Sucrose and Weight of Root in Tetraploid Monogerm and Multigerm Sugar Beet Populations Under Different Mating Systems

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Introduction

During he last decade polyploid varieties of sugar beets have been planted on a large scale in Denmark, Netherlands, Austria, Italy, Germany, and other countries. Replacing of diploid varieties by polyploids in these countries was prompted by the higher productivity of polyploids and by better combinations with high yield and high sucrose percent (3, 5, 27, 28, 35, 36, 37, 39, 43, 50, 69, 83, 84, 87, 88)[2]. According to the opinions of European breeders a better combination of high sucrose and yield can be obtained at the polyploid than at the diploid level (35). Therefore, in many European countries polploidy has become a new and widespread method in sugar beet breeding (36, 65).

The breeding of polyploid varieties includes the four following stages: a) obtaining tetraploids by colchicine treatment, control of the ploidy level, and the propagation of new tetraploids in certain generations (5, 6, 7, 36, 38, 62, 74, 75, 76, 78, 79, 80, 85); b) improvement of the biological characters of tetraploid populations and lines along with the economic value (73); c) evaluation and selection of tetraploid and diploid parental strains according to their ability to combine as in triploids (polyploids) (88); and d) the composition of polyploid varieties from diploid, triploid, and tetraploid beets, or obtaining pure triploid male-sterile hybrids (5, 15, 36, 60, 61, 80, 82).

Tetraploidy offers new possibilities in the breeding of monogerm sugar beets. Tetraploid strains of monogerm self-fertile and self-sterile beets obtained by Helen and V. F. Savitsky developed much larger fruits with larger germs than the original diploid strains. The same appearance was observed in tetraploid hybrids resulting from crosses of tetraploid multigerm and monogerm beets. Tetraploid F_2 monogerm segregates showed much larger fruits than F_2 diploid monogerm segregates from crosses of the same strains at the diploid level.

New possibilities have been opened for genetic study and for breeding work in monogerm polyploids by the production of

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the first monogerm tetraploid self-fertile inbreds and a corresponding monogerm male-sterile equivalent (80, 82) by H. Savitsky. Monogerm and multigerm diploids and corresponding tri- and tetraploid self-fertile, self-sterile, and male-sterile strains have now been provided for experimental use.

The genetic effect of autopolyploidy conditioned by the tetraploid type of heredity was theoretically studied by mathematical genetics. However, genetic changes occurring in the polyploid hybrid populations, even in the first generations, have not been studied experimentally in beets and have been studied to only a small extent in other crops.

Doubling of the chromosome number in sugar beets involves two types of changes: a) detectable changes of different characters which can be observed immediately in the first generations after colchicine treatment and which are caused by doubling of the chromosome set; and b) changes of phenotypic and genotypic structure of populations which occur in the following generations which are caused by the replacement of diploid inheritance with a polysomic one.

Polysomic inheritance observed in polyploids is characterized by several peculiarities absent in diploid organisms. The laws of polysomic inheritance differ from Mendel's rules. Gametes in a tetraploid plant may carry more than one representative of the same parental gene. Position of the gene in the chromosome, the process of pairing, multivalent formation, non-disjunction, and chiasmata formation influence the type of segregation in tetraploids (8, 20, 21, 24, 26, 29, 33, 45, 53, 63, 77, 94, 95). Because of polysomic inheritance, reaction toward different types of matings is not equal in diploids and tetraploids. The difference is caused by slower segregation in tetraploids (1, 2, 23, 34, 44, 48, 49, 70, 90). Correlations caused by linkage are also changed in tetraploids. Differing from diploids, which have only two types of linkage (coupling and repulsion), tetraploids possess many distinct types of gametic series (22, 25, 54, 93). These secondary genetic variations in tetraploid populations, which occur as a consequence of polysomic inheritance, lead to a situation in which it is reasonable to employ, in some cases, different methods of breeding and mating than in diploids. It is known that tetraploids in certain species changed their original type of mating (89). In spite of this, in the majority of outbred species such as *Secale cereale*, *Brassica*, *Raphanus*, and *Kok-saghyz*, as well as in *Beta vulgaris*, autotetraploids maintained outbreeding as a type of mating. Self sterility in sugar beet autotetraploids derived from self-sterile diploids was confirmed in many of our

experiments conducted in different environments during the last 5 years.

The type of mating—inbreeding or outbreeding—defines the genetic structure of a given species (55, 56, 57, 59). The genetic mechanism controlling vigor in outbreeding species is based upon selective advantages of heterozygotes (12, 13, 14, 18, 41, 42). Therefore, the maximum expression of productiveness in polyploid hybrids and populations may be obtained in the process of breeding only at certain levels of heterozygosity. The genetic effect of inbreeding and outbreeding has not been studied experimentally in sugar beets. This paper is devoted to a study of variations in percent sucrose and root weight in tetraploid monogerm and multigerm populations obtained by different mating systems (selfing, sibbing, backcrossing, and outcrossing).

Materials and Methods

To study the variation in percent sucrose and weight of root in tetraploid self-fertile and self-sterile beets, several inbred lines and experimental hybrid populations between monogerm and multigerm beets were obtained. These populations differed in their origin and in the type of mating employed for their propagation.

Tetraploid self-sterile experimental populations studied represent typical tetraploid sugar beet populations, with the exception that the "genetic conditions" involved in their formation had been predetermined (sibbing or open pollination) and were controlled from the beginning of their development. Therefore, it was possible to study the variation of percent sucrose and of weight of root in tetraploid populations under different types of matings: hybridization, sibbing, and open pollination.

Self-fertile tetraploid monogerm inbreds and monogerm self-sterile populations have not been developed and studied previously.

The experiments included the following six tetraploid strains obtained by H. Savitsky (79, 80) by using the colchicine treatment: $4n$ US 35/2 self-sterile multigerm; $4n$ US 22/3 self-sterile multigerm; $4n$ SLC 15 self-sterile monogerm; $4n$ SLC 31 self-sterile monogerm; $4n$ SLC 91 self-fertile monogerm inbred line; and $4n$ monogerm male-sterile equivalent of SLC 91.

The following diploids were also used: $2n$ SLC 15 self-sterile monogerm; $2n$ SLC 91 self-fertile monogerm inbred line; $2n$ F_2 or S_1 population from hybridization of self-fertile $2n$ SLC 91 monogerm to $2n$ US 35/2 multigerm (Table 1).

The following tetraploid hybrids were obtained by hybridization:

(a) F_1, F_2 (sib), and F_2 open pollinated between $4n$ self-sterile SLC 31 monogerm and $4n$ self-sterile US 35/2 multigerm, b_1 crosses between F_1 to monogerm parent, and b_1 crosses between F_1 to the multigerm parent US 35/2.

(b) F_2 (sib) and F_2 open pollinated and b_1 between $4n$ self-sterile SLC 31 monogerm and $4n$ self-sterile US 22/3 multigerm.

(c) F_1, F_2 (selfed F_1) and F_2 open pollinated and b_1 between $4n$ self-fertile SLC 91 monogerm and $4n$ self-sterile US 35/2 (Table 1).

To obtain F_1 hybrids about 30 plants in a corresponding monogerm population were pollinated (by exchanging pollinating bags) by the pollen of the same number of plants taken at random in a multigerm population. The authenticity of F_1 hybrids was controlled by the type of fruit. During the production of all following generations and backcrosses, conditions providing for random reproduction were observed. In all backcrosses within self-sterile beets F_1 hybrids were used as the female parent. In sib-crosses 2 sister plants from the same F_1 family were crossed. By selfing, the plants were self-pollinated (bagged). F_1, F_2, and F_3 tetraploid hybrids between self-sterile beets and self-fertile SLC 91 were highly self fertile and selfed seed was obtained without any difficulty. In self-fertile beets tetraploid male-sterile plants equivalent to the tetraploid SLC 91 were used as the female parent to obtain F_1 seed, which was used only for testing the F_1 and backcross hybrids SLC 91 $\times$ US 35/2.

A test of tetraploid F_1 hybrids between monogerm male-sterile SLC 91 and US 35/2 and monogerm self-sterile SLC 31 $\times$ US 35/2 was conducted under the numbers 17-1 and 17-2 (Table 1). Each of these F_1 hybrids was planted in 20 replications, each of which occupied one row of a two-row plot (entry number 17-1 and 17-2). These hybrids were similar in sugar and in yield. For analysis of variance both rows of entry number 17 were calculated as were all other entries which had two-row plots. Mean percent sucrose and mean weight of root for each of the mentioned F_1 hybrids were given on the basis of analysis of 20 one-row plots.

All the basic parental or hybrid populations, e.g., the F_1 $4n$ SLC 91 $\times$ $4n$ US 35/2, were grown for seed in isolation plots. To control possible chromosome deviations in every tetraploid population, seed was harvested from individual plants and individual progenies were planted in separate plots. Cases with noticeable chromosome disturbances were not observed in this experiment.

Table 1.—Origin of sugar beet populations and code number of entries.

Code number of entry	Population	Number of chromosomes	Symbol
	Series A—Tetraploid hybrids between self-sterile monogerm SLC 31 and US 35/2		
18	Population of monogerm self-sterile tetraploid SLC 31	36	P_1
19	Population of tetraploid US 35/2	36	P_2
17-2	F_1 hybrids between monogerm SLC 31 and US 35/2	36	F_1
4	Sib F_2 progenies between monogerm SLC 31 and US 35/2	36	F_2 Sib (US 35/2)
5	Open-pollinated F_2 progenies between monogerm SLC 31 and US 35/2	36	F_2 open pollinated
6	Backcross F_1 to monogerm parent SLC 31	36	F_1 to P_1
7	Backcross F_1 to US 35/2	36	F_1 to P_2
	Series B—Hybrids between self-fertile inbred line SLC 91 monogerm and US 35/2		
16	Tetraploid inbred SLC 91 monogerm	36	P_3
17-1	Tetraploid F_1 MS monogerm hybrid SLC 91 × US 35/2	36	MS F_1
11	Selfed S_1 tetraploid hybrid progenies (F_2) between monogerm SLC 91 and US 35/2	36	F_2 91 selfed
12	Open-pollinated F_2 progenies between monogerm SLC 91 and US 35/2	36	F_2 91 open pollinated
13	Backcross F_1 to monogerm parent SLC 91	36	F_1 to P_3
15	Diploid inbred SLC 91 monogerm	18	Diploid inbred
14	Selfed S_1 diploid hybrid progenies between diploid SLC 91 and diploid US 35/2	18	Diploid S_1
20	Triploid monogerm hybrid between diploid MS monogerm SLC 91 and tetraploid US 35/2	27	MS triploid
	Series C—Tetraploid hybrids between self-sterile monogerm 31 and US 22/3		
8	Sib F_2 progenies between monogerm SLC 31 and US 22/3	36	F_2 Sib (US 22/3)
9	Open-pollinated F_2 progenies between monogerm SLC 31 and US 22/3	36	F_2 US 22/3 open pollin.
10	Backcross progenies F_1 to monogerm parent SLC 31	36	F_1 US 22/3 to F_1
	Series D—Diploid and tetraploid populations originating from SLC 15 self-sterile monogerm		
1	Open-pollinated population of diploid SLC 15 monogerm	18	Diploid 15
2	Open-pollinated population of tetraploid SLC 15 monogerm	36	Tetraploid 15
3	Open-pollinated population of tetraploid SLC 15 monogerm	36	Tetraploid 15

Because seed of individual plants was tested separately, variability in different replications within a population was caused by environment and by a sampling variation of progenies composing a given population. Therefore, the number of replications for each population was increased to 20. Some populations (2*n* and 4*n* inbred SLC 91, 4*n* self-sterile monogerm SLC 31, 4*n* US 35/2, triploid hybrid 2*n* MS 91mm × 4 *n* US 35/2) were planted in 20 replications with seed of the same sample. The experiment was conducted at the Salt Lake City Station of the USDA.

Experimental design and analysis of variance for mean weight of root and sucrose percentage.

Twenty populations were planted in two-row plots doubly grouped into 20 replicates (Latin-square design) (Table 2). In each plot 50 plants were expected; in every population or block, 1000 plants (20 × 50) were expected. A total of 20,000 plants were expected in the experiment. In fact, 19,452 plants were actually harvested.

Mean percent sucrose for each plot was calculated from two samples containing 14 beets each. Mean weight of root for every plot was estimated by dividing weight of root from the whole plot by the number of plants in this plot.

Analysis of variance shows that population differences were highly significant for both percent sucrose and weight of root since the F ratio was 10.7 for percent sucrose and 11.9 for weight of root. These ratios are larger than the corresponding F value at the 1% point (Table 2). The F ratio between rows was small and not significant. The F ratio between columns was only one-third as large as the corresponding ratio for population but still significant and equaled 3.1 for weight of root and 5.6 for percent sucrose.

The value of the LSD for the weight of root equals 0.3066 pound at the 5% point and 0.4037 pound at the 1% point. For percent sucrose the value of the LSD will be correspondingly 0.523 percent and 0.6897 percent.

The values of the LSD for the weight of root and for percent sucrose do not differ essentially from the value of the least significant ranges or Duncan's new multiple range test, LSR. For the weight of root, at the comparison of two adjacent values of populations' yield, LSR equals 0.31, for 5 populations LSR equals 0.34, for 10 populations 0.37, for 16 populations 0.38, and for 20 populations 0.38 pound. Thus, even for the weight of root, the maximal value of LSR exceeds the value of LSD by 0.0754 pound only. For percent sucrose the value LSR equals 0.52 for 2 populations, 0.59 for 5 populations, 0.62 for 10 populations,

Table 2.—Mean squares, degrees of freedom and sources of variation in analysis of variance for mean weight of roots in pounds and for percent of sucrose in sugar beets.

	Degrees of freedom	Mean root weight (pounds)			Sucrose percent		
		Sum of squares	Mean squares	Variance ratio F	Sum of squares	Mean squares	Variance ratio F
Total	399	161.0760			489.3644		
Between columns	19	14.3485	0.7552	3.1078	76.0479	4.0025	5.6448
Between rows	19	8.5805	0.4516	1.8584	26.0929	1.9368	0.8320
Between populations	19	55.0363	2.8966	11.9202	144.7259	7.6172	10.7425
Residual	342	83.1107	0.2430	------	242.4977	0.7091	------

Table 3.—Sucrose and weight of root in sugar beet strains in diploid and tetraploid self-sterile SLC 15 monogerm and in diploid and tetraploid self-fertile inbred SLC 91 monogerm.

	Diploid		Tetraploid		Difference of ploidy levels	
	Weight (pounds)	Sucrose (percent)	Weight (pounds)	Sucrose (percent)	Weight (pounds)	Sucrose (percent)
SLC 15 monogerm self-sterile	2.7420	13.7400	------	------	------	------
Early-maturing progenies	------	------	3.0790	13.6700	+ 0.3370	— 0.0700
Late-maturing progenies	------	------	2.7640	13.7900	+ 0.0220	+ 0.0500
Progeny differences			0.3150	0.1200	------	------
SLC 91 monogerm self-fertile inbred	2.1030	13.9550	1.9215	14.0300	— 0.1815	+ 0.0750
Variety difference	0.6390	0.2150	1.1575	0.3600	------	------
			0.8425	0.2400	------	------
LSD	0.3066	0.5238				
MSD	0.4037	0.6897				

and 0.64 for 16 populations. For 20 populations LSR equals 0.65 percent sucrose, while LSD equals 0.52 percent.

Experimental Results

Sucrose and weight of root in monogerm diploid and autotetraploid self-sterile and self-fertile populations

Many tetraploid beet populations in the first generation after colchicine treatment showed, according to European data, a lower weight of root than the original diploids (35, 43, 73, 74, 86). The tetraploid components of the polyploid variety "Poly-Beta" showed a lower weight of root than diploid and triploid components of the same variety (37).

Variation of percent sucrose and weight of root in two monogerm strains obtained by colchicine treatment and propagated by different matings (self-sterile population SLC 15 and self-fertile inbred SLC 91) were studied in this experiment (Table 3). Plants composing the tetraploid population SLC 15 differed widely in the time of flowering, therefore, they were divided into two groups (each one containing an equal number of plants) according to the time of flowering. Seed was harvested separately from the plants of each group.

Doubling the chromosome number did not modify the percent sucrose in the self-fertile SLC 91 inbred or in the self-sterile population SLC 15. Both diploid and tetraploid self-sterile populations SLC 15 are characterized by a higher percent sucrose than the multigerm tetraploid US 35/2 and US 22/3 populations (Table 3).

Diploid and tetraploid inbreds of SLC 91 monogerm also exhibited the same percent sucrose but were significantly lower than the diploid and tetraploid self-sterile monogerm populations of SLC 15 in root weight. In diploids these differences in the weight of root reached 0.6390 pound and the value of MSD equaled 0.4037 pound. In tetraploids the difference in weight of root between two self-sterile populations and self-fertile inbreds equaled 0.8425 and 1.1575 pounds, respectively. Thus, big differences in the yield between self-sterile and self-fertile beets were maintained after colchicine treatment (Table 3).

In spite of this, several genotypes exhibited different reactions toward doubling of chromosome number. Diploid and tetraploid inbreds of SLC 91 do not differ significantly in root weight. A somewhat different reaction toward doubling of chromosomes occurred in a self-sterile population of SLC 15. A diploid population of SLC 15 did not show noticeable variability in terms

of flowering within the population, but the tetraploid population SLC 15 was not uniform in terms of flowering, therefore, we were obliged to test the progeny from early (C_1) and late (C_1) maturing plants separately. Monogerm progenies obtained from late-maturing tetraploid plants did not differ in the weight of root from the original diploid population of SLC 15. Tetraploid progenies obtained from early-maturing plants exceeded significantly in weight of root the original diploid population SLC 15 by 0.3370 pound (Table 3).

In such a way different genotypes from the same diploid population reacted differently to chromosome doubling. Therefore, it is not accidental that chromosome doubling causes a different reaction in different varieties relative to increase or decrease of weight of root. The effect of tetraploidy may be neutral, positive, or negative in different varieties. Different reactions of individual genotypes within a species to chromosome doubling is known also in other crops. For instance, in flax tetraploid races of the linseed oil type greatly increased their size, whereas the tetraploid races of the flax type decreased their size in comparison with corresponding diploids.

It may be theoretically expected that differences in size (consequently, in weight) between related diploids and tetraploids may occur in connection with the number of propagations of tetraploids. When a self-sterile panmictic population is propagated for several generations, the weight of root of its components may change from generation to generation and this appearance may be explained by the fact that equilibrium in different genes is not reached simultaneously in diploid and tetraploid populations.

A random mating of two mixed diploid panmictic populations, each homozygous in one allele, will always give 50% homozygotes and 50% heterozygotes. In the same mixed tetraploid self-sterile panmictic populations, only one generation will consist of 50% homozygotes and 50% heterozygotes. In succeeding generations the percent of heterozygotes will increase and the percent of homozygotes will decrease as follows: 50%, 22.2%, 15.43%, 13.44%, 12.81%, 12.60%, etc. (29). The number of homozygotes is rapidly reduced during the first generation and slows down until the stage of equilibrium is approached.

Equilibrium in tetraploids does not occur simultaneously for different genes because different genes exhibit different ratios in tetraploid segregation (chromosome and chromatid segregation). The rate of the approach to equilibrium is two-sevenths per generation for random chromatid segregation and one third for chromosome segregation (44).

Because many heterozygotes in beets, as in other self-sterile species, have selective advantage (12, 13, 14, 41, 42), fresh tetraploids propagated for several generations may improve their vigor and productiveness. Rasmusson (73) reported on this appearance by propagation of tetraploid beet populations.

In tetraploids under random mating, equilibrium is reached when gametes are produced in the proportion of n^2AA:2nAa:Iaa and the proportion of zygotes equals n^4AAAA:4n^3AAAa:6n^2AAaa: 4nAaaa:Iaaaa, where n is a ratio of dominant to recessive allelomorphs (29, 44).

Some other characters in beets show a more or less identical reaction when diploid strains are transformed into tetraploids, differing in percent sucrose or weight of root. This may be caused by the increase in the volume of the nucleus and the cell, a phenomenon manifested in beet tetraploids as well as in tetraploids of other crops. Therefore, tetraploid beets develop larger pollen grains than diploids (19, 79). Tetrapolids and triploids have more chloroplasts in stomata cells (6, 7, 62). The size of tetraploid multigerm and especially monogerm fruits is also much larger in tetraploids than in diploids.

Contrariwise, some other characters in tetraploids show a diminished size when compared to diploids. For instance, tetraploid beets develop shorter petioles, the seedstalks are shorter, although the stalks and leaves are thicker; the root in tetraploids does not branch as much as in diploids (therefore, the shape of the root is often better in tetraploids). Percent sucrose and weight of root are not characters showing identical reaction in all genotypes when turned into tetraploids. Interactions between percent sucrose, weight of root, and the level of ploidy are different for different genotypes in beets. Moreover, such interactions may change under different environment, which explains the relatively different productiveness of polyploid varieties in comparison with diploids in European countries, countries which differ in temperature and humidity (27, 28, 36).

The effect of chromosome doubling in corn is different between varieties and is unpredictable for several metric traits. In spite of this, the size of cell, pollen and earliness always show the same type of alteration caused by chromosome doubling (72). Differences in the manifestation of quantitative characters as a consequence of a reaction of a genotype toward chromosome doubling was observed also in tomatoes (16, 17) and in many other crops (40, 65, 66, 86, 89). Genetic cause of the difference in the manifestation of individual characters in different genotypes and species after chromosome doubling is unknown. There

are several hypotheses suggesting that the observed differences are caused by different phylogenetic development of a given species or races or different ontogenetic development of individual characters (17, 35, 40, 65, 66, 86, 89). The different reaction of individual genotypes and varieties from doubling of chromosomes is very important in beets. Further investigations may give helpful information for detecting sugar beet types with the most effective reaction to chromosome doubling.

Percent sucrose and yield in hybrids between tetraploid monogerm and multigerm self-sterile populations.

Weight of root in F_1 and F_2 hybrids.

The monogerm self-sterile population SLC 31 was crossed to two tetraploid multigerm populations, US 35/2 and US 22/3. The tetraploid US 35/2 showed a higher mean weight of root (2.8830 pounds) than the monogerm tetraploid SLC 31 (2.4860 pounds). The difference in yield between these two populations equals 0.3970 pound and is significant at the 5% level of probability (Table 4). The difference in sucrose between these two populations is even more significant because the percent sucrose in the monogerm tetraploid exceeds the percent sucrose in tetraploid US 35/2 by 1.1700 percent (while 1% equals only 0.6897) (Table 4). Differences in percent sucrose and in weight of root between these two tetraploid parents are as large as the differences in these characters in diploid varieties of different types (E and Z types).

The average weight of root of F_1 hybrids between these populations (SLC 31 and US 35/2) equaled 3.1235 pound. F_1 hybrids exceed the monogerm parental population (SLC 31) by 0.6375 pound with significance at the 1% level and the multigerm population US 35/2 by 0.2405 pound, which is not a significant difference.

The calculated mean weight of roots of the F_1 hybrid is

$$\frac{2.4860 + 2.8830}{2} = 2.6845 \text{ pounds.}$$

This value is 0.4390 pound lower than that obtained in the experimental test.

Heterosis for weight of root is well known in diploid beets. Heterosis has not yet been described for tetraploid beets, however, in this experiment heterosis in weight of root was observed also after hybridization of two tetraploid sugar beet populations. The effect of heterosis was established also in the hybridization of tetraploid rye populations. The yield of F_1 hybrids in this case significantly exceeded the yield of the parents by 18.4% and 19.8% (64, 65). In *Antirrhinum* some diploids exhibit

Table 4.—Sugar beet tetraploid hybrids between self-sterile monogerm strain SLC 31 and US 35/2.

Code number of entry	Population	Mean root weight	Mean sucrose
		(pounds)	(percent)
18	Monogerm self-sterile SLC 31-P_1	2.4860	13.7050
19	US 35/2 - P_2	2.8830	12.5350
17-2	$F_1 = P_1 \times P_2$	3.1235	12.9150
4	F_2 Sib	2.9240	13.3700
5	F_2 open pollinated	2.7995	13.3950
6	Backcross F_1 to P_1	2.6370	13.5550
7	Backcross F_1 to P_2	3.0060	12.5650
LSD at 5% point		0.3066	0.5238
MSD at 1% point		0.4037	0.6897

heterosis. The effect of heterosis is repeated also after hybridization of analogous genotypes at the tetraploid level (91).

As a rule heterosis in the weight of root observed in the F_1 hybrids in diploid beets cannot be maintained in the F_2 generation (81). Heterosis in diploid F_2 hybrids usually falls somewhere between the F_1 and mid-parent values.

In connection with manifestation of heterosis in the F_1 tetraploid self-sterile hybrids, it is important to study weight of root in F_2 hybrids obtained after sibbing or open-pollination of numerous F_1 hybrid families (Table 4).

The differences in weight of root between F_1 and F_2 hybrids is only 0.1995 pound, which is not significant. F_2 hybrids similar to F_1 showed good yield, exceeding significantly the weight of root in the monogerm parent by 0.4380 pound. The F_2 hybrid as well as the F_1 hybrid showed a higher weight of root than the second tetraploid parent US 35/2, but in both cases this excess was not significant.

The observed weight of root in F_2 hybrids obtained by sibbing equaled 2.9420 pounds (Table 5). This yield almost equaled the calculated yield, according to the formula $\frac{P_1 + P_2 + 2F_1}{4}$ = 2.9040 pounds. This formula is used for the calculation of a theoretical mean for a genetic model when assumptions are made for a normal diploid meiosis and segregation of only those genes which show an additive type of reaction (i.e., the absence of all types of non-allelic gene action, multiple alleles, linkage, selection, and polysomic heredity) (18, 32, 34, 44, 58, 68). By using the above mentioned, or other similar formulae, it is possible to

determine the distinctions in the individual characters among diploid and tetraploid hybrids. However, such distinctions might be caused by factors other than the differences in the type of reaction of the additive genes, such as the different rate of increasing homozygosity in diploid v.v. tetraploid hybrids.

When numerous diploid F_2 hybrids (obtained from crosses of different sugar beet genotypes or from the hybridization of sugar beets to mangels or red table beets) are studied, the calculated weight of root of F_2 hybrids is always higher than that observed in experiments. This indicates that in diploid beets, genetic control of weight of root is conditioned mainly by the reaction of genes which do not show an additive type of reaction.

Propagation of tetraploids by sib mating of a few generations cannot change their genetic structure because genetic structure is determined by the natural and artificial selection and by the method of mating (11, 30, 55, 56, 57, 59). Therefore, F_2 tetraploid hybrids possess similar genetic mechanism which controls vigor in all outbreeding species and which is based on selective advantage of heterozygotes in polygenic traits (12, 13, 14, 18, 41, 42). In such a case, differences between observed and calculated yields in diploid and tetraploid F_2 or backcross hybrids is conditioned not by alteration of the relative value of heterozygotes and homozygotes in diploid and tetraploid F_1 and F_2 generations and by the highly-increased role of additive elements in tetraploid genotypes, but mainly by the effect caused by propagation of tetraploid hybrids, i.e., by tetrasomic heredity itself. In the given case this difference was conditioned by slower elimination of heterozygotes in tetraploids than in diploids.

In diploids, a heterozygous population approaches the homozygous condition in about ten generations by selfing and in thirty generations by brother-sister mating. In tetraploids, 10 generations of sib-mating are needed to halve the proportion of heterozygotes and 31 generations are needed to reach 90 percent of homozygosity (1, 31). The following data give a more exact idea of the proportion of zygotic types in different generations of an autotetraploid propagated by the sib method (1):

Type of zygotes	Percent of different types of segregates							
	F_1	F_2	F_3	F_4	F_5	F_{10}	F_{20}	F_{30}
Simplex and triplex (Mm^3 and M^3m)	00	44	49	49	47	34	15	7
Duplex (M^2 m^2)	100	50	41	35	31	19	9	4
Homozygotes (M^4 and m^4)	0	5.6	10	16	22	47	76	89

The approach to homozygosity in tetraploids is slow. By sib-mating in the F_2 only 2.8% recessives or complete dominants appear for every locus. Therefore, the effect of heterosis observed in F_1 tetraploid hybrids was maintained at a higher level in the tetraploid F_2 population than it usually was in corresponding diploid hybrids. The effect of heterosis for weight of roots in diploid beets is conditioned by genes which usually do not show an additive type reaction. In tetraploids this reaction of genes is not "fixed" by sib-mating because of the slow decrease in heterozygosity.

Another interesting fact observed in the study of yield in F_2 tetraploid hybrids was that the weight of root in the F_2 obtained by sib-mating and by open pollination was practically the same (Table 4). The inbreeding effect caused by sib-mating was so insignificant that it did not decrease the yield of roots in the F_2 sib population in comparison with the open-pollinated F_2 progenies.

The fact that the inbreeding effect by one sib-mating in tetraploids does not decrease the weight of root in comparison with open pollination was confirmed also by another tetraploid hybrid in the given experiment. The same tetraploid monogerm population SLC 31 was crossed with tetraploid population US 22/3. Tetraploid US 22/3 is characterized by a lower weight of root than tetraploid US 35/2. F_2 hybrids between SLC 31 and US 22/3 were lower in yield than the F_2 hybrids SLC 31 and US 35/2 (Table 5).

The weight of root in F_2 hybrids obtained by sib-mating of F_1 (SLC 31 $\times$ US 35/2) equaled 2.9240 pounds and of F_2 hybrids obtained by sib-mating of F_1 (SLC 31 $\times$ US 22/3) 2.5205 pounds. The difference in weight of root between these F_2 populations was 0.4035 pounds, which is significant.

Also, the second F_2 hybrid did not lose yield after one sibbing in comparison with the yield of the F_2 obtained under open pollination (Table 5). The yield of roots in the F_2 after sibbing equaled 2.5205 pounds and the yield of the roots in F_2 after open pollination was 2.5755 pounds. Thus, for two different F_2 tetraploid hybrids sib-mating used once did not decrease the yield of root in comparison with open pollination. In diploid F_2 hybrids the decrease in yield after sib-mating in comparison with open pollination was usually observed (81).

Weight of root in backcross hybrids.

Backcross tetraploid hybrids between monogerm and multigerm beets are as interesting for study as the corresponding diploid hybrids. Therefore, in all the hybrid combinations

Table 5.—Sugar beet tetraploid F_2 and backcross hybrids between self-sterile monogerm SLC 31 crossed to US 35/2 and to US 22/3.

Population	Mean root weight (pounds)			Mean sucrose (percent)		
	Hybrids: SLC 31 monogerm to			Hybrids: SLC 31 monogerm to		
	US 35/2	US 22/3	Differences	US 35/2	US 22/3	Differences
F_2 sib	2.9240	2.5205	0.4035*	13.3700	12.6100	0.7600**
F_2 open pollinated	2.7995	2.5755	0.2240	13.3950	12.6050	0.7900**
Difference	0.1245	0.0550	.....	0.0250	0.0050	.....
Backcross F_1 to monogerm parent SLC 31	2.6370	2.6375	0.0005	13.5550	13.5200	0.0350
Backcross F_1 to multigerm parent US 35/2 and US 22/3	3.0060	.....	.....	12.5650	.....	.....
Difference	0.3690*	.....	.....	0.9900**	.....	.....
LSD	0.3066			0.5238		
MSD	0.4037			0.6897		

studied in this experiment, backcross hybrids obtained from crosses of F_1 to monogerm parents, were included. At the same time only one backcross hybrid derived from F_1 crosses back to the multigerm parent was studied (SLC 31 × US 35/3) (Table 5).

Backcross hybrids to the monogerm parent are of special interest because of the possibility of obtaining from them a "second backcross," which, according to Fisher (22), is extremely powerful in polysomic inheritance. The importance of the "second backcross" for polyploids, contrary to backcross diploids, is that the first backcross in tetraploids does not allow one to distinguish between the offspring from gametes Ab-aB and AB-ab. The genotypes of such gametes may be recognized by the performance of a second backcross by crossing to a multiple recessive in two successive generations so that each gamete is recognized, not by the appearance of a single individual, but by a frequency distribution observed in a family. Besides this, backcross hybrids to the monogerm parent are important also from the point of view of selection for monogerm character because of the increased number of monogerm segregates in comparison with their number in tetraploid F_2 hybrids.

The ratio of multigerm to monogerm plants in F_2 tetraploid monofactorial hybrids may be affected by several cytological variables (8, 21, 24, 26, 29, 53, 54, 67). This ratio depends upon chiasma formation between centromere and the locus studied. Because of different distances between the centromere and different genes (loci), the monofactorial segregation ratio may vary from 35:1 by chromosome assortment to 20.8:1 by chromatid assortment. The percent of monogerm segregates in F_2 tetraploid hybrids ($4n$ monogerm × $4n$ multigerm) varied in our experiments within the indicated limits. (A special paper will be devoted to the inheritance of the monogerm character in tetraploid beets.)

A backcross to the recessive increases strikingly the number of recessive segregates in the following generation in comparison with their number in the F_2. According to Haldane (29), the ratio of dominants to recessives in the backcross, when different heterozygous types are crossed with recessive, will change as follows: by crosses aaaa × AAaa, 5:1; by crosses aaaa × Aaaa, 1:1. A selfed tetraploid F_2 population will produce only 2.8% of homozygous recessive lines and 22.2% of lines segregating in the ratio 3:1. Fifty percent of F_3 lines will segregate as the F_2 population. About 30% of F_3 lines will be practically useless for selection of recessive characters, because they will segregate the

recessive to dominant plants in the ratio 1:784, or they will be constantly dominant.

After selfing F_1, the ratio of segregation in F_2 (obtained from two homozygous lines differing in two non-linked dominant factors) is 9:3:3:1 in diploids. This ratio in tetraploid heredity alternates in F_2 to 1225:35:35:1, and in tri-hybrids the ratio will change to 1 recessive : 45,000 dominants. The best method of obtaining homozygotes at both loci in F_3 consists in obtaining selfed progenies from all F_2 plants carrying recessive homozygotes for one allele (29). In the cases when it is impossible to self F_2 tetraploid hybrids, the method of sib-mating is usually used; but sib-mating, low in effectiveness even for diploid heredity, appears to be ineffective for tetraploids. In such cases the backcross method remains practically the only possible way.

However, our experiments showed that the sib-method is satisfactory for the segregation of monogerm plants in tetraploids because all monogerm F_2 segregates produce F_3 sib lines which do not segregate more multigerm plants. Plants of Mmmm genotype developed multigerm fruits.

A study of the weight of root in backcross hybrids showed that hybridization also causes changes in tetraploids. Hybridization of F_1 hybrids (SLC 31 $\times$ US 35/2) with both parents produced two backcross populations differing significantly from each other (Table 6). The difference in weight of root between them equaled 0.3690 pound. This difference in weight of root between two backcross hybrids is caused mainly by a drastic reduction in yield of backcross hybrids with the monogerm parent. This backcross hybrid is significantly lower in productiveness than the F_1 hybrids. In another backcross hybrid from crosses to multigerm US 35/2 the weight of root equaled 3.0060 pounds. This yield differs insignificantly from the yields of the F_1 hybrid (3.1235 pounds), the F_2 hybrid (2.9240 pounds), and the backcross recurrent parent US 35/2 (2.8830 pounds). At the same time, weight of root of this backcross hybrid significantly exceeded (at the 1% point) the yield of the monogerm SLC 31 parent (the difference equaled 0.5200 pound).

In tetraploid sugar beet hybrids not only the observed yield of roots in F_2 but also the observed yield of roots in both backcross hybrids does not differ from the calculated yield of roots (Table 6). However, even in the presence of this interrelation between observed and calculated values, there is no reason to think that weight of root in tetraploid beets increases significance of genes causing the additive type of reaction. This problem is highly important because the presence of additive types of

Table 6.—Mean weight of root in sugar beet tetraploid hybrids between self-sterile SLC 31 monogerm and US 35/2.

Population	Observed mean	Calculated mean	Difference between observed and calculated	Formula to which weight of root was calculated	Significance of differences
Hybrids SLC 31 × US 35/2:					
Backcross F_1 to monogerm SLC 31	2.6370	2.80475	0.16775	$\frac{P_1 + F_1}{2} \pm \frac{\sqrt{(\Sigma P_1)^2 + (\Sigma F_1)^2}}{4}$	Not significant
Backcross F_1 to multigerm US 35/2	3.0060	3.0035	0.00275	$\frac{P_2 + F_1}{2} \pm \frac{\sqrt{(\Sigma p_2)^2 + (\Sigma F_1)^2}}{4}$	do.
F_1 SLC 31 × US 35/2	3.1235	2.6845	0.4390	$\frac{P_1 + P_2}{2} \pm \frac{\sqrt{(\Sigma P_1)^2 + (\Sigma P_2)^2}}{4}$	Not significant
F_2 SLC 31 × US 35/2 (sib)	2.9240	(a) 2.9040	0.0200 (a)	$\frac{P_1 + P_2 + 2F_1}{4} \pm \frac{\sqrt{0.5(\Sigma P_1)^2 + 0.5(\Sigma P_2)^2 + (\Sigma F_1)^2}}{4}$	do.
		(b) 2.8215	0.1025 (b)	$\frac{b_1 + b_2}{2} \pm \frac{\sqrt{(\Sigma b_1)^2 + (\Sigma b_2)^2}}{4}$	
P_1 SLC 31 monogerm	2.4860				
P_2 US 35/2	2.8830				

heredity usually indicates that the given character may be fixed in the homozygote in the following generations by selfing. Stabilization of yield in the following generations at a higher level is conditioned, as it was indicated, by the peculiarities of polysomic heredity. On the other hand, yields observed in F_1 and F_2 tetraploid hybrids will decrease relatively slowly in the following four generations by sib-mating because of delayed segregation of deleterious homozygotes. In these four generations by sib-mating the percent of homozygotes will not exceed 12. It means that there will be only one half the homozygotes appearing in the diploids after one selfing.

Percent sucrose in hybrids.

The monogerm self-sterile tetraploid SLC 31 significantly exceeds in percent sucrose the tetraploid US 35/2 (Table 4). F_1 hybrids between these two tetraploids showed intermediate sucrose. The percent sucrose in F_1 hybrids was 12.9450, which differed only slightly from the mean percent sucrose of the parents (13.1200) (Tables 4 and 7).

In F_2 hybrids, obtained by sib-mating, the percent sucrose was a little higher than in the F_1 and equaled 13.3700. However, this difference in percent sucrose between F_1 and F_2, equaling 0.4250%, does not reach the 5% point of significance.

In such a way the percent sucrose obtained in F_2 tetraploid hybrids (13.3700%), as well as the percent sucrose in F_1 hybrids (12.9450%), does not differ significantly from the mean sucrose of the parents (13.1200%). A similar type of inheritance of percent sucrose was often observed in diploid sugar beet hybrids. In diploid hybrids, which show almost the same percent sucrose in F_1, F_2, and the middle parent $\frac{(P_1 + P_2)}{2}$, the backcross hybrids derived from crosses to both parents differed very much from each other. This has been shown for many diploid hybrids derived from parents differing in percent sucrose.

The same relationship in percent sucrose in parental strains in F_1, F_2, and both backcross hybrids is observed in tetraploids (Tables 4 and 7). In this case, the percent sucrose in backcross hybrids to the monogerm parent and in backcross hybrids to the multigerm parent differed very much. Recurrent hybridization of F_1 hybrids to the monogerm population SLC 31, i.e., to the higher sucrose parent, increased the percent sucrose in the hybrids to 13.5550 (Tables 4 and 7). This backcross population exceeded significantly by 0.9900% the other backcross population obtained from crosses to the lower sucrose second parent (Tables 4 and 7).

Table 7.—Sucrose percent in sugar beet tetraploid hybrids between self-sterile SLC 31 monogerm and US 35/2.

Population	Observed mean	Calculated mean	Difference between observed and calculated	Formula to which percent sucrose was calculated	Significance
Backcross F_1 to monogerm SLC 31	13.5550	13.3250	0.2300	$\frac{F_1 + P_1}{2} \pm \frac{\sqrt{(\Sigma P_1)^2 + (\Sigma F_1)^2}}{4}$	Not significant
Backcross F_1 to multigerm US 35/2	12.5650	12.7400	0.1750	$\frac{F_1 + P_2}{2} \pm \frac{\sqrt{(\Sigma p_2)^2 + (\Sigma F_1)^2}}{4}$	do.
F_1 SLC 31 × US 35/2	12.9450	13.1200	0.1750	$\frac{P_1 + P_2}{2} \pm \frac{\sqrt{(\Sigma P_1)^2 + (\Sigma P_2)^2}}{4}$	do.
F_2 (SLC 31 × US 35/2) sib	13.3700	(a) 13.0325	0.3375	$\frac{P_1 + P_2 + F_2}{4} \pm \frac{\sqrt{0.5(\Sigma P_1)^2 + 0.5(\Sigma P_2)^2 + (\Sigma F_1)^2}}{4}$	do.
		(b) 13.0600	0.3100	$\frac{b_1 + b_2}{2} \pm \frac{\sqrt{(\Sigma b_1)^2 + (\Sigma b_2)^2}}{4}$	do.
P_1 SLC 31 monogerm	13.7050				
P_2 US 35/2	12.5350				

In these tetraploid hybrids, sucrose observed in both backcross hybrids was very close to the sucrose calculated according to the formula where percent sucrose of the F_1 and a corresponding parent was divided by 2.

The percent sucrose observed in the F_2 did not differ from the calculated percent. Percent sucrose was calculated according to the formula $\frac{(b_1 + b_2)}{2}$ and equaled 13.0600% which did not differ significantly from the sucrose of 13.3700% observed in F_2 (Table 7).

Thus, the percent sucrose in tetraploid F_1, F_2, and backcross hybrids modified in such a way that in any case a deviation could not be stated from the limits usually observed in many diploid hybrids in which the percent sucrose in $F_1 = F_2 = \frac{P_1 + P_2}{2}$.

In our self-sterile hybrids, phenotypical differences between diploids and tetraploids in different generations by sib-mating were manifested only for weight of root, not for percent sucrose.

Two F_2 hybrid combinations and corresponding backcross hybrids from crosses of F_1 to the monogerm parent were studied. Both hybrid combinations derived from hybridization of the same tetraploid population (SLC 31) to multigerm populations (US 35/2 and US 22/3) differed greatly in percent sucrose. This difference in sucrose of the multigerm parent was evident also in F_2 hybrids obtained from sibbing and from open pollination of the F_1.

Table 8.—Percent sucrose in hybrids between SLC 31 × US 35/2 and SLC 31 × US 22/3.

Hybrid	F_1	F_2 sib	F_2 open pollinated	Backcross To mono-germ	Backcross To multi-germ
Monogerm SLC 31 × US 35/2	12.9450	13.3700	13.3950	13.5550	12.5650
Monogerm SLC 31 × US 22/3	.....	12.6100	12.6050	13.5200	.....
Difference	.....	0.7600	0.7900	0.0350	.....
LSD		0.5238			
MSD		0.6897			

Hybrids with a higher sucrose parent (US 35/2) showed significantly higher sucrose. On the other hand, both hybrid combinations when crossed back to the high sugar recurrent parent (monogerm) increased their percent sucrose.

Thus, in contrast to comparatively little changes in percent sucrose or in weight of root in different generations of tetraploid hybrids by propagation *inter se*, the effect of hybridization of F_1 with different varieties or backcrosses to different parents is evident.

Hybrids between tetraploid self-fertile monogerm inbred SLC 91 and multigerm tetraploid population US 35/2

Weight of root in F_1 tetraploid and triploid hybrids.

It was established by experiments compatible with those of H. Savitsky that the self-fertile tetraploid monogerm inbred line SLC 91 (as well as other tetraploid inbreds), when crossed to different tetraploid self-sterile strains, produced self-fertile F_1, F_2, F_3, F_4, and subsequent generations. On the other hand, tetraploid multigerm varieties US 35/2 and US 22/3 remained self sterile like their original diploid ancestors.

Therefore, it is very desirable to incorporate in different tetraploid populations the gene of self fertility derived from the original monogerm beet SLC 101. Only in this way is it possible to study the effect of inbreeding in different tetraploid hybrids because sib-mating shows a very low effect by polysomic heredity.

In comparison with the tetraploid self-sterile population US 35/2, the tetraploid inbred SLC 91 showed a higher sucrose and a very reduced weight of root. The weight of root in tetraploid SLC 91 equaled 1.9215 pounds; the weight of root in US 35/2 was 2.8830 pounds. The difference between these two tetraploid strains was significant at the 1% level (0.9615 pound) (Table 9). The weight of roots in F_1 hybrids between these two tetraploids was 3.2135 pounds (Table 9).

These F_1 tetraploid hybrids between SLC 91 × US 35/2 exceeded in weight of root not only the calculated mean yield of both parents, 2.4022 pounds, but also the yield of every individual parent (Table 9). Thus, heterosis in the weight of root was observed in F_1 tetraploid hybrids.

F_1 hybrids between SLC 91 and US 35/2 yielded more than the F_1 hybrid between self-sterile populations SLC 31 × US 35/2. Crow (9) and Falconer (18) indicated that an increase in vigor in hybridization depends on the presence of a large number of homozygous recessive loci in the parents. The manifestation of higher vigor in hybrids between the inbred line SLC 91 and US 35/2 than in the hybrid SLC 31 with US 35/2 may be explained from this point of view by the higher number of homozygous loci in SLC 91.

Table 9.—Sugar beet hybrids between self-fertile monogerm inbred line SLC 91 and US 35/2.

Code number of entry	Population	Mean root weight	Mean sucrose
		(pounds)	(percent)
	A. Tetraploid populations		
16	Inbred SLC 91 monogerm - P_3	1.9215	14.0300
19	US 35/2 - P_2	2.8830	12.5350
17-1	F_1 - $P_3 \times P_2$	3.2135	13.0400
11	F_2 selfed (S_1)	2.5435	13.1950
12	F_2 open pollinated	2.6155	13.6550
13	Backcross F_1 to P_3	2.0435	14.9100
	B. Diploid populations		
15	Inbred SLC 91 monogerm	2.1030	13.9550
14	SLC 91 mm × US 35/2 selfed (S_1)	1.9835	14.3750
	C. Triploid hybrid		
20	2*n* MS SLC 91 mm × 4*n* US 35/2	3.2180	13.4850
LSD at 5% point		0.3066	0.5238
MSD at 1% point		0.4037	0.6897

The production of self-fertile tetraploids makes possible the application of inbreeding and the subsequent selection for combining ability at the triploid and tetraploid levels. Heterosis in diploids, as well as in polyploids, remains a central problem in sugar beet breeding. Therefore, one of the main reasons for the application of polyploidy in sugar beet breeding is the possibility of obtaining hybrid vigor in triploid hybrids.

In many species, a genetic barrier was demonstrated between diploids and the autotetraploids derived from them. In corn (71), rye (51), *Lycopersicum* (10, 46), and *Datura stramonium* (4) diploids do not cross with tetraploids or produce inviable hybrids. In beets, diploids crossed with tetraploids easily when planted together and vice versa.

Peto and Boyes (69) first indicated in 1940 that triploids had an advantage over diploids. Later this advantage was noticed in almost all the investigations in different countries (27, 35, 36, 37, 60, 83, 87, 92). Knapp (35) states that "Generally speaking, however, there can be no doubt that, in the first place, triploids are superior both to diploids and to tetraploids." Knapp considers that doubling of the chromosome number in tetraploids disturbs the physiological harmony inherent in the genetical constitution

of the diploids. On the other hand, according to Knapp, an increase in the number of genomes in triploids makes possible an additional heterosis effect. It is more difficult for the breeder to obtain tetraploid strains than diploids having the same performance. In principle, however, this must be possible, and it probably will be only a question of time as to when such tetraploids will be created.

In this experiment only one triploid hybrid with the same gene pool as the diploid and tetraploid hybrids (SLC 91 × US 35/2) was studied. This triploid hybrid differed from F_1 tetraploid hybrids in that the female parent involved in hybridization was the diploid inbred SLC 91. Triploid hybrids showed the greatest root weight in the experiment (3.2180 pounds) and also a high sucrose percent (13.4850) (Table 9). The monogerm triploid produced a significantly higher yield than the higher yielding parent US 35/2 (difference of mean 0.3350 pound) and showed at the same time a significantly higher percent sucrose (difference of mean 0.9500%). Therefore, for the same gene pool, the triploid level favored in these beets a better expression of the polygenic balance of sucrose and root weight than the corresponding tetraploid level.

The genetic structure of heterozygosity is dissimilar in diploids and tetraploids. A diploid may have for each allele only one type of heterozygotes (Aa). A tetraploid has three different kinds of heterozygotes for every locus, depending on the number of recessives and dominants in the zygote: triplex AAAa, duplex AAaa, simplex Aaaa.

In beets, at many loci, these relations are still more complicated because of the presence of multiple alleles which are already known for several beet characters. In such a case, for instance, in the triplex, all three dominant genes belonging to one locus may be represented by three different genes of one multiple allele.

Triploids for every digenic locus (i.e., in the absence of a multiple allele) will have two types of heterozygotes (AAa and Aaa). In such a way genic balance and interrelation between dominants and recessives in heterozygotes appear to differ at different ploidy levels. Something common in the genic balance of heterozygotes may be noticed in diploids (Aa) and in tetraploids (AAaa) only, and only for digenic loci (not for multiple alleles). Triploids possess a completely new genic balance for every heterozygous locus, which is not peculiar to diploid heredity.

Thus, genetic control of heterosis in triploids is determined by the action of heterozygotes of different genetic structure,

namely, AAa and Aaa, which are not identical to diploid heterozygotes Aa. This constitutes the main difference in physiological significance of gene relations in triploid genetics in comparison with diploid and tetraploid heredity.

A shift of diploid genetics to tetraploid may not increase the level of heterozygosity in F_1 hybrids derived from the same lines because all heterozygous loci in diploids remain the same in tetraploids. Only by special selection of tetraploid hybrids or by the selection of tetraploid lines for combining ability can tetraploid hybrids with a higher degree of heterozygosity than the original diploids be obtained. Triploid hybrids always possess a new genic balance for all heterozygous loci. Triploid heredity is thus able to modify genetic reaction of the most valuable part of the genotype in plants produced by outbreeding, namely, its heterozygosity. In other words, triploid heredity modifies the mechanism which directly controls the phenomenon of heterosis itself. Such changes caused by triploid heredity concern intra- and also inter-allelic reaction of genes.

A shift from the usual genic balance within a heterozygote itself, i.e., from 1:1 to 2:1, or 1:2 in triploids, may increase or decrease the genetic or physiological difference in the action of recessive and dominant genes. By testing for combining ability, triploids may be selected in which twice as many biochemical substances will be produced for dominant genes in relation to recessive if compared to their diploid ancestors. In such cases a genetic difference in the action of genes within an allele will be increased. Difference in the biochemical substances between 2 genes within an allele represents just a factor causing true heterosis (euheterosis) (13, 14).

Weight of root in F_2 tetraploid hybrids.

A study of the grade of depression in quantitative characters in selfed tetraploids is of great interest. For this study, F_1 hybrids between SLC 91 × US 35/2 were selfed and F_2 selfed seed obtained (Table 9). Mean weight of roots in the F_2 (S_1) hybrids equaled 2.5435 pounds, i.e., 0.6700 pound lower than in F_1 hybrids from which they descended.

A reduction in yield by 0.6700 pound resulted after one selfing of F_1 tetraploid hybrids. This indicates that sugar beets are very sensitive to the alteration of the grade of heterozygosity and that the effect of heterosis may fall down even at a relatively slow increase of homozygosity which occurs in S_1 by tetraploid heredity.

Let us be reminded that by one sib-mating of self-sterile F_1 hybrids (SLC 31 × US 35/2) a reduction of the mean weight

of roots in F_2 in comparison with F_1 equaled only 0.1995 pound (Table 4). This reduction in yield caused by one sibbing was so small that it was statistically insignificant. Thus, a negative effect of very low inbreeding, caused by one sibbing in tetraploids, could not be established significantly. But when the intensity of inbreeding increased after one selfing of tetraploids, the difference between yield in F_1 and F_2 (S_1) generations was significant.

It is important to trace the degree of depression caused by inbreeding in S_1 tetraploids in comparison with the diploids. In this experiment these were tested along with the F_2 (S_1) hybrids obtained after one selfing of diploid hybrid SLC 91 to US 35/2 (Table 9).

The yield of roots in diploid S_1 hybrids (1.9835 pounds) and tetraploid S_1 hybrids (2.5435 pounds) differed significantly, and both S_1 hybrids differed significantly from the sib-progeny (2.9240 pounds).

The mean weight of root in diploid F_2 hybrids obtained after one selfing was 0.5600 pound lower than the mean weight of roots in corresponding tetraploid selfed hybrids. These data indicate that selfing decreases the weight of root in tetraploids to a higher degree than sib-mating. Such a decrease occurred in tetraploids to a smaller degree than in corresponding diploid hybrids.

In sib-mating, as in selfing S_1, the degree of modification of weight of root from F_1 to F_2 in tetraploids is dissimilar to that in diploids (Table 10). The same is indicated also by calculated values for weight of root in F_2 tetraploids obtained after selfing according to the formula $\frac{P_1 + P_2 + 2F_1}{4}$. According to this formula, the calculated mean weight of roots must equal 2.8079 pounds. The weight of roots in S_1 tetraploids observed in this experiment equaled 2.5435 pounds. The difference between observed and calculated yields is not significant (Table 10). In diploids S_1 the reduction in yield in comparison to heterosis in F_1 is always very noticeable and its significance is easily proven, even in the experiments with lower accuracy.

In tetraploids, even by selfing, the inbreeding effect expressed in weight of roots increases much slower than in diploids. This is conditioned mainly by the slower increase in homozygosity by the selfing of tetraploids.

Demolition of heterozygotes in selfed tetraploids at random chromosome assortment occurs in different generations as follows:

in F_1—100% heterozygotes, in F_2 -91%, in F_3—80.5%, in F_4 - 67.44%, in F_5%56.25%, in F_6 46.85%. After five generations of selfing, a tetraploid hybrid population will carry 26.6% recessives, i.e., almost as much as a diploid population carries after one selfing. The percent of heterozygotes after self-fertilization decreases in a diploid at the rate of 0.5 while in a tetraploid because of random chromosome distribution this coefficient equals only 0.83 for each generation (1, 29). By this random chromosome segregation in tetraploids, heterozygotes disappear quite slowly. This process will be especially delayed if complete homozygotes of aaaa type are low in viability or lethal, as may be expected for many defective recessive genes (32).

In random assortment of chromatids, the proportion of heterozygotes by inbreeding will increase rather fast, but also in this case homozygotes will grow very slowly if compared to diploids (26, 54, 77). With maximum chromatid segregation only 4.6% recessives will occur in F_2 (AAAA, 4.6%; AAAa, 24.5%; AAaa, 41.8%; Aaaa, 24.5%; aaaa, 4.6%) (47).

A pure chromosome assortment or a pure chromatid assortment is of rare occurrence for the majority of genes. Therefore, for the majority of genes responsible for the hereditary variations in the weight of root, a segregation intermediate between these extreme types must be expected.

It is important from the practical point of view that tetrasomic inheritance modifies the significance of a different type of mating for the weight of root as well as for some other characters. Selfing applied to inbreeding produces almost the same effect as sib-mating in diploids. Therefore, tetraploidy offers new possibilities for the alteration of the reproduction system in sugar beet tetraploids. This leads to a re-evaluation of the effect of the action of the gene of self fertility in the breeding of tetraploids. In contrast to diploid beets, the use of inbreeding is practically impossible in the breeding of self-sterile tetraploids (sib-mating is not effective). It is necessary to include the gene of self fertility in the tetraploid populations destined for inbreeding (for instance, to obtain monogerm male-sterile strains) with the purpose of making use of heterosis. The gene of self fertility itself, although influencing the characters in the same way but only slowly as in diploids, does not produce in the first generations of inbreeding such a negative effect on vigor of tetraploids as in diploids. Therefore, tetraploid inbreds in the same number of inbred generations are often more vigorous than corresponding diploid inbreds of the same gene pool Therefore, it is possible

to use in the breeding program more tetraploid than diploid inbred lines.

The rate of increase of homozygosity in tetraploids may be accelerated by backcrossing to parental homozygous inbred lines. In the backcross of a tetraploid F_1 hybrid with an inbred line, homozygosity increases faster than after segregation in an S_1 tetraploid. Therefore, when F_1 hybrids were crossed back to the monogerm inbred line SLC 91, a decrease in yield was greater than in the S_1 generation (Table 10). In a population obtained after such a backcross, the mean root weight was 0.5000 pound lower than in the S_1 and 1.1700 pounds lower than in the F_1. A large decrease in yield of backcross hybrids with inbred lines showed that the phenotypical expression of certain homozygote alleles in tetraploid beets can be even greater than the same effect in diploid beets.

For the improvement of self-sterile diploid sugar beets at the majority of the breeding stations, sib-mating is largely used; self-fertile beets are not used in many cases because of too large a depression caused by inbreeding and the necessity of developing male-sterile equivalents. It it more convenient to use selfing in a breeding program with tetraploids because the bagging of one plant excludes crossing. After 3 to 5 generations of selfing, tetraploid inbred lines are propagated, as well as diploids, in isolated plots where tetraploid plants may intercross within an inbred line, a method also used for the propagation of diploid inbreds. Similar to sugar beets, tetraploids in other species also showed better resistance to the inbred depression. For instance, tetraploid self-fertile lines of rye did not reach their maximum value of depression fall, even after 10 generations of selfing (51, 52).

Percent sucrose in hybrids.

Tetraploid monogerm inbred line SLC 91 is higher in sugar than the tetraploid US 35/2. The difference in percent sucrose between these two strains equaled 1.4950% and was highly significant (Table 9).

The calculated mean percent $\frac{(P_1 + P_2)}{2}$ for both parents was 13.2825%. Percent sucrose actually observed in F_1 hybrids was a little lower than the calculated sucrose of the mean of the parents (13.0400%).

The calculated sucrose of the middle parent in diploids is often close to the sucrose observed in F_1 hybrids derived from crosses of high- and low-sugar parents (81). Usually S_2 to S_3 lines

Table 10.—Mean weight of roots in sugar beet tetraploid self-fertile populations.

Population	Observed mean	Calculated mean	Difference between observed and calculated	Formula to which weight of root was calculated	Significance
F_1 SLC 91 × US 35/2	3.2135	2.4022	0.8113	$\frac{P_1 + P_2}{2} \pm \frac{\sqrt{(\Sigma P_1)^2 + (\Sigma P_1)^2}}{4}$	Significant
F_2 (S_1) selfed	2.5435	2.8079	0.2644	$\frac{P_1 + P_2 + 2F_1}{4} \pm \frac{\sqrt{0.5(\Sigma P_1)^2 + 0.5(\Sigma P_2)^2 + (\Sigma F_1)^2}}{4}$	Not significant
Backcross: F_1 to monogerm SLC 91	2.0435	2.5675	0.5240	$\frac{P_1 + F_1}{2} \pm \frac{\sqrt{(\Sigma P_1)^2 + (\Sigma F_1)^2}}{4}$	Significant
P_1 SLC 91 monogerm	1.9215				
P_2 US 35/2	2.8830				

produced from selfing of such F_1 hybrids showed a somewhat higher sucrose but lower yield. The same was observed in F_2 (S_1) tetraploid hybrids (Table 9).

In our tetraploid hybrids obtained by selfing, sucrose observed in F_2 (S_1) was somewhat higher when compared with the F_1 generation but was not significant (Table 9). A big increase in sucrose was observed when F_1 tetraploid hybrids were crossed back to the monogerm inbred line SLC 91; the backcross hybrids showed 14.9100% sucrose. They had the highest percent sucrose in the experiment and differed significantly from F_1 and F_2 hybrids (Table 9). Next highest in sucrose percent was a diploid S_1 hybrid (14.3750%) (Table 9). The difference between sucrose of diploid and tetraploid populations was significant at the 5% level (0.5350%). In this way, hybridization and further selection in later generations of hybrids make possible the development of high-sugar tetraploid lines.

Discussion and Conclusion

A study of percent sucrose and yield in autotetraploid sugar beet populations showed that tetraploid and triploid strains open new possibilities in sugar beet breeding. These possibilities are provided not only by alteration in sucrose and weight of root caused directly by chromosome doubling, but also by the shift from diploid heredity to tetraploid heredity. As a consequence, in autotetraploid sugar beets carrying the same gene pool as their diploid ancestors, percent sucrose and weight of root modify differently under different types of matings than in their diploid ancestors.

Initial changes of percent sucrose and weight of root after doubling of chromosomes by colchicine.

Individual characters of sugar beets respond differently to doubling of chromosomes. Several characters, such as size of seeds, buds, and flowers, length and thickness of petioles, thickness of leaves, and height and thickness of seedstalks always show the same tendency to change their manifestation in different tetraploid populations and varieties, although the grade of such alteration is not always of the same order.

Percent sucrose and weight of root do not manifest a uniform response when diploids are turned into tetraploids. In comparison with the genetic structure of diploids, percent sucrose and weight of root may increase, decrease, or remain at the same level. Monogerm self-sterile and self-fertile strains studied in this experiment did not show a definite tendency in the changes of percent sucrose influenced by the alteration of the chromosome number.

Weight of root in individual progenies derived from the same self-sterile population reacted differently to chromosome doubling. Weight of root of fresh tetraploid populations may rise because of the augmentation of the percent of heterozygotes in following generations due to panmixing mating.

Secondary changes in yield and sucrose in tetraploids caused by different kinds of mating.

Independent of the initial changes in percent sucrose and weight of root which occurred after chromosome doubling, these characters will change in the following hybrid generations differently in diploids and tetraploids. Differences occurring in diploids and tetraploids during their propagation are not similar and depend on the methods used for propagation of diploid and tetraploid hybrids (sibbing, selfing, backcrossing, open pollination).

Weight of root is much reduced in diploids after inbreeding. In tetraploid hybrids these changes could not be established after sibbing. The decrease in vigor and in weight of root in F_2 hybrids is much lower in tetraploids than in diploids after selfing. Tetraploids are more resistant to inbreeding than diploids which is manifested by a lower reduction of their vigor and yield. Therefore, sib progenies show the same yield as progenies obtained after open pollination.

Favorable genetic reaction of increased heterozygosity, which increased vigor and weight of root, was established in tetraploids. As a consequence, heterosis in the weight of root was shown in F_1 tetraploid hybrids. Heterosis was established by hybridization of self-sterile monogerm tetraploids with multigerm tetraploid populations, and also by the hybridization of male-sterile monogerm inbreds with the same multigerm population. Heterosis observed in F_1 tetraploid hybrids could be maintained at a much higher level in the F_2 generation than in diploids.

The highest yield of roots and high sucrose were observed in male-sterile monogerm triploid hybrids.

The additive type of reaction of genes is more important for percent sucrose than for weight of root, the maximum expression of which is determined by the presence of heterozygotes. Percent sucrose increased in many tetraploid hybrids in proportion to increased homozygosity. This opens possibilities for the selection of high sugar hybrid lines. Tetraploid self-fertile lines and backcross progenies from hybridization with monogerm inbred parents showed the highest percent sucrose obtained in this experiment.

The experiment showed that sib-mating as a method of inbreeding appeared to be very low in effectiveness in tetraploids.

If it is desirable to use inbreeding in tetraploids, the gene of self fertility must be incorporated in the tetraploid strains. The self-fertility gene, originating from monogerm SLC 101, makes possible the application of inbreeding in tetraploids.

A study of inheritance of weight of root and of percent sucrose in tetraploid hybrids indicated that hybridization causes extensive changes in these characters in F_1 and backcross hybrids. At the same time, because of a tetraploid type of segregation, these heterogenic characters remain more stable and do not change in the following generations as much as in diploids.

As was shown in this experiment, tetraploids developed by application of different types of mating differed from the fresh tetraploids obtained by colchicine treatment. Of special interest for polyploid selections are triploid hybrids because triploid hybrids possess a new gene balance for all heterozygous loci. Triploid heredity permits the control of the phenomenon of heterosis itself.

Literature Cited

(1) BARTLETT, M. S. and J. B. S. HALDANE. 1934. The theory of inbreeding in autotetraploids. J. Genet. 29: 175-180.

(2) BENNETT, J. H. 1954. Panmixia with tetrasomic and hexasomic inheritance. Genet. 39: 150-158.

(3) BEYSEL, D. 1957. Osmotischer Wert und Viskosität des Protoplasmas diploider und polyploider Zuckerrüben. Deut. Bot. Gesell. Ber. 70: 109-120.

(4) BLAKESLEE, A. F., Y. BELLING and M. E. FARNHAM. 1923. Inheritance in tetraploid *Daturas*. Bot. Gaz. 76: 329-373.

(5) BØGH, H. 1954. Om fremstilling af polyploide stammer af bederoer. Planteforaedling. Pajbjergfondens forsøgs-og Foraedlingsarbejbe: 1-39.

(6) BUTTERFASS, T. 1958. Die practische Ermittelung des Ploidiegrads von Zuckerrüben durch Zählen der Schliesszellen-Chloroplasten. Der Züchter 28: 309-314.

(7) BUTTERFASS, T. 1959. Ploidie und Chloroplastenzahlen. Deut. Bot. Gesell. Ber. 72: 440-451.

(8) CATCHESIDE, D. G. 1956. Double reduction and numerical non-disjunction in tetraploid maize. Heredity 10: 205-218.

(9) CROW, J. F. 1952. Dominance and overdominance. *In* Gowen, J. W. ed. Heterosis. Ames, Iowa State College Press, p. 282-297.

(10) COOPER, D. C. and R. A. BRINK. 1945. Seed collapse following matings between diploid and tetraploid races of *Lycopersicon pimpinellifolium*. Genet. 30: 376-401.

(11) DARLINGTON, C. D. 1956. Natural populations and the breakdown of classical genetics. Royal Soc. London, Proc. Ser. B. Biol. Sci. 145: 350-364.

(12) DOBZHANSKY, T. 1946. Genetics of natural populations. XIII. Recombination and variability in populations of *Drosophila pseudoobscura*. Genetics 31: 269-290.

(13) DOBZHANSKY, T. 1950. Genetics of natural populations. XIX. Origin of heterosis through natural selection in populations of *Drosophila pseudoobscura*. Genetics 35: 288-302.

(14) DOBZHANSKY, T. 1952. Nature and origin of heterosis. *In* Gowen, J. W. ed. Heterosis. Ames, Iowa State College Press, p. 218-223.

(15) ELLERTON, S. and A. J. T. HENDRIKSEN. 1959. Note on the probable cause of the occurrence of tetraploid plants in commercial triploid varieties of sugar beet. Euphytica 8 (2): 99-104.

(16) FABERGE, A. C. 1936. The physiological consequences of polploidy. I. Growth and size in the tomato. J. Genet. 33: 365-382.

(17) FABERGE, A. C. 1936. The physiological consequences of polyploidy. II. The effect of polyploidy on variability in the tomato. J. Genet. 33: 383-399.

(18) FALCONER, D. S. 1960. Introduction to quantitative genetics. New York, Ronald. 365 p.

(19) FELTZ, H. 1953. Untersuchungen an diploiden und polyploiden Zuckerrüben. Zeitsch. für Pflanzenzücht. 32: 275-300.

(20) FISHER, R. A. 1941. The theoretical consequences of polyploid inheritance for the mid style form of Lythrum salicaria. Ann. Eugenics II: 31-38.

(21) FISHER, R. A. 1944. Allowance for double reduction in the calculation of genotype frequencies with polysomic inheritance. Ann. Eugenics. 12: 169-171.

(22) FISHER, R. A. 1947. The theory of linkage in polysomic inheritance. Royal Soc. of London. Philos. Trans. B. 233: 55-87.

(23) FISHER, R. A. 1949. The theory of inbreeding. Edinburgh, Oliver. 120 p.

(24) FISHER, R. A. and K. MATHER. 1943. The inheritance of style length in *Lythrum salicaria*. Ann. Eugenics 12: 1-23.

(25) GEIRINGER, H., 1949. Contribution to the linkage theory of autopolyploids. I and II. Bull. Math. Biophysics II: 59-82 and II: 197-219.

(26) GEIRINGER, H. 1949. Chromatid segregation of tetraploids and hexaploids. Genetics 34: 665-684.

(27) GRAF, A. 1956. Die Bedeutung der polyploiden Zuckerrüben in Oesterreich. Zeitschr. für Zuckerindus. 6: 477-480.

(28) GRAF, A. 1958. Zuckerrübensortenbericht, Zusammenfassung 1957. Verein für Zuckerrübenforschung :1-4.

(29) HALDANE, J. B. S. 1930. Theoretical genetics of autopolyploids. J. Genet. 22: 359-372

(30) HALDANE, J. B. S. 1936. The amount of heterozygosis to be expected in an approximately pure line. J. Genet. 32: 375-391.

(31) HALDANE, J. B. S. 1937. Some theoretical results of continued brother-sister mating. J. Genet. 34: 265-274.

(32) HORNER, T. W., R. E. COMSTOCK, and H. F. ROBINSON. 1955. Non-allelic gene interaction and the interpretation of quantitative genetic data. Tech. Bull. N.C. Agric. Exp. Sta., No. 118: V+ 117 p.

(33) KEMPTHORNE, O. 1955. The correlation between relatives in a simple autotetraploid population. Genetics 40: 168-174.

(34) KEMPTHORNE, O. 1957. An introduction to genetic statistics. New York, Wiley. 545 p.

(35) KNAPP, E. 1957. The significance of polyploidy in sugar beet breeding. Internatl. Genet. Symp. Proc. 1956. 300-304.

(36) KNAPP, E. 1956. Beta-Rüben Bes. Zuckerrüben. *In* Roemer, T., und Rudorf, W. Handbuch der Pflanzenzüchtung, ed. 2. V.3, p. 196-284.

(37) KNAPP, E. und H. WIEBALCK. 1957. Über den Anteil der Diploiden, Triploiden und Tetraploiden an den Leistungseigenschaften einer polyploiden Zuckerrübensorte (Kleinwanzlebener Polybeta). Zeitschr. für die Zuckerindus., 7 (4) : 166-169.

(38) KLOEN, D., and G. J. SPECKMANN. 1954. The creation of tetraploid beets. II. Selection in the first generation (the C_1) from the treated material. Euphytica 3: 35-42.

(39) KRÜGER, W. 1956. Untersuchungen über die Leistung der "Kleinwanzlebener Polybeta." Zucker 9: 524-529.

(40) KUCKUCK, H. und A. LEVAN. 1951. Vergleichende Untersuchungen an diploiden und tetraploiden Leinsippen und an tetraploiden Kreuzungsnachkommenschaften nach vieljahriger Selektion. Der Züchter 21: 195-205.

(41) LERNER, I. M. 1954. Genetic homeostasis. New York, Wiley. 134 p.

(42) LERNER, I. M. 1958. The genetic basis of selection. New York, Wiley. 298 p.

(43) LEVAN, A. 1942. The effect of chromosomal variation in sugar beets. Hereditas 28: 345-399.

(44) LI, C. C. 1955. Population genetics. Chicago, University of Chicago Press. 366 p.

(45) LI, C. C. 1957. The genetic variance of autotetraploids with two alleles. Genetics 42: 583-592.

(46) LINDSTROM, E. W. 1932. A fertile tetraploid tomato: cross-sterile with diploid species. J. Hered. 23: 115-121.

(47) LINDSTROM, E. W. 1935. Segregation of quantitative genes in tetraploid tomato hybrids as evidence for dominance relations of size characters. Genetics 20: 1-11.

(48) LITTLE, T. M. 1945. Gene segregation in autotetraploids. Bot. Rev. 11: 60-85.

(49) LITTLE, T. M. 1958. Gene segregation in autotetraploids. II. Bot. Rev. 24: 318-339.

(50) LÜDECKE, H. 1956. Sortenprüfung mit Zuckerrüben in Bundesgebiet 1956. Institut für Zuckerrübenforschung. Göttingen. :1-16.

(51) LUNDQVIST, A. 1947. On self-sterility and inbreeding effect in tetraploid rye. Hereditas 33: 570-571.

(52) LUNDQVIST, A. 1953. Inbreeding in autotetraploid rye. Hereditas 39: 19-32.

(53) MATHER, K. 1935. Reductional and equational separation of the chromosomes in bivalents and multivalents. J. Genet. 30: 53-78.

(54) MATHER, K. 1936. Segregation and linkage in autotetraploids. J. Genet. 32: 287-314.

(55) MATHER, K. 1941. Variation and selection of polygenic characters. J. Genet. 41: 159-193.

(56) MATHER, K. 1942. The balance of polygenic combinations. J. Genet. 43: 309-336.

(57) MATHER, K. 1943. Polygenic inheritance and natural selection. Cambridge Phil. Soc. Biol. Rev. 18: 32-64.

(58) MATHER, K. 1949. Biometrical genetics. New York, Dover. 158 p.

(59) MATHER, K. 1953. The genetical structure of populations. Soc. Expt. Biol. Symposia 7: 66-95.

(60) MATSUMURA, S. 1953. Improvement work with sugar beets by means of triploidy. A concluding review. *In* Matsumura, S., ed. (Improvement of sugar beets by means of triploidy). Nat. Inst. Genet. and Kihara Inst. Biol. Res., Tokyo. No. 14, p. 120-129.

(61) MOCHIZUKI, A. 1953. (Cytological and genetical studies on sugar beet. V. Cytogenetical studies on the production of triploid sugar beet seed). *In* Matsumura, S., ed. (Improvement of sugar beets by means of triploidy). Nat. Inst. Genet. and Kihara Inst. Biol. Res., Tokyo. No. 14, p. 14-39.

(62) MOCHIZUKI, A. and N. SUEOKA. 1955. Genetic studies on the number of plastid in stomata. I. Effects of autopolyploidy in sugar beets. Cytologia 20: 358-366.

(63) MULLER, H. J. 1914. A new mode of segregation in Gregory's tetraploid Primulas. Amer. Naturalist 48: 508-512.

(64) MÜNTZING, A. 1954. An analysis of hybrid vigour in tetraploid rye. Hereditas 40: 265-277.

(65) MÜNTZING, A. 1956. Polyploidiezuchtung. In Roemer, T., and Rudorf, W. Handbuch der Pflanzenzüchtung, ed. 2, v.l, p. 700-731.

(66) NOGGLE, G. R. 1946. The physiology of polyploidy in plants. I. Review of the literature. Lloydia 9: 153-173.

(67) OKA, H. 1955. Studies on tetraploid rice VI. Fertility variation and segregation ratios for several characters in tetraploid hybrids of rice, *Oryza sativa*, L. Cytologia 20: 258-266.

(68) POWERS, LE ROY. 1955. Components of variance method and partitioning method of genetic analyses applied to weight per fruit of tomato hybrid and parental populations. U.S. Dept. Agr. Tech. Bull. 1131. 64 p.

(69) PETO, F. H. and J. W. BOYES. 1940. Comparison of diploid and triploid sugar beets. Canadian J. Res. Sec. C. Bot. Sci. 18: 273-282.

(70) PARSONS, P. A. 1959. Some problems in inbreeding and random mating in tetrasomics. Agron. J. 51: 465-467.

(71) RANDOLPH, L. F. 1935. Cytogenetics of tetraploid maize. J. Agr. Res. 50: 591-605.

(72) RANDOLPH, L. F. 1941. An evaluation of induced polyploidy as a method of breeding crop plants. Biol. Symposia 4: 151-167.

(73) RASMUSSON, J. 1953. Autotetraploid sugar beets: vitality changes in subsequent generations. Hereditas 39: 257-269.

(74) RASMUSSON, J. and A. LEVAN. 1939. Tetraploid sugar beets from colchicine treatments. Hereditas 25: 97-102.

(75) ROSEN, G., VON. 1949. Problems and methods in the production of tetraploids within the genus *Beta*. Socker Handl. II. 5: 199-217.

(76) REITBERGER, A. 1956. Ruhekernuntersuchungen bei gesunden and viruskranken Diploiden und Polyploiden von *Beta vulgaris*. Züchter 26: 106-117.

(77) SANSOME, F. W. 1933. Chromatid segregation in *Solanum lycopersicum*. J. Genet. 27: 105-132.

(78) SAVITSKY, H. 1940. Cytology and embryology of the sugar beet. Vsesoiuzni Nauchno-issledovatel' skii Institut Sakharnoi Promyshlenosti, Sveklovodstvo. (All Union Scientific Research Institute of the Sugar Industry. Sugar Beet Culture 1: 453-548.

(79) SAVITSKY, H. 1952. Polyploid sugar beets-cytological study and methods of production. Am. Soc. Sugar Beet Technol. Proc. 7: 470-476.

(80) SAVITSKY, H. 1954. Obtaining tetraploid monogerm self fertile, self sterile and male sterile beets. Am. Soc. Sugar Beet Technol. Proc. 8 (2): 50-58.

(81) SAVITSKY, V. F. 1940. Genetics of the sugar beet. Vsesoiuzni Nauchno-issledovatel' skii Institut Sakharnoi Promyshlenosti. Sveklovodstvo (All-Union Scientific Research Institute of the Sugar Industry). Sugar Beet Culture 1: 549-684.

(82) SAVITSKY, V. F. 1958. Genetische Studien und Züchtungsmethoden bei monogermen Rüben. Zeitsch. für Pflanzenzüchtung. 40: 1-36.

(83) SCHLÖSSER, L. A. 1952. Polyploidie in der Zuckerrübenzüchtung. Landwirt. Gesell. Mitt. 67: 551-552.

(84) SCHLÖSSER, L. A. 1956. Stand der "Polybeta"-Züchtung. Zuckerrübe und Zuckerrübensamen Kleinwanzlebener Saatzucht, Einbeck : 8-16.

(85) SCHWANITZ, F. 1938. Die Herstellung polyploider Rassen bei Beta-Rüben und Gemüsearten durch Behandlung mit Colchicin. Der Züchter 10: 278-279.

(86) SCHWANITZ, F. 1951. Untersuchungen an polyploiden Pflanzen. Der Gigas-Charakter der Kulturpflanzen und seine Bedeutung für die Polyploidiezüchtung. Züchter 21: 66-75.

(87) SEDLMAYR, K. 1955. Polyploide Zuckerrüben. Die Bodenkultur 8: 235-243.

(88) SEDLMAYR, K. 1957. Rekurrente Selektion auf reciproke Kombinationsfähigkeit, Ein Beitrag zur Züchtung polyploiden Heterosispopulationen bei *Beta vulgaris*. Züchter 27: 65-69.

(89) STEBBINS, G. L. 1950. Variation and evolution in plants. 1-643. New York.

(90) STEBBINS, G. L. 1956. Artificial polyploidy as a tool in plant breeding. Brookhaven Symposia in Biology 9: 37-53.

(91) STRAUB, J., VON. 1946. Die Züchtung von Polyploiden mit positivem Selektionswert. Zeitschr. für Naturforschung. 1: 342-345.

(92) STEWART, D. and J. O. GASKILL. 1952. Results of field tests with triploid sugar beets in 1951. Am. Soc. Sugar Beet Technol. Proc. 7: 452-453.

(93) WINTON, D. De and J. B. S. HALDANE. 1931. Linkage in the tetraploid *Primula sinensis*. J. Genet. 24: 121-144.

(94) WRIGHT, SEWALL. 1937. The distribution of gene frequencies in populations. Proc. Nat. Acad. Sci. 23: 307-320.

(95) WRIGHT, SEWALL. 1938. The distribution of gene frequencies in populations of polyploids. Proc. Nat. Acad. Sci., Wash. 24: 372-377.