

SIZE INHERITANCE AND GEOMETRIC GROWTH PROCESSES IN THE TOMATO FRUIT

JOHN W. MACARTHUR AND LEONARD BUTLER
Department of Biology, University of Toronto, Toronto, Canada

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INTRODUCTION

THE literature on size inheritance contains but few references to what seems to be an important clue to its study, namely, a frequent tendency for F_1 and F_2 hybrids to approach the geometric mean of the parent sizes (GROTH 1914, 1915). It is almost universally assumed and taught that the ideal hybrid will "blend" in size to the arithmetic mean. The reasons for the comparative neglect of geometric relationships seem to be mainly that the studies of size inheritance hitherto made have been with few exceptions confined to crosses between parents so similar in size that arithmetic and geometric means are not easily distinguished. Such confusion is but natural, since size fluctuates widely under environmental influences, and is often confusingly increased over its true value by heterosis.

The classic data are in fact mainly drawn from crosses where the parent races or species differed by not more than 2, 3 or 4 to 1. Approximately such a ratio characterizes the parental differences in the bulk of the published crosses involving linear measurements or proportions, surface areas, volumes or weights of the body as a whole or of some part or organ. Witness the many studies on rodents and fowls among animals and the even more numerous similar observations on the inheritance of size of flowers, seeds, fruits, leaves, stems or roots of both cultivated and wild plants.

Much greater size differences than these are obtainable in crossable parents in selected cases. For instance artificial selection has produced an extremely large size range in fruits of apples, peppers and tomatoes, in tubers of potatoes, and a striking contrast in body size between bantam and Asiatic breeds of fowls, etc. Hybrids between such extremes generally show not blending but "dominance of small size," or inheritance by some geometric rule.

The tomato fruit provides especially favorable material for size study, since there are enormous differences between the small one gram fruits of "Red Currant" (*Lycopersicon pimpinellifolium*) and the comparatively gigantic 100 to 400 gram fruits of some commercial varieties of *L. esculentum*. During the last twelve years we have accumulated a vast amount of size data, and from them evolved a theory of size inheritance (MACARTHUR 1935, BUTLER 1937), here applied in the hope that it will clarify

TABLE I
 Mean fruit weight in grams of the different tomato crosses.

CROSS NUMBER	LARGER PARENT	SMALLER PARENT	NO. OF F ₂ PLANTS	LARGE P ₁	SMALL P ₁	F ₁	F ₂	GEOMETRIC MEAN	ARITHMETIC MEAN	
<i>Parents Differing Greatly in Size</i>										
449	Yellow Pear	XRed Currant	84	12.4	1.1	4.2	4.2	3.7	6.7	
3413	Large Pear	XRed Currant	210	54.1	1.1	7.4	6.4	7.4	27.6	
25A	Grape Cluster	XRed Currant	75	55.8	1.1	7.9	8.0	7.6	28.5	
3313	902 selection	XRed Currant	914	56.2	1.1	7.2	7.3	7.6	28.0	
34T	Putman's Forked	XRed Currant	124	57.0	1.1	7.1	7.5	7.7	29.0	
3316	745 selection	XRed Currant	650	57.5	1.1	7.4	7.8	7.7	29.3	
452	Honor Bright	XRed Currant	143	150.0	1.1	9.4	6.9	12.3	75.5	
441	Golden Queen	XRed Currant	136	152.4	1.1	10.1	10.2	12.3	76.7	
3210	Tangerine	XRed Currant	720	173.6	1.1	8.3	9.5	13.2	87.3	
414	Albino	XRed Currant	219	312.0	1.1	12.0	12.3	17.5	156.5	
3415	Tangerine	Xr y f H selection	140	173.6	5.0	38.1	50.0	29.4	89.3	
729	r o r y selection	XBurbank Pres.	58	36.0	5.1	14.0	15.8	13.5	30.6	
901	l c u h selection	XBurbank Pres.	238	55.0	5.1	21.0	22.3	10.8	30.0	
721	Devon Surprise	XBurbank Pres.	66	58.0	5.1	23.0	22.9	17.2	32.5	
403	Dwarf Aristocrat	XYellow Pear	222	112.6	12.4	35.5	41.0	37.4	62.5	
445	McMullen Pink	XYellow Pear	286	148.8	12.4	44.0	45.2	43.0	80.0	
451	Honor Bright	XYellow Pear	136	150.0	12.4	47.5	40.1	43.3	81.2	
<i>Parents Differing Slightly in Size</i>										
3409	r y f H selection	XRed Currant	86	5.0	1.1	3.3	3.4	2.5	3.0	
405	Peach	XYellow Pear	495	42.6	12.4	23.1	26.2	23.0	27.5	
410	Honor Bright	XWhite Apple	183	150.0	39.1	49.9	57.2	70.5	94.5	
401	Dwarf Aristocrat	XPeach	103	112.4	42.6	67.1	73.3	69.5	77.5	
450	Honor Bright	XPeach	390	150.0	42.6	68.1	61.6	80.0	96.3	
434	Dwarf Aristocrat	XGrape Cluster	90	112.4	55.8	73.3	81.1	79.0	84.1	
3209	Tangerine	X902 selection	534	173.6	68.0	112.3	86.3	99.0	114.9	
3201	Tangerine	XR. N. H.	359	173.7	68.0	91.2	81.1	100.0	120.8	
409	Albino	XDw. Aristocrat	216	312.0	112.4	137.9	160.4	188.0	212.2	
438	Albino	XHonor Bright	80	312.0	150.0	160.0	151.3	217.0	231.0	
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some aspects of the problem and also suggest other avenues of research. As a good deal of this material is embodied in the thesis to be published later by the junior author, this paper will be confined to a statement of the theory with a modicum of supporting data. The observations will be presented first and will treat the subject from four different angles.

I. THE INHERITANCE OF FRUIT WEIGHT

There is a large amount of variation between the weights of fruits even on the same plant, but, as will be shown in a later paper, each variety or inbred line has its own average inherited weight. By crossing lines of different fruit weights we can see how the various contrasting fruit sizes are inherited. The average fruit weight was determined by weighing ten fruits from each plant, a certain amount of selection being exercised to avoid using obviously atypical fruits. These abnormal fruits were of two types, undersized ones due to faulty pollination or lop-sided growth, and those that were oversized owing to an increase in the locule number.

The crosses presented (table 1) are divided into two categories, first the cases where the two parents differ greatly in fruit size, and second, those in which the parents differ only slightly. It will be noticed that the resulting hybrids cover the whole range of possible behaviors, illustrating at the one extreme the geometric mean and at the other extreme typical blending. Closer scrutiny of this table will show that the cases that conform most closely to the arithmetic mean of the two parents are crosses in which the parents did not differ greatly in fruit size (small by small, medium by medium, or large by large). It will also be noted that only one F_1 weight is given; it was found that even when the parental size contrast was greatest the reciprocal crosses never differed significantly in F_1 fruit weight.

The main purpose of the table is to bring out the close agreement in both the interspecific and intraspecific crosses between the observed F_1 and F_2 means and the calculated geometric means, and the poor agreement with the arithmetic means. The greater the parental contrasts, the larger become the discrepancies between arithmetic and geometric values and the more the F_1 and F_2 values favor the geometric mean.

That a similar geometric relationship applies equally well in the case of backcrosses is shown in table 2.

Analyzed from this point of view numerous crosses and "grading up" backcrosses in other species show a similar behavior. This is illustrated in SAUNDER'S and MACOUN'S breeding project with the wild Siberian crab; by large commercial varieties of apples (CHIPMAN 1933); in peppers (DALE 1929); and in F_1 hybrids of bantam fowls by large Asiatic breeds (JULL and QUINN 1931).

In these varied materials the approach of the F_1 , F_2 and backcross sizes to the geometric means may be taken to be the general rule, the seeming approach to the arithmetic mean being really limited to those special cases in which parental differences are comparatively small. Since the latter happen to be most numerous in the genetic literature they have come to be considered typical, possibly obscuring thereby an essential feature of size inheritance.

TABLE 2
Mean fruit weights in grams of two tomato crosses and their respective backcrosses.

	P_1	B.C.	F_1, F_2	B.C.	P_1
Red Currant×Tangerine	$1.12 \pm .005$	$3.14 \pm .09$	$9.03 \pm .13$	$32.2 \pm .78$	173.6 ± 3.6
Geometric mean		3.19	13.8	39.5	
Arithmetic mean		5.08	87.3	91.3	
Red Currant×902 selection	$1.12 \pm .005$	$2.5 \pm .15$	$7.41 \pm .10$	$19.8 \pm .95$	$56.2 \pm .05$
Geometric mean		2.9	7.9	20.4	
Arithmetic mean		4.27	28.6	31.8	

2. THE F_2 DISTRIBUTION OF FRUIT WEIGHTS

A prime essential for the study of problems of inheritance of size and other important features of organization is the merging of the physiological, developmental and genetic points of view. The problem thus becomes primarily one of determining the physiology of gene effects during the development of such quantitative characters.

In the recent literature there has been a tendency to attack the problem from the standpoint of gene action and to subject the older view of blending inheritance to considerable criticism. KAPTEYN (1916) long ago pointed out, with numerous appropriate biological examples, that causes depending on size produce proportional or positively skew distributions, instead of normal frequency curves. RASMUSSEN'S (1933) theory of genic interaction assumes that the total effect of the genotype is not determined by the direct simple addition of the effects of quantity genes, but that they interact with one another in such a way that the cumulative effect of all the genes is less than the sum of their individual effects; the net result is inevitably a negatively skew curve. POWERS (1936) in his work on barley actually obtained data directly opposing this view and concluded that the cumulative effect of a number of genes was greater than the sum of their individual effects. Recently SINNOTT (1937) has shown that his F_2 frequency distributions in summer squashes are positively skewed and has interpreted this to indicate that the effects of the size genes are geometrically cumulative.

The form of the F_2 distribution is thus often used as an index of the type of inheritance and the mode of operation of the size genes; for these purposes data are given from two F_2 populations, each consisting of more than a thousand plants. In both cases the curves (fig. 1) are positively skew, and on the basis of such large numbers this skewness is significant. Since in cases of blending inheritance a normal curve is always attained

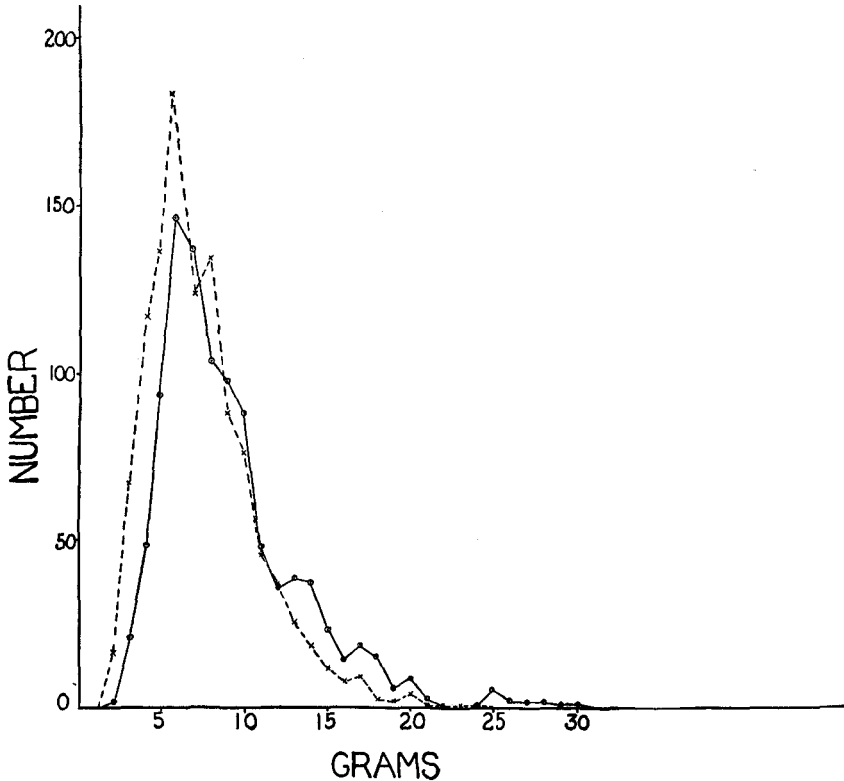


FIGURE 1. Positively skew distributions of mature fruit weights (grams) in two F_2 tomato populations:

Cross	Number of plants	Arithmetic means	Geometric means	Median	$g_1 = \frac{k_3}{k_2^{3/2}}$
3313 F_2 ---x---	1107	$7.41 \pm .10$	6.73	6.24	+1.105
3210 F_2 —•—	994	$9.03 \pm .09$	8.24	7.49	+1.596

unless interaction takes place, some explanation must be given for the skewness. Obviously RASMUSSEN'S theory does not apply in this case. But if the factors react with one another on a geometric or percentage basis, each adding a definite proportion to the already existing capital, then such addition to a small capital will make very little difference, while the same percentage increases based on a large capital will result in large increases.

The result of such a scheme will be that the weights crowd together at the lower end of the scale and spread out at the upper end. This is just what happens in many of the crosses that we have studied. From the means and statistical constants of the data given in the legend of figure 1 it will be seen that the geometric means of the distributions are much closer to the median than are the arithmetic means. This would indicate that the distribution is almost normal around the geometric mean, so that if the data were plotted logarithmically the curve would be nearly symmetrical.

TABLE 3
Mean fruit weights in grams of tall and dwarf F₂ segregates, and their absolute and percentage differences.

Tall parent	Dwarf parent	Mean F ₂ fruit weights		Differences	
		Tall	Dwarf	Absolute (grams)	Proportional (percent)
Red Currant	×902 selection	6.9 ± .10	8.4 ± .30	1.4 ± .31	20.5
Tangerine	×902 selection	81.8 ± 1.4	101.6 ± 2.0	19.8 ± 2.5	23.0
Devon Surprise	×B. Preserving	24.0 ± 1.0	18.1 ± 2.5	5.9 ± 2.7	26.2
Yellow Peach	×Dwarf Aristocrat	76.8 ± 1.5	61.2 ± 1.9	15.6 ± 2.4	21.1
740 selection	×"Primula"	24.8 ± 1.4	18.0 ± 1.3	6.8 ± 1.9	30.0
97M selection	×3213 selection	54.0 ± 1.4	38.0 ± 2.3	16.0 ± 2.7	32.0

3. THE LINKAGE OF QUALITATIVE AND QUANTITATIVE FACTORS

The results of LINDSTROM (1928) and our own extensive data (mainly unpublished) show that there are a number of definite genetic linkages between the known qualitative factors and fruit size genes; for the present purpose part of the first chromosome linkages are chosen (table 3) to illustrate some novel features of gene relationship. These are all crosses of a dwarf parent with a tall one; in some cases the fruits of the dwarf F₂ segregates are larger than those of the tall ones, while in other cases, where expected, the converse relationship is true. Therefore this linkage of fruit size with the dwarf gene must be interpreted as truly genetic and not physiological. The important point now concerns a comparison of the values in the last two columns of table 3. It will be noted that, whereas the absolute difference in grams (next to the last column) between the means of the two segregate classes varies a great deal, the percent increases (in the last column) are relatively constant. Since this percentage is found by putting the difference between the class means over the F₂ mean it would appear probable that the action of the true fruit size gene or genes linked in this first chromosome is to cause an increase in growth which is proportional to the basic fruit size. This illustrates clearly the

difference in such a situation between simple additive growth and proportional or geometric growth. The geometric type of increase prevails in this case, and our results show further that the same type of relationship is exhibited with at least eleven other genes.

Not only the true size genes, but also those influencing size through shape, or general physiological effects display the same action. In our more recent studies (MACARTHUR 1934 a, 1935) we have observed that at least two factors, fasciated fruit (*f*) and lutescent foliage (*l*), show a physiological association with size. The fasciation factor always tends to make the fruits of the fasciated segregates larger than those of the respective smooth-fruited ones, regardless of whether the fasciated parent is the larger or the smaller fruited. Lutescent, on the other hand, tends to make the fruits smaller than those on the green plants in the same F_2 . It is interesting to note that though the differences of the F_2 class means of the fasciated and smooth in the one case and the lutescent and green in the other are erratic when considered in terms of grams, they are rational and subject to analysis when considered on a percentage basis. The rough fasciated fruits are 60 to 80 percent larger than the regular smooth ones, while the fruits of the lutescent plants are 15 to 20 percent smaller than those of the corresponding green plants, carrying similar residual genes.

It is interesting to anticipate here what is taken up more fully in section four and the discussion, namely, the physiological mechanism involved. The evidence to date regarding the action of the fasciated gene indicates that it exerts its effect in the early primordial stage by proliferating more locules; and indeed it would seem logical to infer from observations of the number of fasciated flowers that contain two, three, or even four separate or partly fused ovaries, that the mechanism is more properly characterized as ovary proliferation rather than locule proliferation. No matter which of these mechanisms is operating the net result of imposing this system on the basic fruit size is the same; that is, the effect of this increase in locule number on final fruit size is proportional to the already determined locule size and final cell size. Lutescent on the other hand seems to retard the later developmental processes so that its effect is also proportional to the capital involved.

4. THE GROWTH OF THE TOMATO FRUIT AS RELATED TO CELL NUMBER AND CELL SIZE

Since 1925 it has been our established practice (without at first realizing its significance) to classify tomato plants segregating for fruit shapes (oval, pear, fasciated, etc.) and in a general way for fruit size by an inspection of the ovary primordium at anthesis. This naturally directed attention to growth phenomena during the early period, and in the summer of 1934

the junior author made a histological study of cell number and cell size during this period and of the influence of these factors on the subsequent development of fruit size. Since the majority of our conclusions, though derived in a different manner, are essentially the same as Miss HOUGHTALING'S (1935) the reader is referred to her paper for a detailed discussion of the influence of cell number and cell size on the mature fruit size.

Our conclusions may be summarized as follows:—

1. The period prior to anthesis is characterized by cell division, and any differences in ovary size at anthesis are associated entirely with cell number and not with cell size.
2. The post-anthesis period is characterized chiefly by cell expansion, cell division being a minor factor which just suffices to maintain the epidermis, the cells of which do not expand.
3. The differential cell expansion takes place early in the post-anthesis period and the maximum cell expansion varies greatly in the several varieties.

Since in arriving at these conclusions we made use of the probable number of cells present at each stage, some of the figures of which are included in table 4, it is advisable to give the method employed in calculating them. The variety Yellow Cherry has an ovary diameter of 1.1 mm and a cell wall thickness of .1 mm, the diameter of the cells at this stage is .01 mm. From these data the following computations are made, assuming the fruit to be a sphere:—

External volume $1.1^3 \times .5236$	= .6969	cu. mm
Internal volume $(1.1 - .2)^3 \times .5236$	= <u>.3817</u>	cu. mm
Volume of ovary wall	= .3152	cu. mm
Volume of cell $.01^3$	= .000001	cu. mm
Number of cells $.3152 / .000001$	= 315,000	cells.

By the above method of calculation the cells in the central septa are omitted but this does not introduce any serious error, and in our estimation is preferable to any method that treats the ovary as a solid body.

Table 4 shows that the tomato species and varieties can be divided into three more or less well defined groups as regards cell numbers, with *L. pimpinellifolium* representing the first group, yellow cherry the second, and the *esculentum* varieties the third. The two F₁ hybrids between Red Currant and *esculentum* types as well as Burbank Preserving, known to be a selection from such a cross, fall into the second or intermediate group. Our more recent data show that all F₁ hybrids of *L. pimpinellifolium* X *L. esculentum* have cell numbers between 300,000 and 400,000 and fall into this class, even when the *esculentum* variety is Beefheart which has a relatively enormous 400 gram fruit.

In general the larger the fruit the greater the number of cells in its ovary; there are however exceptions to this rule which are explained by reference to the fifth column where the diameters of the mature cells are given. Therefore cell number and cell expansion together account for most of the final fruit size, as may be tested by computing the cell mass (from the diameters) and multiplying by the cell number.

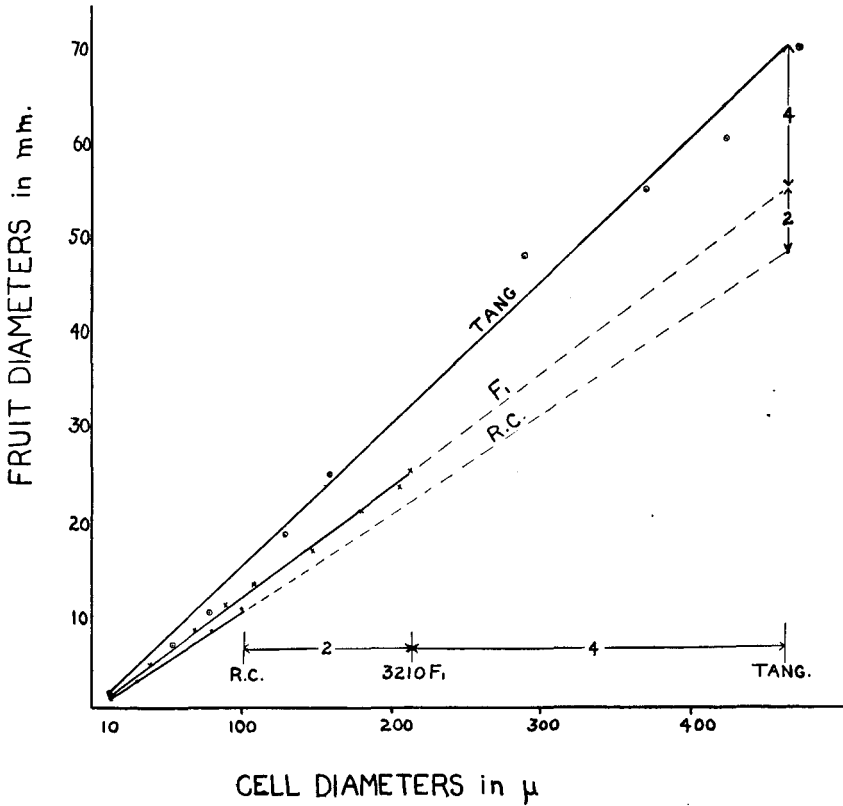


FIGURE 2. Graphs indicating that cell expansion and cell size both operate as geometric processes. A differential increase in cell numbers is seen in the divergent slopes of the three lines and a differential cell expansion in unequal extensions of these lines (see text).

As cell expansion also plays an important part in the determination of fruit size something should be said about its mode of inheritance. Table 4 shows that the mature cell diameters are also divisible into three classes and that these classes bear a geometric relationship to one another.

The effect of these two factors, cell number and cell size, on the final fruit size is brought out clearly in figure 2, where cell diameter is plotted against fruit diameter. The relationship between cell and fruit diameter is evidently a straight line, the slope of the line in the case of the two parents being very different and the F_1 being intermediate. The differences

in slope indicate that for any given cell size the Tangerine has a much larger fruit than does the Red Currant, because of the greater number of cells present in the Tangerine variety. The amount of divergence between the three lines is therefore the effect of initial cell number; the greater the cell expansion the larger the absolute differences between the three lines, but the relative differences remain the same. By observing the end points on each line the effect of cell expansion on fruit size can be studied. If we hold cell number constant, by plotting the final cell sizes all on a line with the same slope, such as the extrapolated Red Currant and F₁ lines,

TABLE 4

The number of cells in the pericarp wall of tomato fruits at flowering time and the cell diameters in mature fruits. The cell size at anthesis in all varieties is taken as .01 mm.

VARIETY	FRUIT WEIGHT (GRAMS)	OVARY DIAMETER (MM)	THICKNESS OF WALL (MM)	NUMBER OF CELLS IN THOUSANDS	MATURE CELL DIAMETERS (MICRA)
Red Currant	1.1 ± .005	.85	.086	164	110
3313 F ₁ (902×R.C.)	7.2 ± .06	1.08	.10	303	200
3210 F ₁ (Tang×R.C.)	8.3 ± .07	1.09	.10	309	220
Yellow Cherry	4.2 ± .11	1.1	.10	315	120
Burbank Preserving	5.2 ± .09	1.2	.09	401	140
Yellow Peach	42.6 ± 2.0	1.5	.08	507	400
Devon Surprise	58.0 ± 2.2	1.4	.10	531	400
Banalbufor	33.1 ± 1.0	1.5	.10	617	350
902 selection	56.2 ± .05	1.6	.08	640	400
Stirling Castle	98 ± 5.4	1.7	.08	659	360
Tangerine	173 ± 3.6	1.8	.08	745	550
John Baer	69.6 ± 3.4	1.8	.09	829	470

we find that the fruit diameters read from these points show geometric progression. Hence we are dealing with two geometric factors, which together would account for the observed relationship between parents and F₁ shown in table 1, and the effect of cell expansion superimposed on cell number is to accentuate the geometric relationship. A similarity may be seen in the time of operation of these two factors, differential cell division taking place in the early part of the pre-anthesis period, and differential cell expansion taking place in the early part (first nine days) of the post-anthesis period.

From the P₁ and F₁ data there at first appeared to be a correlation between cell number and cell size. But in the F₂ population the apparent association between cell number and cell size proved to be a pseudo-correlation; for when the weight is held constant by partial correlation methods

we may safely conclude that cell number and cell expansion are really two separate genetic entities.

Letting w =mature weight, s =cell size, and n =cell number, the correlations are as follows:

$$r_{ws} = +.674 \pm .038$$

$$r_{sn} = +.411 \pm .059$$

$$r_{wn} = +.523 \pm .051$$

$$r_{sn.w} = +.0009 \pm .70$$

Thus the study of cell number and size, and of the growth of the tomato fruit through all but the earliest primordial stages of its development, has led to some definite results which may be associated with the genetic findings. Parents of different fruit size, and their reciprocal crosses in F_1 , F_2 and backcross generations come early to differ in cell numbers in their growth. This early difference in cell number is followed by a subsequent brief period of differential cell expansion. The growth in the long final period is approximately equal both in rate and duration in all varieties and hybrids.

The data presented under headings 1 to 4 draw attention to four lines of approach to the problem of fruit size inheritance, each leading to the same conclusion. Collectively they form a substantial support to the following hypothesis.

A WORKING HYPOTHESIS OF FRUIT SIZE INHERITANCE

A view has already been proposed (MACARTHUR 1935, BUTLER 1937) that appears tenable for the tomato data and adequate to explain the principal results described. The basic size factors are considered as rate genes, one group of which governs the rate of division (or the duration of active mitosis) in the formative stages from the earliest establishment of the fruit primordium to anthesis. Earlier or later in this limited time-effective period a large-fruited variety or species undergoes a few more cell divisions than a smaller-fruited one. The differences of cell numbers found in fruits of typical varieties (table 4) are such as would be caused by a difference of one or two divisions out of at the most 17-19 divisions. Each extra division at this stage doubles the initial capital. Ovary proliferation and formation of additional locules may both increase this capital. On the basis of such differences in cell number at anthesis, the size increases occurring later by expansion of each of the cells is therefore proportional to the cell number. Increase of capitals at equal rates over equal periods of time by the compound interest rule results in comparatively vast absolute differences in final fruit sizes. There is, however, the further evidence suggesting that other factors governing cell expansion itself may be also geometric in their action (fig. 2). Since both basic processes, con-

trolling cell number and cell size, are probably geometric in nature, the mature fruit sizes would be such as were observed (tables 1 and 2).

From the genetic aspect, the allelic size factors from parents of different size would control the rate and number of divisions in the corresponding formative period of the F_1 hybrid. Thus a blending of mitotic rates results in the "dominance of small size" (wild type) factors in the fruit of the hybrid, that is, in a geometric mean of ultimate size as far as cell number is involved; a partial dominance of the slower rate would reduce the F_1 size even below the geometric mean (table 1).

A small parent with cells from x mitotic divisions crossed with a large parent with $x+2$ divisions would produce an F_1 with fruit size characterized by $x+1$ divisions. This latter number is also the average of the F_2 generation, but with factor segregation increasing the variability as in the usual theory. To illustrate with an actual case, the cross of the 164,000-celled Red Currant with the 745,000-celled Tangerine was observed to produce an F_1 hybrid bearing fruits of 309,000 cells. In the two backcrosses the expected less-than-intermediate number of cells are evidently formed, as shown by the ovary sizes and the geometric means.

Similar considerations are obviously applicable to cell expansion (data in last column of table 4). In any case a large amount of variation in fruit sizes would be expected for at least two reasons, quite apart from the known modifying effects of environment and of genes controlling shape, locule number, etc (YEAGER 1937): (1) Doubtless mitoses do not continue synchronously in all cells of the anlage, at least after chemo- and histodifferentiation begin. Accordingly cell numbers in varieties and hybrids are not expected to conform strictly to any 1:2:4 series. (2) Cell division and cell expansion appear to be largely independent processes; if so, the possible combinations of cell numbers and sizes would be numerous and varied enough to give a wide range of fruit sizes. An attempt is being made to synthesize and select some of these combinations, for example fruits containing the Red Currant cell number and the Tangerine cell size, etc. Each such selection should theoretically be obtainable with or without fasciation, with high or low locule number, and in varying shapes. Collectively these selections would be expected to duplicate most of the fruit types occurring in the known cultivated varieties and wild species.

DISCUSSION

The familiar view of size inheritance in its simplest form assumes that size genes 1) are numerous, 2) lack dominance, producing a blend as regards size in the F_1 hybrid, 3) are equal, and 4) simply additive in their effect, producing symmetrical F_2 distributions, and that 5) their segrega-

tion and assortment explain the increased variance of the F_2 population and the different means and variance of F_3 selections.

Objection is raised only to attributes 2), 3) and 4). The assumed lack of dominance is patently inconsistent with the observed behavior of the bulk of qualitative genes and with the dominance theory of heterosis, which also deals with the same or similar quantitative factors. The cases actually analyzed have often revealed some major and other accessory or modifying size genes. The F_2 distributions are frequently asymmetrical.

In the tomato where the analysis of fruit size has perhaps been carried farther than in other species, genetic studies have from the first shown clearly that the fruit size is gene-transmitted, size as a character being unusually complex and multifactorial. Many typical recessive mutant factors affecting size have been recognized and located in chromosomes (MACARTHUR 1934b); some of these exert their important size effects by modifying fruit shape or locule number or both (YEAGER 1937); for example, the genes for fasciation (*f*) and those raising the locule number increase fruit size, probably by increasing the basic cell number, while at least two genes which elongate the fruit (ovate, *o*, and "plum") tend to decrease its size. Other recessive genes with marked and distinguishing specific qualitative effects also have a general or physiological influence on size (MACARTHUR 1934a, 1935; CASTLE 1936); lutescent (*l*), a chlorophyll deficiency, slows down both plant and fruit growth and decreases the ultimate size of the fruit; tangerine (*t*) and possibly peach (*p*), on the other hand, appear to enlarge the fruit perhaps by acting on the cell expansion mechanism. Linkage experiments have shown the existence of other factors, for example, in chromosomes I, II and III, which presumably act as "size genes" *per se* for they produce their size effects when fruit shape, locule number, and all known qualitative factors are held constant.

These instances show that the several identified factors controlling size obviously do not necessarily or always lack dominance. Many are known to exhibit a fairly typical dominant-recessive relationship. It is relevant to mention also that the dominance theory of hybrid vigor implies an F_2 asymmetry, but not of the kind observed, since the skewness is negative if large size is dominant (ASHBY 1937c, pp. 432-33).

Some of the factors isolated are certainly unequal, for they have been shown to affect size by varying amounts. Several of the genes determining size or number of cells are apparently distinct in nature and mode of influence, inasmuch as they affect different processes and act at different times in ontogeny. The histological analysis of fruit development, though still far from complete, already directs attention not to one process only, but to many (rate and duration and localization of cell division, rate of

advancing differentiation, time and amount of cell expansion, etc). It is certainly clear that some of the chief size factors influence ovary proliferation (f), or locule number, others localization of differential growth (f , o , plum); and still others probably determine fruit cell expansion (t , p) or fruit cell division rate or general plant growth (l). These factors being dissimilar in nature and unequal in effect, no linear relation would be expected or possible between the number of factors and the size of the fruits. What they have in common is that most of them act comparatively early in fruit growth, and probably all of them act, whether directly or indirectly, on processes of a geometric nature.

Since the F_2 distributions are strongly and positively skew the interaction of the various size factors can hardly be either arithmetically cumulative in total effect or according to a law of diminishing returns. Both the F_1 positions and the F_2 distributions are features associated with geometric growth, and show the likelihood that consideration of geometric processes will prove indispensable for an understanding of size inheritance. Since cell number and size are of widespread importance in many processes involving embryological organization and physiological functions, it is possible that quantitative characters other than size may also have a geometric basis.

It deserves some notice that conclusions in many ways parallel have been reached recently by several investigators working with quite different materials and objectives. In mutant races of *Drosophila*, an eye size directly proportional to that characteristic of the imago has been fixed and is already detectable in the anlage by the time the first 11.6 percent of the total development period is completed (MEDVEDEV 1935). The breed differences in body size of rabbits are evident when only five or six cleavage divisions have occurred (CASTLE and GREGORY 1929, GREGORY and CASTLE 1931); and in chickens such cell number differences are discernible in the embryos before hatching (BLUNN and GREGORY 1935). The latest work on the physiology of heterosis (ASHBY 1937a, b, c; LUCKWILL 1937; but contrast EAST 1936) has again referred the greater size of F_1 plants displaying a marked hybrid vigor to an initial advantage in size of the embryo primordium. Such cases from both animals and plants suggest that some common and consistent explanation may be found to account for the genetically determined size differences characteristic of parts or of whole organisms.

These observations concentrate attention on the present need for researches 1) to discover just how early and by what factors the differences in amount of capital, that is, the number and size of cells comprising the primordium of the organ anlage or embryo, are determined; 2) to demonstrate more precisely by linkage studies the existence and nature of factors

more or less specifically controlling cell number and cell size, and obtain such factors in their various combinations, and 3) to unify the theory underlying heterosis and quantitative inheritance in general.

SUMMARY AND CONCLUSIONS

The tomato provides especially favorable material for the study of fruit size inheritance from the combined genetic and developmental aspects. Many qualitative and quantitative factors have been identified and mapped whose specific or general size effects have been localized as to time, site and general mode of action.

That fruit size fundamentally involves geometric processes is indicated by four different lines of approach:

1) The average F_1 , F_2 and backcross fruit sizes approach more closely to the geometric mean of the parent varieties or species crossed, than to their arithmetic means, as is usually supposed.

2) Linked size genes, as well as fruit shape and other genes affecting size, appear to operate on a percentage basis.

3) The F_2 distributions are positively skew.

4) Histological analysis of developing fruits shows that the basic phenomena involved are those controlling cell number and cell size, both of which appear to act during limited time-effective periods (p. 260), and in a geometrical manner.

The characteristic variety or species fruit sizes are anticipated in the size of the ovary primordium, which in turn is determined by differences in cell number (brought about by different rates of cell division in the pre-anthesis period), and by varying amounts of cell expansion (fixed in the first days after anthesis). On the basis of the unequal cell numbers and sizes established in the early anlage the later observed proportionate or percentage increases produce relatively enormous absolute differences in mature fruit size.

A theory proposed to account for the histological observations and the genetic results is that rate genes control in the main two basic geometric processes, some determining the number of cell divisions, others the amount of cell expansion. Together the factors govern differential growth in size of the primordia, creating unequal amounts of initial capital. It is such genes acting geometrically the heterozygous combinations of which produce the F_1 fruit sizes noted and the assortment of which explains the means and skewness of the F_2 distributions.

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