight of the ripe berries. It appears from the table that the size of the berries in *Solanum nodiflorum* remained unchanged despite the doubling of the chromosome number, while in *Solanum gracile*, it decreased considerably. The amphidiploid hybrid between *Solanum gracile* and *S. insulae-*

Table 19.
Number of berries per hectare, *medio* September.

Year		Amount of reproductive organs per hectare; hkg. dry matter	Number of berries, (ripe + unripe), millions per hectare
1939	<i>Solanum nodiflorum</i> 2n	22.8	125.6
	» » 4n	21.0	101.5
1939	<i>Solanum gracile</i> 2n	14.04	39.6
	» » 4n	3.68	19.0
1940	<i>Solanum gracile</i> 2n	20.17	56.8
	<i>S. gracile</i> × <i>S. insulae-pascalis</i> ; amphidiploid 4n	5.81	10.8
	<i>Solanum insulae-pascalis</i> 2n	5.38	13.2
1940	<i>Solanum nigrum</i> 2n	34.40	40.0
	<i>S. nigrum</i> × <i>S. nitidibaccatum</i> ; amphidiploid 4n	33.18	72.7
	<i>Solanum nitidibaccatum</i> 2n	16.06	33.5

pascalis possesses berries, which are increased in size as compared to the parent species, while on the other hand the size of the berries in the second hybrid, *S. nigrum* × *S. nitidibaccatum*, is intermediate.

In order to make an estimation of the fertility of the various plants feasible, the number of berries per hectare is given in table 19. The calculation of these figures was based on the determinations of the weight of the reproductive organs per hectare (cf. figs. 8, 13, 16, and 17) in connection with counts of the berries per gram of dry matter in the reproductive organs. It must be emphasized that "reproductive organs" include, too, the flower stalks and the fruit stalks. The remarkable fertility of the tetraploid *S. nodiflorum* and of the amphidiploid hybrid between *S. nigrum* and *S. nitidibaccatum*, and the reduced fertility in the tetraploid *S. gracile* appear from the table. The figures would correspond still better to the fertility, if they were completed by counts of the number of seeds per berry. Examinations of this kind will be published by M. WESTERGAARD, Ph. D.

Summary.

The production of dry matter in stocks of some diploid and autotetraploid and also of diploid and amphidiploid forms of *Solanum* has been studied in field experiments. Moreover, the rates of photosynthesis and respiration as well as the development of leaf area have been compared in the experimental plants.

A. Autotetraploid Plants.

1. Setting the amount of dry matter of each of the diploid plant species at the end of the season equal to 100, the following relative amounts were found in the corresponding autotetraploids: *S. nodiflorum* 99, *S. gracile* 108, *S. alatum* 78, and *S. nigrum* 84. Hence, in *S. gracile*, only, a small excess was found in the tetraploids. In *S. nodiflorum*, the final result was practically the same in diploids and tetraploids. Otherwise, the capability of production of the tetraploids was smaller than that of the diploids (table 3 p. 19).

2. While the distribution over the individual plant organs of the matter produced was almost the same in $2n$ and $4n$ plants of *Solanum nodiflorum* (fig. 13), a considerable decrease in the production of berries and an increase in the production of stem and leaf were caused in *S. gracile* (fig. 8) and *S. nigrum* through the doubling of the chromosome number.

3. The relative rates of photosynthesis of diploid and tetraploid plants of *Solanum nodiflorum*, on an average, are as 100 to 89. Moreover, the variation is markedly greater in the tetraploids (table 8). (Also in *Sinapis alba*, (table 9), the rate of photosynthesis was found to be smaller in the tetraploids, viz. 85 per cent of that of the diploids.)

4. From May 20th until the middle of June, the average rate of respiration of a whole plant per gram of dry matter was in the tetraploid *Solanum nodiflorum* 79 per cent of that of the diploid; during the next month, this figure was 87 per cent and 99 per cent during the last part of the season.

5. The size of leaf area of the tetraploid *Solanum nodiflorum* was almost identical with that of the diploid during the whole season (fig. 7).—On the 38th day of vegetation, the leaf area of the diploid *Solanum gracile* was almost twice that of the tetraploid, on the 102nd day, however, the leaf area of the tetraploids was $1\frac{1}{2}$ times that of the diploids (table 14).

B. Amphidiploid Plants.

1. In the beginning, the amount of dry matter per hectare in the amphidiploid hybrid between *Solanum gracile* and *S. insulae-pascalis* was about the same as in the smaller of the parent species, viz. *S. insulae-pascalis*; however, during the development, it approached gradually that of *S. gracile*, finally becoming almost as high as in this plant (fig. 14 and table 7).—In the amphidiploid hybrid between *S. nigrum* and *S. nitidibaccatum*, the amount of dry matter per hectare during the last part of the experimental period was 25—35 per cent higher than in *S. nigrum*, and much higher than in *S. nitidibaccatum*, which species rather early stopped developing, although it grew very vigorously in the beginning (fig. 15 and table 7).

2. The amphidiploid hybrid between *Solanum gracile* and *S. insulae-pascalis* produced somewhat more stem than did the parent species. The production of berries was exactly that of *S. insulae-pascalis*, amounting to about one fourth, only, of that of *S. gracile* (fig. 16).—The amphidiploid hybrid between *S. nigrum* and *S. nitidibaccatum*, as compared with *S. nigrum*, has a greater production of root, stem, and leaf, while the production of

berries is equal. Compared with *S. nitidibaccatum*, it has twice the production of root and berries, while the production of stem and leaf in these plants is equally great (fig. 17).

3. The maximum rate of photosynthesis of the amphidiploid hybrid between *S. gracile* and *S. insulae-pascalis* was smaller than that of both original species; in the case of the amphidiploid hybrid between *S. nigrum* and *S. nitidibaccatum*, however, it was about the same as in the superior of the two parent species (table 10). The ratio of the maximum rate of photosynthesis of the leaves to that of the respiration of the leaves was about the same in all these plants (tables 12 and 13).

4. During the period of vegetation, the leaf area of the amphidiploid hybrid between *Solanum gracile* and *S. insulae-pascalis* increased continuously, in contradistinction to the original species, in which the leaf area at last had highly decreased (fig. 18). In *Solanum nigrum* and *S. nitidibaccatum* as well as in the amphidiploid hybrid between these species, a shedding of part of the leaves took place during the last part of the experimental period. This shedding was much more marked in *S. nitidibaccatum* than in the two other forms. In this case, too, the hybrid finally had a larger leaf area than any of the parent species (fig. 19).

C. Addendum.

The relative content of dry matter in the various plant organs and also the size and the number of fruits are given in tables 16—19.

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