THE PHYSIOLOGICAL CONSEQUENCES OF POLYPLOIDY[1]

I. GROWTH AND SIZE IN THE TOMATO

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(With Two Text-figures)

Introduction

Ever since the discovery of polyploidy, descriptions of the properties which distinguish one member of a series from another member have been published. Polyploidy, as a variation, is quite general throughout the vegetable kingdom, and it is clearly of great interest to derive some generalization which would enable one to predict the effect of chromosome doubling in any given case. As a result of modern cytogenetic work, such predictions can be made with great certainty as regards the genetical and cytological consequences, and the effect on self- and cross-fertility. The physiological results of polyploidy, on the other hand, are only known very superficially. The present paper is an account of an investigation of the effect of polyploidy on growth and total size in the tomato. The same data will be re-examined from the point of view of variability in a separate paper.

The tomato is one of the few plants in which it is possible to induce tetraploidy at will, and therefore to obtain rigorously comparable material (Jørgensen, 1928). From the moment the chromosomes of an organism are doubled, it begins to exist under what may be termed a new genetic régime. It is difficult to estimate how important the effects of the early stages of this process are as compared with the effects of polyploidy as such. Therefore, in the present investigation, no material was used which had existed as a tetraploid for more than three generations. All critical conclusions were derived from material in the first generation after somatic doubling.

[1] In part adapted from a thesis accepted for the degree of Ph.D. of the University of London.

Review of literature

For the reasons stated above, it is difficult to obtain valid information from polyploids found in nature. Müntzing (1936) has given a very full review of literature on autopolyploids in general. Only polyploids produced experimentally will be considered here.

The work on mosses has been reviewed by Schwarzenbach (1926), v. Wettstein (1932) and Allen (1935). Cell volume is usually roughly proportional to chromosome number, but there are exceptions to this, and in the case of *Anthoceros laevis* the diploid has smaller cells than the haploid (Schwarzenbach, 1926). Becker (1932) has found that osmotic pressure decreases as cell size increases. The situation in ferns has been reviewed by Andersson-Kottö (1936); cell sizes behave in the same way as in the mosses.

In the tomato, differences in appearance and growth have frequently been reported (e.g. Sansome, 1933), but usually no actual measurements were taken. There is no doubt that tetraploids can be recognized from diploids with a good deal of certainty, but the difference is hard to define. According to Sansome & Zilva (1933, 1936) the vitamin C content of tetraploid fruits appears to be greater, though this has been questioned by MacHenry and Graham (1935). Kostoff & Aksamitnaja (1935) have published chemical analyses of diploid and tetraploid petunia and tomato, but used only two replicates, so that it is difficult to base any conclusions on their work.

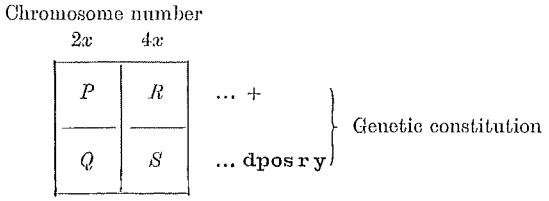
Experimental results

The numerical data accumulated in this work are bulky, and every effort has been made to summarise them as briefly as possible. Consequently, tests of significance alone are most often given. Fisher's (1935, 1936) statistical notation is used throughout. In the experiments about to be described all populations which have been inbred under controlled conditions for a few generations are called pure lines, for the sake of convenience.

1934 Growth-rate experiment

This was a preliminary experiment, principally designed to show whether tetraploids differ consistently from diploids in their growth. Information was also desired, in order to establish a technique for future experiments, on the relation between the dry and fresh weight throughout the period considered, and on the relation between roots and shoots.

Description of material. Four pure lines, *P*, *Q*, *R* and *S*, were used, which had been inbred for five generations. These may be classified in a fourfold table:



where **d** = dwarf, **p** = peach (hairiness), **o** = oval fruit, **s** = compound inflorescence, **r** = red colour of fruit, **y** = colourless skin of fruit. Full descriptions of these factors are given by MacArthur (1931). The two tetraploid lines were doubled in 1932.

Methods and technique. The plants were grown in water culture ($\frac{1}{2}$ strength Knop) in paraffined earthenware pots 23 cm. across and 26 cm. deep, each holding 5·25 litres. The solution was renewed each week; aerating was found unnecessary for tomatoes. The lids, of compressed cork 8 mm. thick, had twenty 2·5 cm. equally spaced holes bored in them. The lids were soaked in paraffin, and a sheet of muslin placed on one side while the wax was still melted; small seedlings could then be pushed through a small hole in the muslin. When samples were taken, the whole 2·5 cm. disc of muslin was cut out with the plants. Seeds were germinated on moist filter paper in Petri dishes. The pots were kept on the staging of a greenhouse, the temperature of which was kept at about 24° C.

The experiment was laid out in eight randomized blocks, four pots of twenty plants each per block. Samples were taken every 4 days, and always at the same time of the day; nine samples were taken altogether. Within each pot the plants were taken in a predetermined systematic way in order to ensure their gradual spacing and to avoid bias. Each plant was cut in two at cotyledon level and the fresh weight of both "roots" and "shoots" recorded separately. Plants were then dried in flat aluminium dishes in a water oven ($\pm$ 98° C.) for 20 hours; they were then weighed again. All the weighings were done on a battery of Joly balances of phosphor bronze wire (Bolas & Melville, 1933) so that each weighing is accurate to at least 0·01 of its value. Weighing is very rapid and consequently no precautions need be taken against the absorption of moisture.

Thus four measurements were taken on each individual. It was

originally intended to take only one plant from each pot at each time. Actually twelve plants of each line were taken on each occasion instead of eight. Of these twelve, eight were taken one from each block, and four from each of four blocks, the particular groups of four blocks being a different one on successive occasions. This results in a partial confounding of "times", and of 32 of the 88 degrees of freedom for the "lines" × "times" interaction with one of the 7 degrees of freedom for blocks on each occasion. The total contribution for blocks is quite insignificant, as the following table shows; dry weights of the shoots of eight individuals sampled, one from each block, are used:

TABLE I[1]

Variance	D.F.	S. of S.	M.S.	z	0·05 point of z
Blocks orthogonal to times	7	0·2588	0·0370	0·2172	0·3565
Error (from replication within blocks)	394	9·4187	0·0239		

[1] In this, and in all following tables D.F. = degrees of freedom, S. of S. = sum of squares, M.S. = mean square, 0·05 point of z = that value in the distribution of z the probability of obtaining which by random sampling is 1 in 20, from Fisher's table (Fisher, 1936).

On the strength of this information, the sum of squares for blocks is not subtracted from error in any of the following analyses, and all twelve measurements in each line on each occasion are included.

All the computations are made on logarithms to base 10 of the weight, 0·1 mg. being the unit. The result of using a logarithmic scale is that increase of weight with time is very nearly linear, depending on the constancy of the environment. The plants were in the so-called "grand" period, and grew exponentially, as it is expressed by Blackman's equation:

$$W_t = W_o e^{rt},$$

where W_o is the initial weight, W_t the weight at time t, and r the relative growth rate or efficiency index (Blackman, 1919). In the analysis of variance, the sum of squares for times is determined by all the differences between samples taken at different times. These differences will be largely a function of the relative growth rate, but will also arise from changes of environment with time. The relative importance of these two may be examined by separating the sum of squares for times into two portions: one accounted for by a linear regression and a remainder. This is done in Table II. It will be seen that although by far the greater part is accounted for by that one degree of freedom for the linear regression, the remainder, based on 7 degrees of freedom, is still highly significant. This means that the relative growth rate was not constant.

The times × lines interaction is made up of differences in the effect of time on the different populations. This will consist of differences in relative growth rate and of differences in response to changes of environment. It is not unreasonable to suppose, *a priori*, that differences of the effect of environment on different strains will be small in comparison with the effect of changes of environment as a whole. That this is in fact so can be seen from Tables VIII and IX, in which a component due to a linear regression is separated from the sums of squares corresponding to various comparisons. In two cases the remainders are not significant, and in two others they are not very large.

TABLE II

Decomposition of times

Variance	D.F.	S. of S.	M.S.	z	$0{\cdot}01\ z$
Times	8	296·6730	37·0841	—	—
Linear regression	1	292·3482	292·3482	—	—
Remainder	7	4·3482	0·6212	1·6289	0·4963
Error	394	9·4187	0·0239	—	—

TABLE III

Dry weight of shoots: main analysis

Variance	D.F.	S. of S.	M.S.	z	$0{\cdot}01\ z$
Total	429	309·2647	0·7209	—	—
Times	8	296·6730	37·0841	—	—
Lines	3	1·7827	0·5941	1·6067	0·6717
T. × L.	24	1·3903	0·0579	0·4424	0·3014
Error	394	9·4187	0·0239	—	—

Such a procedure results in a gain of precision, to the extent to which changes in environment will tend to affect different lines to the same extent. It is the existence of this method which made it possible deliberately to change the environment of a whole experiment by transferring the plants from a greenhouse to a patch of land out of doors in 1935.

The criterion of classification "lines" gives a means of testing differences in the total amount of weight produced. Biologically it is a function of both the initial weight W_0 and the growth rate r of the compound interest law.

The main analysis of variance is given in Table III. As will be seen later, the correlation between the four measurements taken on one plant is so high that one of them may safely be taken as representative. The dry weight of shoots alone is used.

Two plants were accidentally lost in sample 3 of line *P*, hence the total number of degrees of freedom is not 431, but 429. Owing to the trivial difference, the samples are treated as if they were orthogonal, for the sake of simplicity.

A decomposition of the three degrees of freedom for lines is given in Table IV. Fisher's factorial notation is used (Fisher, 1935). The letters *p*, *q*, *r*, *s* represent the four lines. The comparisons:

$$p+q-r-s,$$
$$p-q+r-s,$$
$$p-q-r+s,$$

are orthogonal to one another. The first represents the effect of polyploidy, and its mean square is actually less than that for error, so that the tetraploids did not differ significantly from diploids in the total amount of matter produced. The second comparison represents the effect

TABLE IV

Dry weight of shoots: decomposition of "lines"

Variance	D.F.	S. of S.	M.S.	*z*	0·01 *z*
Lines (total)	3	1·7827	0·5942	1·6067	0·6717
$p+q-r-s$	1	0·0005	0·0005	—	
$p-q+r-s$	1	0·8469	0·8469	1·7838	0·9511
$p-q-r+s$	1	0·9350	0·9350	1·8333	
$p+q+r-3$	1	1·2089	1·2084	1·9616	
Remainder	2	0·5743	0·2872	1·2431	0·7695
Error	394	9·4187	0·0239	—	—

of the factor **d** (which is the only one of the six factors that might be expected to affect growth appreciably), and is significant. The last comparison represents the extent to which this fourfold classification fails to account for the differences, and it actually gives the biggest mean square of the three.

The comparison $p+q+r-3s$ is not orthogonal to the first three; it is suggested by the graph on Fig. 1, from which it appears that *s* is smaller than the other three lines. This gives a highly significant mean square.

The composition of the times × lines interaction is similarly analysed on Table V. For each comparison, a component accounted for by a linear regression is isolated.

It will be seen that this component is large in the first two comparisons of Table V. $t(p-q+r-s)$ is not itself significant, but it appears quite legitimate to isolate the linear component since there are good *a priori* reasons for so doing. The third comparison, which, as was already seen, tests the failure of the fourfold classification, is significant,

but its linear component is quite small and not significant at all. Thus, polyploidy and the factor **d** account for differences in growth rate, but interact with one another in producing different deviations from a constant growth rate.

The comparison $t(p+q+r-3s)$ is very large, and the remainder from a linear regression is significant, though it fails to reach the 0·01 level of

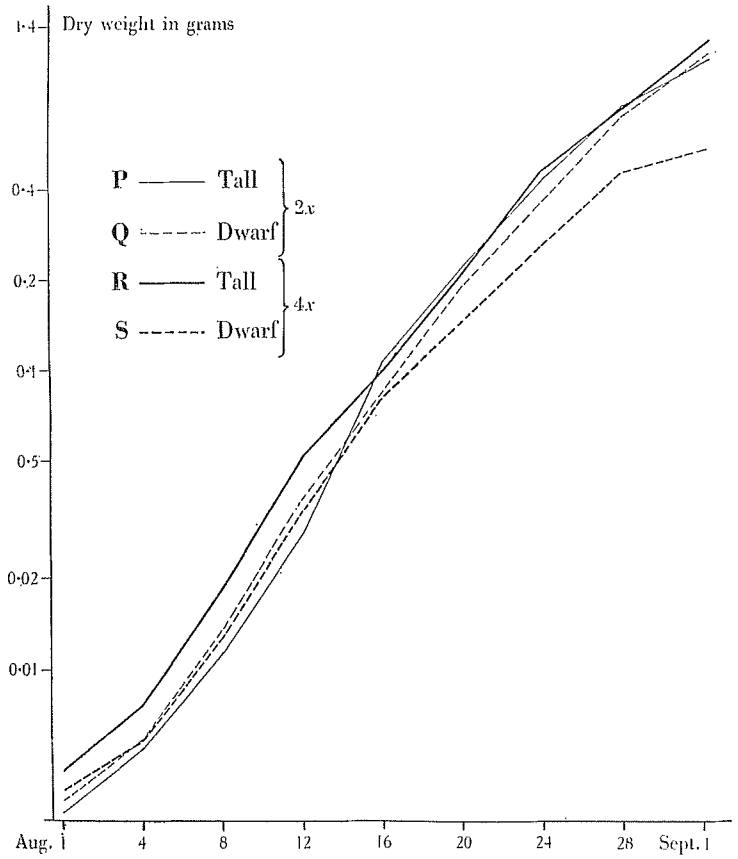


Fig. 1. The growth of the four lines *P*, *Q*, *R* and *S* represented on a logarithmic scale.

probability. The situation is clear on the graph in Fig. 1, where it will be seen that the line *s* grew at a slower rate during the second half of the experiment.

From these analyses the conclusion may be drawn that tetraploids do not produce significantly more material than diploids in the period considered, and that though differences in growth do exist, they are small and represent complex interactions with the genotype and the environment.

TABLE V

Dry weight of shoots: decomposition of "times × lines" interaction

Variance	D.F.	S. of S.	M.S.	z	Points of z	
TL interaction (total)	24	1·3903	0·0579	0·4424	0·01	0·3014
$t\,(p+q-r-s)$	8	0·7983	0·0998	0·7147	0·01	0·4693
Linear regression	1	0·5593	0·5593	1·5764	0·01	0·9511
Remainder	7	0·2391	0·0342	0·1792	0·05	0·3565
$t\,(p-q+r-s)$	8	0·3048	0·0381	0·2332	0·05	0·3369
Linear regression	1	0·2616	0·2616	1·1965	0·01	0·9511
Remainder	7	0·0432	0·0062	—	—	—
$t\,(p-q-r+s)$	8	0·4935	0·0617	0·4742	0·01	0·4693
Linear regression	1	0·0553	0·0553	0·4194	0·05	0·6760
Remainder	7	0·4382	0·0626	0·4814	0·01 0·05	0·4963 0·3565
$t\,(p+q+r-3s)$	8	0·8315	0·1039	0·7348	0·01	0·4693
Linear regression	1	0·4076	0·4076	1·4182	0·01	0·9511
Remainder from L.R.	7	0·4238	0·0605	0·4644	0·01 0·05	0·4963 0·3565
Remainder	16	0·5589	0·0349	0·1893	0·05	0·2523
Error	394	9·4187	0·0239	—	—	—

Covariance of different measurements on the same plant

Similar analyses to the above were made on three other measurements, and gave almost identical results. Of the six possible covariances, only two were calculated: fresh × dry weight of shoots and dry shoots × dry roots. These are given in Tables VI and VII. Regression and correlation coefficients corresponding to each item in the analyses of variance are given, logarithms being used as before. Regression coefficients are there-

TABLE VI

Covariance of fresh and dry weight (shoots)

Source of covariance	D.F.	$S\,(x-\bar{x})\,(y-\bar{y})$	Correlation coefficient	Regression of F.W. on D.W.
Total	429	299·5511	0·989	0·969
Times	8	288·5222	0·999	0·972
Lines	3	1·7902	0·893	1·004
T. × L.	24	1·4505	0·877	1·043
Remainder	394	7·7882	0·672	0·827

TABLE VII

Covariance of roots and shoots (dry)

Source of covariance	D.F.	$S\,(x-\bar{x})\,(y-\bar{y})$	Correlation coefficient	Regression of R. on S.
Total	429	286·5350	0·995	0·927
Times	8	276·3842	0·999	0·931
Lines	3	1·2545	0·913	0·704
T. × L.	24	1·1690	0·857	0·841
Remainder	394	7·7273	0·888	0·820

fore independent of the units in which the two variables are expressed, and tend to unity as correlation increases. It will be seen that the correlations are in all cases very high.

The fact that the four lines do not differ significantly among themselves in water content (92·09 per cent) can be shown more simply by taking for each line the difference between the fresh and dry weight, and calculating a sum of squares for these differences. Since the two measurements are correlated, the variance with which this has to be compared is $V_{(a)}+V_{(b)}-2W_{(ab)}$, where $V_{(a)}$ is the variance of the first variable, $V_{(b)}$ that of the second, and $W_{(ab)}$ their covariance. Table VIII shows that the mean square for differences is actually less than the corresponding error.

TABLE VIII

Lines	*P*	*Q*	*R*	*S*
Mean fresh weight *a*	3·9731	3·9667	4·0981	3·9115
Mean dry weight *b*	2·8723	2·8614	2·9475	2·7666
Difference Δ	1·1008	1·1053	1·1506	1·1449

$S(\Delta-\bar{\Delta})^2=0{\cdot}002024$; M.S. $=0{\cdot}00068$; $V_{(a)}+V_{(b)}-2W_{(ab)}=0{\cdot}01066$.

The relationship between roots and shoots in the four lines may be treated in the same way (Table IX). This again shows a mean square for differences which is less than error, so that shoots may safely be taken as representative of the whole plant. Roots represent 19·10 per cent of the total dry weight.

TABLE IX

Lines	*P*	*Q*	*R*	*S*
Mean dry shoots *a*	2·8723	2·8614	2·9475	2·7666
Mean dry roots *b*	2·2854	2·2939	2·3898	2·2572
Difference Δ	0·5869	0·5675	0·5577	0·5094

$S(\Delta-\bar{\Delta})^2=0{\cdot}00326$; M.S. $=0{\cdot}00109$; $V_{(a)}+V_{(b)}-2W_{(ab)}=0{\cdot}00500$.

Embryo weights of the lines, P, Q, R and S

In the first sample of the 1934 experiment, the plants weighed about 5·5 mg., which is about 5 × the weight of the embryo in the ripe seed. It will also be seen on the graph of Fig. 1 that in the first sample the two tetraploids were heavier than the two diploids, though this is not statistically significant. It appeared of interest to determine the weights of the actual embryos.

Fifty embryos, together with the corresponding seeds, were weighed in each of the four lines. Seeds were first softened (but not germinated) by soaking overnight in 0·1 per cent. $HgCl_2$. The embryos were then dissected out, examined under a binocular microscope, and dried. Thet Su & Ashby

(1929) have described a method for drying very small biological material, and the procedure followed here is partly adapted from theirs. Drying took place at 50° C. under about 5 mm. Hg pressure over P_2O_5. Constant weight was attained in about 10 min., but the embryos, in batches of ten at a time, were left in the drier for half an hour. For weighing, a specially constructed torsion balance was used, which gave a precision by direct reading of 0·01 mg. (3 mm. on the scale) (the author, unpublished).

Seed and embryo weight are highly correlated, as the following table shows:

TABLE X

Covariance	$S(x-\bar{x})(y-\bar{y})$	Correlation coefficient	t
Total	334838	—	—
Between lines	139197	0·8524	23·268
Within lines	195641	—	—

The means of the four lines are given below, in mg.:

TABLE XI

Lines	$P(2x)$	$Q(2x)$	$R(4x)$	$S(4x)$
Mean seed weight	2·4446	2·6730	3·4902	3·1812
Mean embryo weight	0·9744	0·9972	1·3812	1·2470

Only the comparison $p+q-r-s$ need be considered; it is given on Table XII for embryo weights:

TABLE XII

Embryo weight

Variance	D.F.	S. of S.	M.S.	z	0·01 z
Total	199	152791	768·39	—	—
Lines	3	58523	19507·67	1·8514	0·6518
$p+q-r-s$	1	53890	53890·00	2·3595	0·9882
Remainder	2	4633	2316·28	0·7859	0·7755
Error	196	94268	480·96	—	—

Thus it appears that both tetraploid seed and tetraploid embryos are about 1·3 times heavier than the corresponding diploids, and these differences are highly significant. This advantage of increased embryo weight was lost during the eleven days which elapsed between seed sowing and the first sample of the growth-rate experiment. It is possible that the small difference which exists in the first sample is the last trace of the difference found in embryo weight.

1935 GROWTH-RATE EXPERIMENT

This experiment was mainly designed for the measurement of variability (to be dealt with elsewhere), but it is capable of yielding informa-

tion on growth in the same way as the 1934 experiment. In addition, comparisons can be made on heterosis in the F_2 population.

Description of material. Ten genetic populations of tomatoes were used:

A	2*x*	Pure line, inbred for six generations. Genetic constitution: **dpos r y**.
B	4*x*	Pure line inbred for six generations. Doubled in 1932, and taken from same stock as *A* in that year.
C	4*x*	Pure line inbred for six generations. Genetic constitution **dpos r**.
D	4*x*	Pure line inbred for three generations, genetic constitution: +.
E	4*x*	F_2 of **dpos r y** × **cluh**.
F	2*x*	
G	2*x*	F_2 of "Chinaman" × **dpos r y**.
H	4*x*	
I	2*x*	Pure line "Chinaman".
J	2*x*	Pure line inbred for at least six generations. Genetic constitution: **cluh**.

c = compound inflorescence, **l** = lutescent, **u** = uniform, **h** = hairy (MacArthur, 1931). "Chinaman" is a tomato variety originally obtained from Messrs Vilmorin-Andrieux and Cie of Paris. It has been cultivated since about 1860 by Chinese market gardeners in Australia, and is homozygous for several recessives, including *fasciated* and *brachytic*. Tetraploid F_2's were obtained by somatic doubling of the F_1 and selfing. In the case of *G* and *H*, the same F_1 individual is the parent of both; *A* and *B* come from selfing the same individual in 1932.

Description of experiment. The experiment was arranged in four randomised blocks. Seeds were all sown on the same day (13 June 1935), three seeds per pot; 172 pots of each line were sown, forty-three pots per plot. The experiment was started in a greenhouse, and on 11 and 12 July all plants were transferred out of doors, two blocks being transferred on each of these two dates, and the position of lines within blocks was randomized again.

The first sample was taken on 26 July, and subsequently at intervals of one week; samples were always taken at the beginning of the afternoon. On each occasion 12 plants were taken from each of the ten lines, three from each block, thus making 120 plants per sample. The first two samples were taken before thinning out, the choice being random with the restriction that 1 plant only was taken from each pot. In the third

sample, three pots were taken, leaving forty pots per plot. Out-of-doors, the distance between plants was at first 40 cm., but on 6 August every other plant was thinned out, leaving a pattern of diagonal squares. The choice of the individuals to be taken at each out-of-door sample was predetermined systematically, in order to ensure adequate spacing.

The plants were cut off at cotyledon level and dried in an oven built for the purpose. The temperature was first raised to 100° without air current to ensure rapid killing. After half an hour a fan was switched on which drove a stream of hot air over the plants, the temperature being maintained at 70° C. by means of a thermoregulator. Constant weight was attained in a few hours, depending on the size of the samples, but all samples were kept at 70° C. overnight. Plants were weighed on phosphor bronze Joly balances as was done in the 1934 experiment.

Eight samples at weekly intervals were taken. Thus there are 3 individuals × 4 blocks × 10 lines × 8 times = 960 measurements. In such

TABLE XIII

1935 *experiment: main analysis*

Variance	D.F.	S. of S.	M.S.	z	0·01 z
Total	959	1038·131	1·0825	—	—
Times	7	963·324	137·6177	—	—
Lines	9	15·823	1·7582	1·8417	0·4199
T. × L.	63	11·339	0·1800	0·7018	0·2134
Absolute error	640	28·289	0·0442	—	—
Residual error	240	19·356	0·0806	—	—

an experiment there are two kinds of experimental error. One represents differences between individuals classified alike with respect to all other criteria, and will here be called "absolute" and used for tests of significance. The other error is the one commonly used in the standard type of agricultural experiment, and consists of block interactions; it represents discrepancies of behaviour of groups classified alike but in different blocks. This will be called residual error.

Putting L = lines, T = times, I = individuals, B = blocks, the absolute error will contain, I, LI, TI, IB, LTI, LIB, TIB and $LTIB$, and will be based on 640 degrees of freedom. The residual error will contain B and all block interactions not containing I, i.e. LB, TB and LTB, and will therefore be based on 240 degrees of freedom. The two degrees of freedom for individuals cannot of course be separated.

The main analysis is given in Table XIII. Logarithms to the base 10 are again used; 1 mg. is a unit.

Every item in this general analysis is highly significant. In Table XIV

is given a decomposition of the residual error, which shows that the use of blocks did in fact increase the precision of this experiment.

TABLE XIV

Decomposition of residual error

Variance	D.F.	S. of S.	M.S.	z	0·01 z
Residual error	240	19·3557	0·0806	—	—
Blocks	3	3·3387	1·1129	2·7643	0·6655
Block interactions (excluding I)	237	16·0170	0·0676	0·1844	0·1285
Absolute error	640	28·2891	0·0442	—	—

No doubt this is due to the greater heterogeneity of a plot of land as compared with water cultures in a greenhouse. If all blocks and their interactions had been included in error as had been done for the 1934 experiment, the mean square for error would have been 0·05414 instead of 0·04420, the former being based on 880 degrees of freedom. The portion of the sum of squares for times which is taken up by a linear regression is shown in Table XV; it will be seen that the remainder is very significant.

TABLE XV

Decomposition of times

Variance	D.F.	S. of S.	M.S.	z	0·01 z
Times	7	963·3242	137·6177	—	—
Linear regression	1	921·5746	921·5746	—	—
Remainder	6	41·7496	6·9583	3·6808	0·5202
Error	640	28·2891	0·0442	—	—

The growth rates of all ten lines are shown in Fig. 2. The growth rate was slower in the field than in the greenhouse; no doubt this accounts for a large part of the remainder from the linear regression.

Of the 9 degrees of freedom for lines, three give relevant information when isolated. Using Fisher's factorial notation as before, they may be represented as:

$(2x \longleftrightarrow 4x)$	$a- \ b- \ c- \ d- \ e+ \ f+ \ g- \ h+ \ i+ \ j$
(P.L. $\longleftrightarrow F_2$)	$2a+2b+2c+2d-3e-3f-3g-3h+2i+2j$
$(2x \longleftrightarrow 4x)$ (P.L. $\longleftrightarrow F_2$)	$2a-2b-2c-2d+3e-3f-3g+3h+2i+2j$

They are independent of one another and so may be combined into one analysis. The first compares all diploids with all tetraploids. The second compares pure lines with F_2 populations. The third may be called the interaction of the first two degrees of freedom, and it will be seen that it is obtained by cross-multiplication of the coefficients of the first two functions.

The decomposition of the sum of squares for lines is given in Table XVI. The diploid-tetraploid comparison gives a mean square which is less than error. F_2's, on the other hand, produced significantly more dry matter than pure lines. The third comparison is also less than the error, thus showing that heterosis does not differ significantly in diploids and tetraploids. The remainder is still very large, showing that causes other than those included in the above classification introduce big differences. This result entirely agrees with that obtained in 1934, namely that tetra-

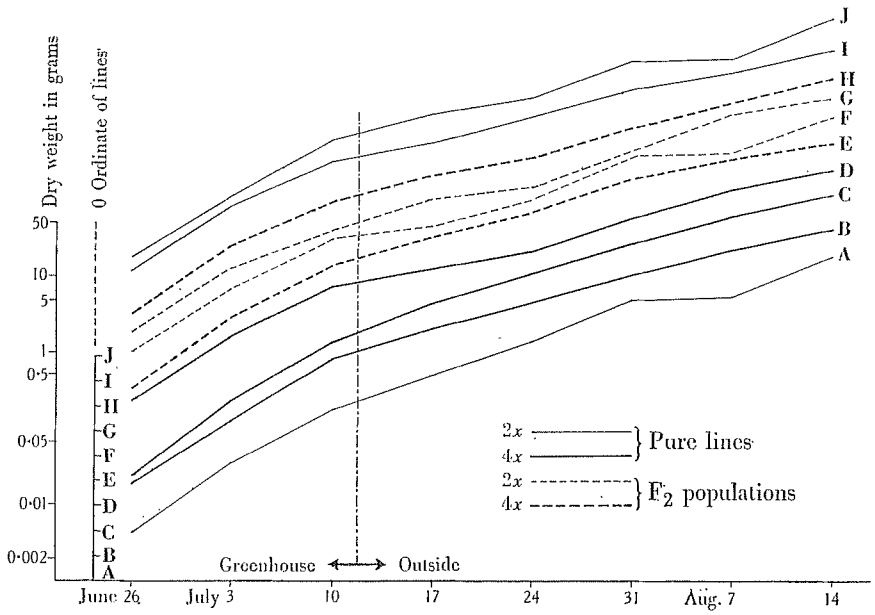


Fig. 2. The growth of the ten lines *A*, *B*, *C*, *D*, *E*, *F*, *G*, *H*, *I* and *J* represented on a logarithmic scale. The origins of the scale for each line are staggered, so as to space the curves.

ploids do not produce significantly more matter than diploids, and extends this conclusion to a period of two months after sowing.

The decomposition of the times × lines interaction is given in Table XVII. Three groups of seven degrees of freedom each, which correspond to the three degrees of freedom of the "lines" analysis, are isolated.

The diploid-tetraploid comparison gives a significant mean square, but that component in it which is due to a linear regression is not significant. It is thus not due to a general difference in growth rate, but to different changes of the growth rate throughout the period. The remainder from the linear regression only just fails to reach the 0·01 level of significance.

Both the variance due to the pure line—F_2 comparison and its linear component are significant, and the remainder, while not very large, is still above the 0·05 level of significance. But the F_2's grew *more slowly* than pure lines, so that the increase in the amount of dry matter produced, which was shown in the "lines" analysis, took place *in spite* of a slightly slower growth rate. It must thus be due to a greater initial weight. In this respect the data are in entire agreement with those of Ashby on maize (Ashby, 1930, 1932). Dr Ashby has kindly shown me some of his

TABLE XVI

Decomposition of lines

Variance	D.F.	S. of S.	M.S.	z	0·01 z
Lines (total)	9	15·8235	1·7582	1·8417	0·4199
($2x \longleftrightarrow 4x$)	1	0·0024	0·0024	—	—
(P.L. $\longleftrightarrow F_2$)	1	1·8799	1·8799	1·8749	0·9492
($2x \longleftrightarrow 4x$) (P.L. $\longleftrightarrow F_2$)	1	0·0249	0·0249	—	—
Remainder	6	13·9163	2·3194	1·9802	0·5202
Error	640	28·2891	0·0442	—	—

TABLE XVII

Decomposition of TL interaction

Variance	D.F.	S. of S.	M.S.	z	Points of z	
T.L. interaction	63	11·3389	0·1800	0·7018	0·01	0·2134
t ($2x \longleftrightarrow 4x$)	7	0·8907	0·1272	0·5286	0·01	0·4931
Linear regression	1	0·1426	0·1426	0·5856	0·05	0·6748
Remainder	6	0·7480	0·1247	0·5184	0·01 0·05	0·5202 0·3740
t (P.L. $\longleftrightarrow F_2$)	7	1·0347	0·1478	0·6036	0·01	0·4931
Linear regression	1	0·4522	0·4522	1·1627	0·01	0·9492
Remainder	6	0·5828	0·0971	0·3934	0·01 0·05	0·5202 0·3740
t ($2x \longleftrightarrow 4x$) (P.L. $\longleftrightarrow F_2$)	7	0·2226	0·0318	—	—	—
Linear regression	1	0·0563	0·0563	0·1209	0·05	0·6748
Remainder	6	0·1663	0·0277	—	—	—
Remainder	42	9·1908	0·2188	0·7998	0·01	0·2345
Error	640	28·2891	0·0442	—	—	—

new and unpublished data, which show that heterosis in tomatoes is of the same nature as in maize.

None of the items of the interaction of the $2x \longleftrightarrow 4x$ and P.L. $\longleftrightarrow F_2$ comparisons are significant, showing that the differences in growth of pure lines and F_2 populations are the same in both diploids and tetraploids.

The remainder from all three comparisons, based on 42 degrees of freedom, is still very significant, so that other factors introduce big differences.

Discussion

From these experiments it appears that the difference in size between diploid and tetraploid tomatoes which has been reported on several occasions is a deceptive appearance. It should be noted that in no case where this difference was described have any actual measurements been given.

In the case of the 1934 experiment, it was seen that the initial advantage of 30 per cent heavier embryos was lost during the 11 days following sowing. It is conceivable that in another environment this would not be so, and that the adult plant would benefit from all or part of this initial advantage. If more definite information is to be gained on this matter, differences in external conditions must be introduced into the experiments as well as the diploid-tetraploid difference. It is a well-known principle in agricultural experimentation that a better variety may only be superior in being able to profit from a better environment. In cereal variety trials differences in sowing distance are often introduced because a higher-yielding variety will only get a chance if given more space. A similar principle may well apply to polyploidy. In this connection it is of interest to note that the geographic distribution of polyploid races is often strikingly different—a subject the data on which have recently been collected together by Müntzing (1936).

In the experiments reported here, the effect of polyploidy on the growth rate showed complex interactions with the genotype. In any case, these effects are relatively small and can only be detected by the special technique used. But the danger of drawing conclusions from experiments with only one genotype is evident.

Summary

1. Experiments are described which are designed to compare diploid and tetraploid tomatoes from the standpoint of growth and total size. The data are treated by analysis of variance.

2. It is shown that tetraploids do not differ consistently from diploids in the total amount of substance produced. Polyploidy interacts in a complex way with the genotype to produce small deviations from a constant growth rate.

3. Tetraploid embryos are about 30 per cent heavier than the diploid, but this advantage is lost during germination.

4. Tetraploids do not differ significantly from diploids in their water content.

5. Heterosis in the F_2 is only due to increased initial weight, and it is of the same magnitude in diploids and tetraploids.

ACKNOWLEDGEMENTS

I wish to express my indebtedness to Dr F. W. Sansome for supplying the material used in this investigation, and for advice in the preparation of the paper. To Prof. R. A. Fisher for his kindness in allowing me to do the statistical work in the Galton Laboratory, and for much valuable advice. To Prof. J. B. S. Haldane for his helpful criticism of the manuscript.

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