

POLYCOTYLEDONY IN THE GENUS LYCOPERSICON

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INTRODUCTION AND LITERATURE REVIEW

Among the large numbers of tomato seedlings grown at the U. S. Regional Vegetable Breeding Laboratory, Charleston, South Carolina, occasional seedlings were found with either notched, cleft, or apparently increased numbers of cotyledons. No special attention was paid to this occurrence, which is commonly known by those who grow and observe large numbers of tomato seedlings, until unusually high percentages of these forms were observed in some fourth generation hybrids from a cross, Lycopersicon pimpinellifolium (Jusl.) Mill. x L. esculentum Mill. var. Marglobe. In certain of these populations the abnormalities appeared in as high as 30% of the seedlings. This fact suggested that the condition was inherited. Since no mention of plurality of cotyledons was found in recently published lists of inherited characters in tomatoes, MacArthur (125) and Boswell (25), it was decided to investigate this easily recognizable character.

The objects of the study were to determine, if possible, the inheritance pattern of the character and any association between such cotyledon characters and other morphological features of the plants, particularly those having to do with greater yield. It would be of value, for example, to know whether these individual seedlings which appear in commercial tomato varieties should be discarded because they were associated with inferior stock, disregarded because of equality with normal seedlings, or saved as superior stock.

A complete discussion of the extensive literature on polycotyledony was impossible in this report since a great majority of the references were but brief notes reporting the sporadic appearance of the condition in various species of plants. Most of the reports were

published in Europe during the 19th century. The last literature survey dealing exclusively with polycotyledony was made by Duchartre (58) in 1848. Penzig (156, 157) in 1921-22, described teratological phenomena, including instances of polycotyledony in approximately 145 species of plants, but did not give special attention to the character. The lack of a complete review of the subject has led many recent investigators to understate the frequency of the occurrence of polycotyledony. Both Litovchenko (119) and Purkayastha (158) made this error, the former finding reference to only 50 species of wild and cultivated plants in which there were reported to be polycotyledons. The author's review of the literature revealed that the phenomenon is quite frequent.

The frequency is shown in TABLE I, which is a summary representing the minimum number of species exhibiting polycotyledony. There were without doubt many more which had been observed without being recorded and others possibly reported in publications not located in this survey. It was evident, however, that polycotyledons are widespread among Dicotyledonous plants, since a total of 295 species in 68 families is included. It should also be noted that the two largest plant families showed the largest numbers of polycot species.

In addition to the reports on the presence of these forms, many investigators described the range of the phenotypic expression of the condition, noting the wide variations found. This variation has been most completely analyzed, however, by DeVries (198, 199) in 1902-03. His classification, which has been generally followed by later workers, follows: The most common form is the tricotyledon which has three separate cotyledons. The next is the hemitricotyledon with one normal and one split cotyledon, the latter of which assumes all conceivable

TABLE I

The occurrence of polycotyledons among families of Dicotyledons.

Families with nine or more species showing polycotyledony

	No. of polycot species	No. of species in family (approx.)
Compositae	28	11,000
Leguminosae	21	7,000
Proteaceae	20	1,000
Cruciferae	18	1,600
Umbelliferae	13	1,500
Caryophyllaceae	12	1,350
Ranunculaceae	12	680
Rosaceae	11	1,500
Scrophulariaceae	9	2,500
Solanaceae	9	1,600

Families with less than nine species showing polycotyledony

No. of polycot species			
Primulaceae	8	Resedaceae	2
Rutaceae	7	Salicaceae	2
Chenopodiaceae	6	Saxifragaceae	2
Euphorbiaceae	6	Sterculiaceae	2
Onagraceae	6	Valerianaceae	2
Aceraceae	5	Verbenaceae	2
Campanulaceae	5	Ampelidaceae	1
Papaveraceae	5	Anacardiaceae	1
Fagaceae	4	Aquifoliaceae	1
Juglandaceae	4	Berberidaceae	1
Urticaceae	4	Betulaceae	1
Convolvulaceae	3	Cactaceae	1
Geraniaceae	3	Combretaceae	1
Labiatae	3	Cornaceae	1
Lauraceae	3	Ebenaceae	1
Loranthaceae	3	Ericaceae	1
Malvaceae	3	Gentianaceae	1
Pittosporaceae	3	Hydrophyllaceae	1
Polemoniaceae	3	Lineae	1
Polygonaceae	3	Lythraceae	1
Rubiaceae	3	Malpighiaceae	1
Tiliaceae	3	Myrtaceae	1
Amarantaceae	2	Papayaceae	1
Balsaminaceae	2	Pedaliaceae	1
Boraginaceae	2	Plantaginaceae	1
Caprifoliaceae	2	Portulacaceae	1
Crassulaceae	2	Sapindaceae	1
Dipsacae	2	Violaceae	1
Oleaceae	2	Zygophyllaceae	1

degrees of division from a slight notch to almost complete separation into two members. Much less frequent than the first two forms are the tetracotyledon, with four cotyledons and the hemitetracotyledon. The latter has three cotyledons, one of which is split, or two cotyledons, both of which are split. Complete series illustrating these types were described by him in Acer Pseudoplatanus, Amaranthus speciosus and other species. Comparison of this series with those described in many other genera by numerous investigators (e.g. 13, 143, 149, 212), showed a striking similarity between them.

In order to more fully describe or to explain the morphological variations, several investigators also studied the vascular systems in normal compared with polycotyledonous plants. This was done as early as 1868 by Junger (101) who noted two "midveins" in tricotyledons instead of one as in normal "dicotyledons" of the same species. More extensive work on this phase of the morphology of polycotyledons was done by Compton (46), Harris et al. (86) and Bexon and Wood (14). No references were found which described abnormal vascular supplies in tomato cotyledons, but the normal disposition of the veins was described by Woodcock (210) in 1936, who found that two principal veins go to each cotyledon.

In addition to various forms of division of the cotyledon and the changes in the vascular supply, a third morphological feature was repeatedly described in the literature. This was the alteration in the leaf placement or phyllotaxy in polycotyledonous plants. Among those citing such changes were Junger (101), Winkler (205) in 1875, Lubbock (121) in 1892, and Weisse (203) in 1921. Recently the idea of the association of leaf placement and increased leaf area, with the

possible increase in yield, has been brought to the fore. The report of Litovchenko (119) indicated that increased yields and larger leaf numbers were associated genetically with the appearance of polycotyledons. The increase was noted in the total number of seeds from tricotyledonous castor bean plants (Ricinus communis) and in the total weight of sugar and fodder beets (Beta vulgaris). In the latter he also noted an increase in the total number of leaves which resulted from altered phyllotaxy in tricotyledonous plants. Any such increases would probably be valuable to beets and leafy vegetables such as lettuce. It would also be of importance to tomato plants in the southern United States, where leaf coverage is often of critical importance in protection of fruits from sun scald.

From the very earliest history of polycotyledony, attempts have been made to secure strains which would show 100% phenotypic polycotyledony. Winkler (205) in 1875, after many carefully repeated attempts, found that he was unable to locate any single sample of seeding in which all the plants manifested this form. Cevidalli (42) in 1900 found polycotyledonous races of beans (Phaseolus vulgaris) and in selecting for greater percentages over a period of five years observed the following percentages: 5%, 20%, 30%, 60% and 93.83%.

Probably the most comprehensive contributions to the subject of polycotyledony, particularly regarding selection, were made by DeVries (198) in 1902 and later. He studied the subject over a period of more than 10 years and his principal conclusions were:

1. The condition expresses itself in a continuous series from normal (Phenotypic) dicotyledons to plants with three or more cotyledons. Tricots, hemitricots and tetracots are thus expressions of

the same condition. Hemitricots are not hybrids between phenotypic dicots and tricots.

2. There are two principal forms of polycotyledonous races. The first, the Halbrasse, has low percentages of abnormal seedlings, rarely going over 5% in spite of long continued selection. The second, the Mittelrasse, has approximately as many polycots as dicots and may, by selection, be brought up to percentages over 90. It is not possible to tell from the appearance of any individual seedling to which of the two forms it belongs. To do this its progeny must be examined.

3. All expressions of polycotyledony are found in both of the forms.

He gave an example of the first form in a line of Oenothera lamarckiana rubrinervis, which, after being inbred for four generations, varied in polycot percentages only from 0.3% to 2.8%. On the other hand, examples of the second form showed results as follows:

	Generation and percentages of polycotyledons		
	<u>First</u>	<u>Second</u>	<u>Third</u>
Clarkia pulchella	16	64	79
Phacelia tanacetifolia	14	58	90
Papaver Rhoeas	20	56	75
Helichrysum compositum	41	51	--

A definite conclusion which DeVries emphasized was that it was futile to attempt to establish lines 100% polycotyledonous, since the apparently normal seedlings were in reality a part of the series showing the visible changes.

A final example of the attempts at such selection was given by the work of Mumerati and Costa (145) in 1933-34. They stated that in trials lasting over a period of twenty years, it was impossible, in spite of over 1,000 plantings of beet seed, to obtain a pure race of polycotyledonous seedlings. They noted, however, that the character increased in frequency as a result of crossing one "deviating" line with another.

The above evidence was ample proof that polycotyledony could be increased through selection, but it must be pointed out, at the same time, that the actual genetic situation was not brought much nearer to a solution.

In spite of the fact that the tomato has been the subject for many inheritance studies, reference to polycotyledony in tomato seedlings was exceedingly rare. Penzig (155) in 1894, under Lycopersicum esculentum Mill., stated, "Herr Dr. Rostan sandte mir Keimpflanzen mit drei Cotyledonen." Agrelius (4) stated, "Out of 428 seeds of previous dicotyledonous plants of Lycopersicon esculentum Mill. but 5 were tricotyledonous, or just over 1 per cent.... ." Gates (76), reporting on the later behavior of the tricotyledons mentioned by Agrelius, remarked, "From the 106 seeds obtained from two tricotyledonous seedlings of tomato in the greenhouse at Manhattan by P. R. White, no, or only very poor plants were obtained, not one of which was tricotyledonous." MacArthur (124), in 1934, speaking of progenies which were derived from X-rayed plants, stated, "One progeny had 25% polycotylous seedlings, but this trait seems to be unfixable." These references indicated failure to increase the incidence of polycotyledony through selection in tomatoes and gave no definite information on its inheritance.

From the preliminary observations made on tomato seedlings at Charleston and from the indications in the literature concerning inheritance and possible yield variations associated with polycotyledony, it seemed probable that a careful study of the material on hand might establish more concrete relationships between these features.

PROCEDURE

Seedling studies. In order to determine the range of expression and frequency of polycotyledony, the associated morphological features and the inheritance pattern, it was necessary to examine thousands of seedlings. Seeds of commercial tomato varieties from the United States and Europe, of Lycopersicon species and other foreign accessions, largely from South America, and of hybrid populations, were planted in sandy soil in flats and the records taken six to twelve days later. Crosses were made in a screened greenhouse.

Mature plant studies. Plants derived from commercial seed of Marglobe and Rutgers, in which polycotyledons occasionally appeared, were used in a test of leaf and fruit number. A field planting was made in the fall of 1942 at Charleston, S. C. Plants of known cotyledon phenotype were used. They were set in six-foot rows, five feet apart in the row, six plants to a row. The rows were arranged in five randomized series, a row of Marglobe and a row of Rutgers included in each series. Within the rows, three normal plants alternated with three polycot plants. Two other separator rows were included in each series to aid in the randomization but only the data from Marglobe and Rutgers rows were used in the analysis of the results. The entire planting was bordered by Rutgers plants. Leaf counts were made at several intervals during the plant growth but only the final values, leaf numbers of the mature plants, were used.

To avoid complications which might arise from disease or other causes, all fruits were picked on the same day, were separated into large, medium, and small sizes, and counted. These three groups were referred to as early, mid-season and late, respectively. Total weight of fruits from each plant was recorded in grams.

RESULTS

Range of expression of polycotyledony in Lycopersicon. Classification of the seedlings according to cotyledon type revealed that many intergrades were distinguishable. The seven principal types, Fig. 1, were found to closely resemble corresponding types in other genera.

During the detailed study of the seedlings, the five types, C to G, Fig. 1, were divided arbitrarily into nine classes shown in Fig. 2, and were known collectively as polycotyledons or polycots. That many more classes were actually detected is indicated in Fig. 3, in which several gradations in the division of a hemitricotyledon are shown. Actual representatives of several cotyledon classes are pictured in Figs. 4 and 5.

The appearance of several cotyledon classes raised the question of the relative frequency of each. This was determined by analysis of hundreds of populations and may be shown by an example from the complete classification of a group of populations which originated in a family with high percentages of polycotyledons, TABLE II.

The results in this table indicated that the various cotyledon phenotype classes of the parent plants, listed in the first column, were not exclusively reproduced in the progenies. This is shown by the numbers in each class in the last nine columns. For example, the first parent plant with normal cotyledons, gave seedlings with eight different phenotypes in addition to normals. Also, the first hemitricot parent plant of class 5, produced in 100 seedlings, not only several of class 5, but some in each of the other polycot classes. It also produced 63 seedlings phenotypically normal.



Figure 1. Seven principal types of tomato cotyledon phenotypes.

- A. Pseudo-monocot
- B. Dicot (normal)
- C. Hemitricot
- D. Tricot
- E. Hemitetracot (two cotyledons, both cleft)
- F. Hemitetracot (three cotyledons, one cleft)
- G. Tetracot

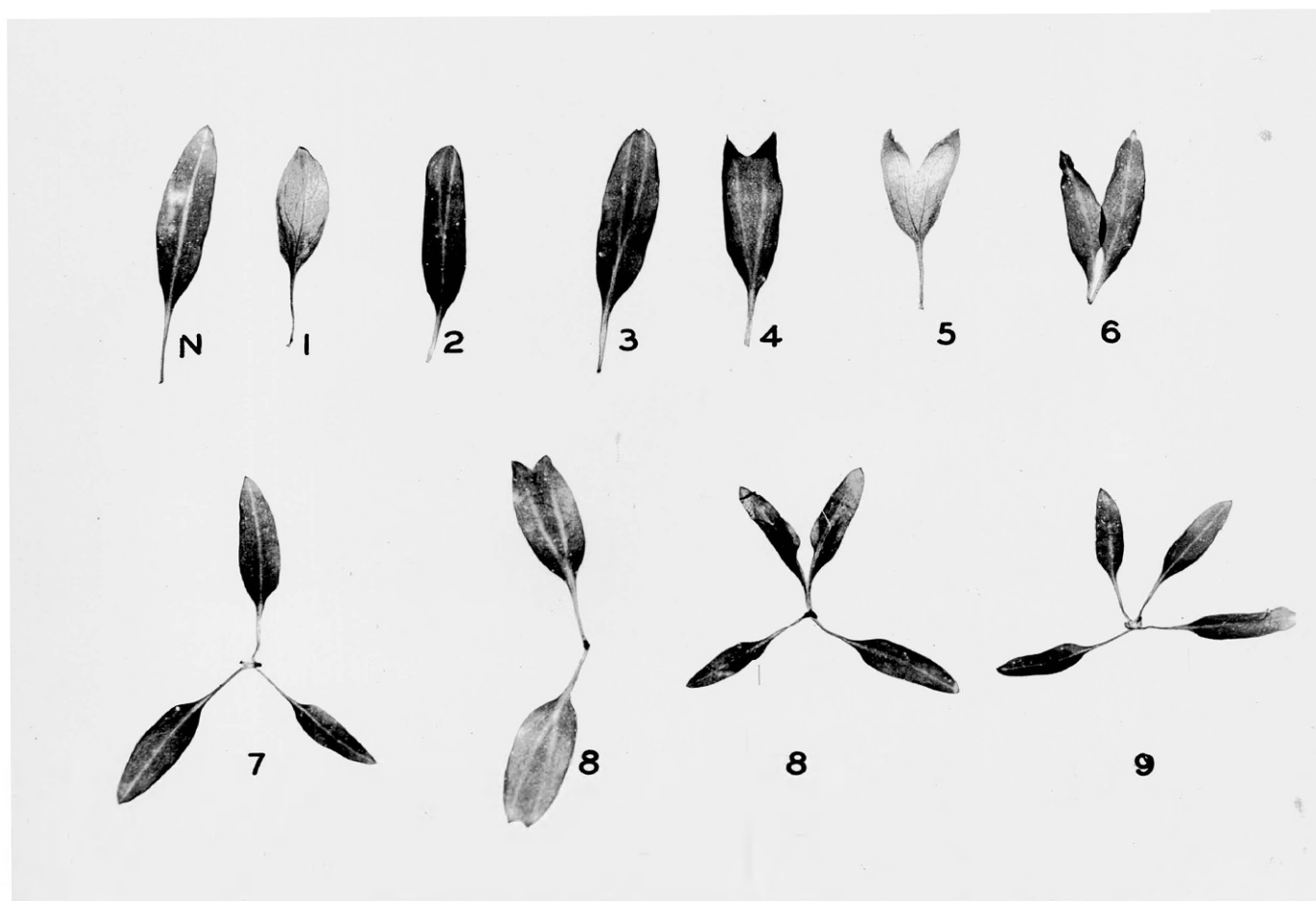


Figure 2. Normal cotyledon (N) and nine classes of Polycothyledony used in classification of tomato seedlings (1 to 6, only the abnormal cotyledon shown; 7 to 9, all cotyledons):

Class

1. Veins separate near apex of cotyledon blade.
2. Veins separate near center of blade.
3. Veins separate at or near base of blade, apex slightly notched or not notched.
4. Notched $1/4$ distance from apex to base of blade.
5. Cleft to center of blade.
6. Cleft to base of blade or into petiole.
7. Three separate cotyledons, arising from distinct points on the axis.
8. (Two types classed together). Three cotyledons, one of which is divided; or two cotyledons, both of which are divided.
9. Four entire cotyledons, arising separately from axis.



Figure 3. The hemitricotyledon in tomatoes. Eleven of the gradations between dicot and tricot phenotype.



Figure 4. Three potted tomato plants from the same population; left to right, tetracot, dicot, and tricot.



Figure 5. Five potted tomato plants. Left, a tricot and two hemitricots; right, two hemitricots.

TABLE II

Complete classification of 1,934 fifth generation seedlings from 15 fourth generation plants of known cotyledon phenotype, F_4 No.244-2-7-3A.

Parent cotyledon class ¹	Total seedlings	Total normal	Total poly-cots	% poly-cots	Distribution of polycot seedlings ¹ in each of nine phenotype classes								
					1	2	3	4	5	6	7	8	9
Normal	144	112	32	22.2	1	3	6	12	2	2	4	2	
Normal	96	35	61	63.5		4	9	26	4	6	4	8	
Normal	187	91	96	51.3	2	20	5	17	12	11	19	9	1
Hemitri-cots													
2	179	88	91	50.8	3	13	12	32	7	6	17	1	
3	85	41	44	51.8	5	5	4	7	5	2	10	6	
4	112	43	69	61.6	3	7	5	20	6	7	13	8	
4	56	29	27	48.2	1	4	4	7	2	4	4	1	
4	66	14	52	78.8	2	3	4	16	10	6	7	4	
4	120	40	80	66.7	2	8	5	21	13	10	8	11	2
5	100	63	37	37.0	1	5	4	5	5	5	9	2	1
5	159	16	143	89.9	1	4	10	32	16	15	38	25	2
Tricots													
6	59	41	18	30.5	2	2	4	7	1		1	1	
7	179	32	147	82.1	2	12	7	45	11	7	26	37	
7	112	15	97	86.6		1	3	15	6	14	27	31	
Hemitet-racot													
8	280	15	265	94.6	11	7	2	51	33	29	66	65	1
TOTALS	1,934	675	1,259		36	98	84	313	133	124	253	211	7
										377			

¹ Low numbers, minor cotyledon division, higher numbers deep splitting. For details, see Fig. 2.

It was also evident from the totals at the bottom of the columns at the right, that the tricotyledon, (classes 6 and 7) represented by 377 seedlings, and the slightly cleft hemitricotyledon (class 4) represented by 313 seedlings, were the types most frequently found. The tetracotyledon (class 9) was only rarely found.

It should be noted that polycots occurred in all fifteen of the progenies listed. The fifteen were taken at random from thirty or more plants of the F_4 parent population. This feature was typical of such populations, in that every plant invariably produced polycots and that the percentages produced always showed differences. Any line of this nature was designated a "polycot producing line."

In the examination of the cotyledons in the present study, in which over 100,000 seedlings were classified, no seedling was observed with more than four cotyledons and in those with four, each cotyledon was entire. Apparently, tetracotyledons are the extreme type of polycotyledony in Lycopersicon.

At the other end of the range of cotyledon types were found extremely rare seedlings with apparently only one cotyledon, Fig. 1, A. These were, in each case, clearly formed of the whole component of two normal cotyledons. Seed from one pseudo-monocotyledon, which had appeared along with 79 normal seedlings from the same source, revealed neither pseudo-monocotyledons nor polycotyledons in 268 seedlings. For this reason, this form was not included as a part of the expression of polycotyledony.

Venation of the cotyledons. A study of venation of normal cotyledons and those with various phases of polycotyledony revealed some differences. In the latter there was often a marked divergence of the main veins in the cotyledon blade and often in the petiole, Fig. 6. This figure also showed that there were four principal veins, two in each cotyledon. That four was the normal number was indicated by the fact that in a normal seedling there were also two pairs of veins, Fig. 7. In seedlings with more than two cotyledons, there was a change in the disposition of the four veins. For example, in a tricotyledon, with three cotyledons arising separately from the axis, one had two veins and the other two had one vein supplied to each, Fig. 7. Thus the total supply was again four principal veins, regardless of the number and form of the cotyledons. This was found to be true in all seedlings examined.

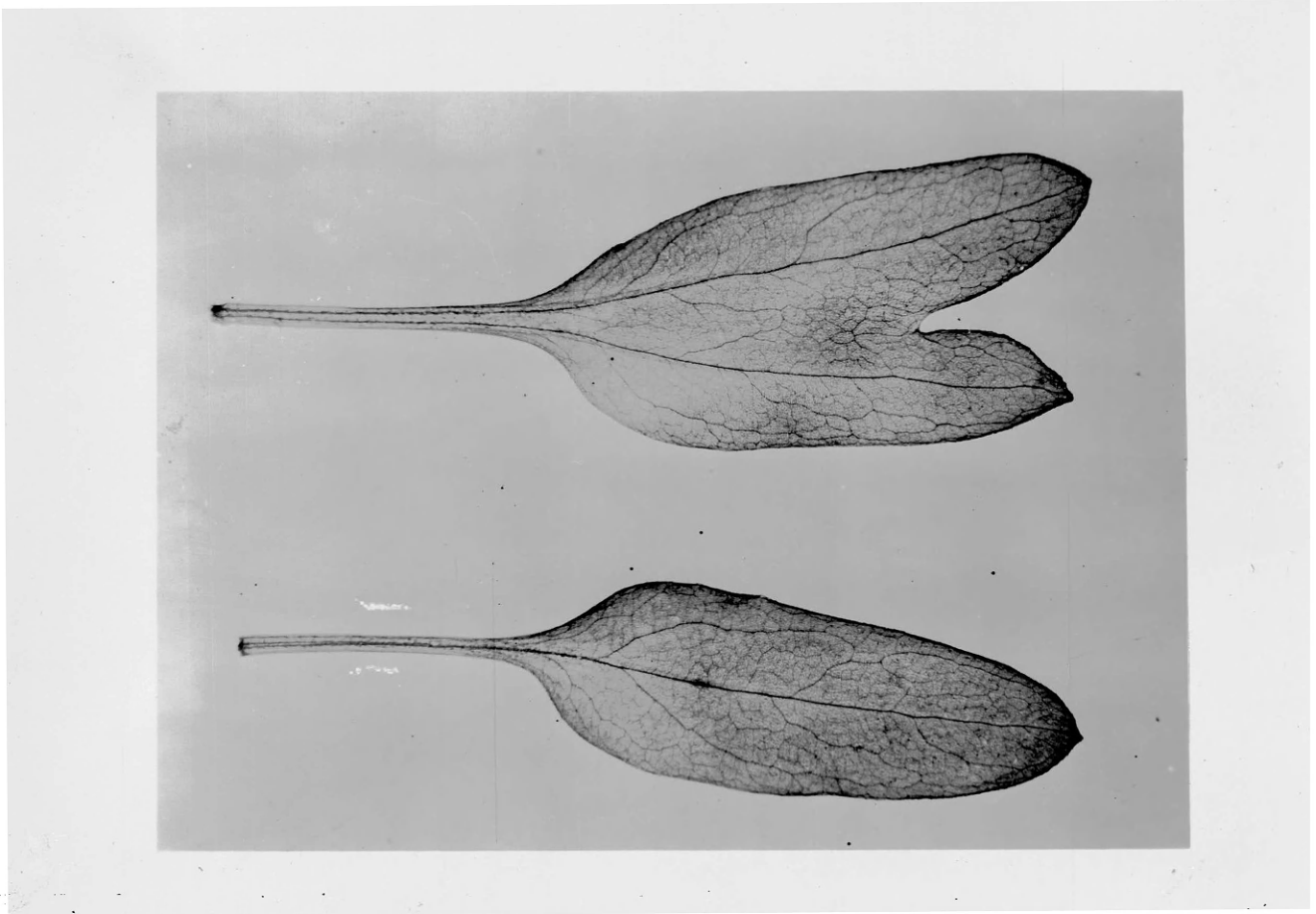


Figure 6. Tomato cotyledon venation. Two cotyledons of a hemitricot, each with two principal veins visible in the petiole. Note divergence of veins in the upper cotyledon compared to that of the normal or entire cotyledon.

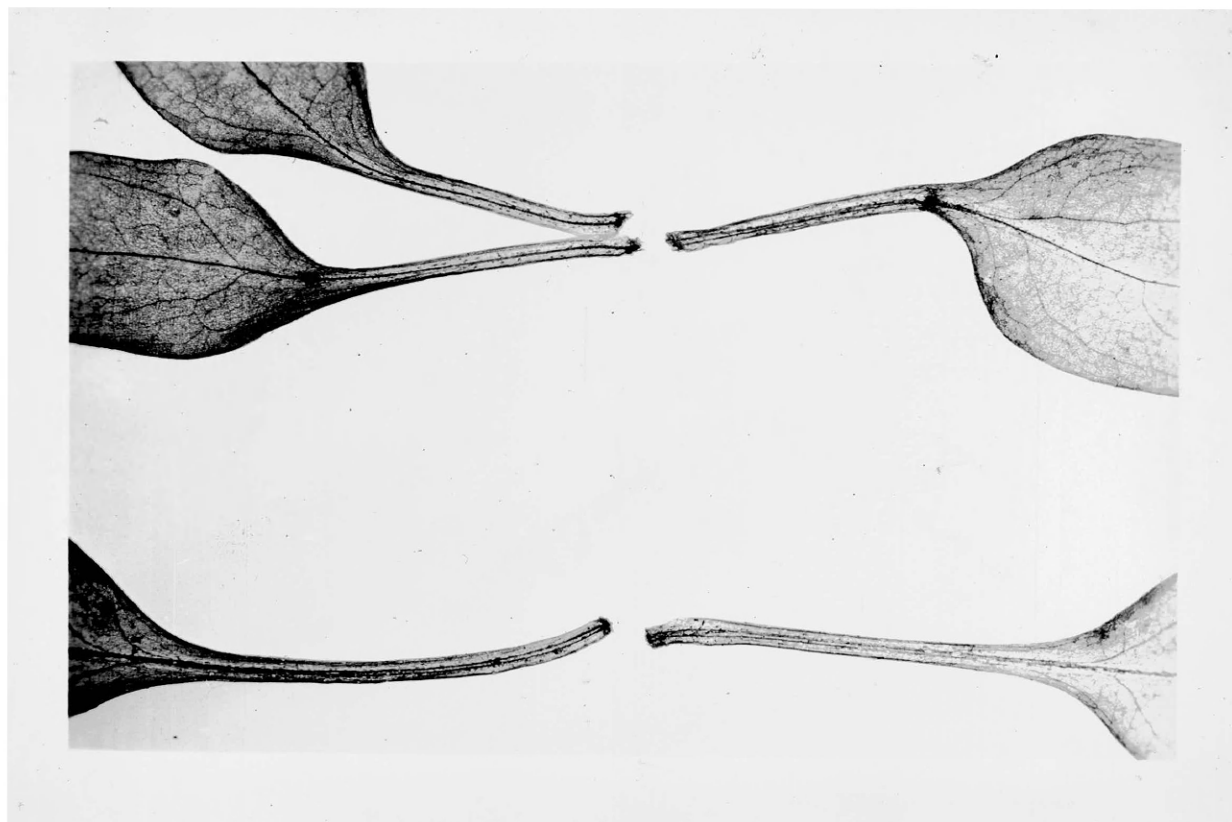


Figure 7. Tomato cotyledon venation. Upper, three cotyledons from a phenotypic tricot, two veins in member at right, one in each of members at left. (Note especially at and near base of petiole) Lower, two cotyledons from a phenotypic dicot, two principal veins in each cotyledon.

The occurrence of polycotyledony in Lycopersicon. In the cotyledon classification of tomato seedlings, 497 different varieties and foreign accessions were examined. In 109 of these, polycots were observed, usually in samples of only one or two hundred seedlings, TABLE III. A total of 17,299 seedlings was included, and of these, 290 or approximately 1.7% were polycots. From the 388 additional lines, none were found in 24,776 seedlings. Many of these lines were represented by only two or three dozen seedlings and it is probable that several of them would have shown the abnormal seedling forms if more had been observed. In all these observations, there were no pure lines of polycotyledons.

Among the 109 lines showing polycotyledony were species of Lycopersicon other than L. esculentum. Some of these have been designated in TABLE III, following the V. B. L. numbers 7 and 8, 533, 541, 545, 550 and 764. The nomenclature follows that of Muller (140). In addition to the above species, the Cherry variety and Pear form of L. esculentum contained occasional polycots. No polycots were observed in approximately 100 seedlings of L. hirsutum H. & B., but some were seen in hybrids involving it, as in V. B. L. No. 591. The appearance of the polycots in the various species cited was similar in all respects to that observed in L. esculentum. The wide geographic range of seed sources and the large number of varieties included in the list gave ample proof of the prevalence of polycotyledons in the genus.

TABLE III

Seedling classification of 109 tomato lines in which Polycotyledons were observed

V.B.L. Number ¹	Identification	Seed- lings	Poly- cots
5-01	Marglobe, #3350 S-2-1-1-6, W. S. Porte	112	1
6	Targinnie Red, Arthur Yates Co., Sydney, Australia	76	1
6-02	Selection from Targinnie Red	757	15
6-02-2	" " " "	157	1
6-02-3	" " " "	138	1
6-02-5	" " " "	56	1
6-02-8	" " " "	97	1
6-03-1	" " " "	54	1
6-03-2	" " " "	62	3
6-06-3	" " " "	109	1
6-08-1	" " " "	105	1
6-09-1	" " " "	85	1
6-010	" " " "	31	1
6-6	" " " "	133	1
6-7	" " " "	166	1
7 & 8	Selections from P.I. ² #79532, Peru <u>L. pimpinellifolium</u> (Jusl.) Mill.	748	10
9-01	Selection from Marglobe, #3311-S-3-3, W. S. Porte	1439	18
10	Commercial Marglobe, W. S. Porte	438	16
21	Burwood Prize, New South Wales	285	3
24	Cameron Canada, Nova Scotia	245	3
31	Danish Export, Denmark	215	1
45	Dobbie's Champion, Scotland	244	1
51	Export, France	67	1
56	Fiaschello, France	626	1
68	Amarillo, Argentina	138	1
73	N.C.D.(Bide's), England	90	1
78	Magnum Bonum, Germany	129	1
87	Vahle Leader, Netherlands	37	7
99	Semperifructifera, Italy	169	1
111	Resista, Germany	433	5
123	Phenomen, Italy	38	1
144	P. I. #92,855, China	18	1
192	Pritchard, Associated Seed Growers	237	6
199	Indiana Marglobe, " " "	56	1
200	Rutgers, " " "	204	8
202	Norduke, W. S. Porte, U.S.D.A.	121	2
204	Comet, W. S. Porte, "	36	1
205	Stirling Castle, W. S. Porte, U.S.D.A.	83	1
207	King George, England	171	2
217	Marvel, W. S. Porte, U.S.D.A.	220	1
218	Penn State, W. S. Porte, "	50	1
222	Gulf State Market, W. S. Porte, U.S.D.A.	157	2
224	Fillbasket, W. S. Porte, "	35	2
226	F ₂ Marglobe x Chinaman	206	2

TABLE III (continued)

Seedling classification of 109 tomato lines in which Polycotyledons were observed

V.B.L. Number ¹	Identification	Seed- lings	Poly- cots
228	Marglobe, Strain 6, Stokes	332	5
230	Dixie, Louisiana Agr. Experiment Station	139	2
231	Louisiana Gulf State #20-5, La. Agr. Exp. Sta.	343	2
234	Montgomery, K. C. Barrons	296	2
239a	Earliana, Associated Seed Growers	189	1
241a	Valiant, Stokes	120	1
242	Stokesdale, Stokes	151	1
243	Bonny Best, Bailey Seed Co.	1362	14
257	P. I. #118,686, Brazil	18	1
262	P. I. #126,409, Peru	42	1
277	P. I. #126,910, Peru	42	1
316	P. I. #128,276, Argentina	42	2
318	P. I. #128,278, "	42	2
355	P. I. #128,285, "	16	1
533	P. I. #126,945, Peru, <u>L. peruvianum</u> var. <u>dentatum</u> Dun.	12	1
541	P. I. #128,649, Chile, <u>L. peruvianum</u> (L.) Mill.	150	1
544	P. I. #128,652, " , <u>L. peruvianum</u> var. <u>dentatum</u>	42	1
545	P. I. #128,653, " , <u>L. peruvianum</u>	232	9
550	P. I. #126,443, Peru, <u>L. glandulosum</u> C. H. Mull.	375	1
570	Everbearing, J. A. Boggs, LaGrange, Kentucky	207	2
572	F ₂ Fruhwonder x Marglobe	117	1
591	Bonny Best x (Bonny Best x <u>Lycopersicon hirsutum</u>) W. S. Porte, U.S.D.A.	28	1
614	P.I. #115,871, U.S.S.R.	38	3
618	U. S. 7W (c20) W. S. Porte selection from P. I. #79532 x Marglobe	88	4
619	U. S. 7W (d5) "	39	2
620	U. S. 16W (a6) "	96	7
622	U. S. 16W (c1) "	145	1
623	U. S. 23W (a20) "	83	2
624	U. S. 23W (b20) "	113	11
625	U. S. 23W (e1) "	129	11
653	P. I. #129,022, Ecuador	45	1
753	P. I. #129,131, Panama	42	1
755	P. I. #129,133, Argentina	57	1
758	P. I. #129,136, "	42	1
764	P. I. #129,143, Peru, <u>L. pimpinellifolium</u>	116	1
768	P. I. #129,689, Argentina	82	1
793	P. I. #117,226, Turkey	27	1
813	P. I. #118,788, Venezuela	26	1
820	P. I. #119,776, Argentina	21	1
887	Summerset, Strain B-1-5-1, Leslie R. Hawthorn, Texas	225	1
888	John Baer, M. C. Strong, Michigan	284	1
889	Pan America, W. S. Porte, U.S.D.A.	155	6

TABLE III (continued)

Seedling classification of 109 tomato lines in which Polycotyledons were observed

V.B.L. Number ¹	Identification	Seed- lings	Poly- cots
890	Essar, M. Shapovalov, Logan, Utah	121	1
974	Marhio, Ohio Agr. Exp. Sta.	113	1
975	Globelle, Ohio Agr. Exp. Sta.	189	1
977	Rouge Naine Native, J. W. MacArthur	23	1
980	Essary, Associated Seed Growers	144	3
982	P. I. #117,900, Brazil	77	1
983	P. I. #118,325, "	35	2
988	P. I. #124,235, India	111	1
1025	P. I. #138,625, Turkey	37	1
1029	Ponderosa, Kilgore Seed Co.	138	2
1030	Cuban Marglobe, " " "	112	1
1046	Bounty, North Dakota Agr. Exp. Sta.	144	3
1114	U. S. 40WFP 35, W. S. Porte, U.S.D.A.	55	4
1116	U. S. 41P.A. 40-1, " "	45	1
1117	U. S. 41P.A. 38-1, " "	96	2
1118	U. S. 41P.A. 36-1, " "	70	1
1119	U. S. 41P.A. 41-11, " "	96	3
1120	U. S. 40WP 2, " "	80	2
1122	U. S. 40WP 4, " "	76	5
1123	U. S. 40WP 16, " "	33	1
1124	U. S. 40WP 17, " "	58	3
1125	U. S. 40WP 41, " "	67	1
1127	U. S. 40WP 63, " "	84	5
1128	U. S. 40WP 87, " "	72	1

¹ Accession number at the U. S. Regional Vegetable Breeding Laboratory, Charleston, South Carolina.

² P. I. refers to the Division of Plant Exploration and Introduction, U. S. Department of Agriculture.

Leaf placement and number in polycotyledons. Comparisons of the leaf placement in normal and polycot plants revealed that abnormalities occurred more frequently in the latter. These were most apparent in young plants, and fell into the following groups:

1. Two leaves at the first, second or third node, instead of one as in most normal plants, Fig. 8.
2. First or second leaf apparently double or cleft along the midrib of the blade, or into the petiole.
3. Opposite leaves at two successive nodes, the first and second or the second and third.
4. Four leaves at the first node, usually accompanied by two growing points.

These changes in placement frequently increased the total number of leaves in plants from two to five weeks old, compared to the number in normal plants of the same age. An indication of this situation is given in Fig. 9, in which a tricot is seen to have its first leaves with closer placement than that of a normal plant.

In a preliminary trial in 1941 leaf counts were made of selected plants of the variety Rutgers at an age of 5 weeks. These were grown in a field plot in 5 randomized series. The counts revealed the following values:

	Mean leaf number	Standard Error
15 tricots	16.06	± 0.42
59 dicots	12.30	± 0.21
Difference of means and its Standard Error	3.76	± 0.92

The difference of 3.76 leaves was significant.



Figure 8. Leaf placement. Tetracot plant showing two leaves at second leaf-node and branching of main axis. Note four cotyledons.



Figure 9. Leaf placement. Right, dicot with first two leaves (both cut off - at right and left of plant) appearing at intervals of 180° . Left, tricot with first three leaves at intervals of 120° .

To test the leaf number at maturity, a second experiment was run in 1942 and involved Marglobe and Rutgers plants. The total number of leaves for each plant, at the time of peak fruit production, were recorded for the two varieties. The values obtained are given in TABLE IV.

The variance analysis of the data revealed that the effects of series and cotyledon class were not significant, normal and polycot plants having essentially the same number of leaves. The mean number of leaves for normal plants was 92.3, for polycot plants, 88.6; the difference of 3.7 leaves was considerably below the value 8.5 required for significance at the 5% point. It is apparent that the number of leaves in mature plants is not associated with the cotyledon class of the seedlings. Variety differences were significant, since Marglobe, with a mean leaf number of 94.9 exceeded Rutgers with 83.6 by a significant margin of 11.3 leaves.

TABLE IV

Total number of leaves in normal and polycot plants of Marglobe and Rutgers. Charleston, S. C., Fall, 1942.

<u>Variety</u>	<u>Class</u>	<u>Series</u>					<u>Totals</u>
		<u>I</u>	<u>II</u>	<u>III</u>	<u>IV</u>	<u>V</u>	
Rutgers	Normal	92	88	103	91	103	
		69	83	73	95	93	
		97	(78) ¹	111	105	61	<u>1,342</u>
Rutgers	Polycot	85	87	77	(64)	75	
		84	65	110	65	77	
		78	87	86	117	79	<u>1,236</u>
Marglobe	Normal	130	126	89	91	79	
		67	112	87	79	73	
		128	107	100	(85)	74	<u>1,427</u>
Marglobe	Polycot	92	67	114	103	85	
		129	112	91	79	79	
		111	92	107	88	72	<u>1,421</u>

¹Numbers in parentheses calculated, 1 degree of freedom removed for each.

<u>Source</u>	<u>D.F.</u>	<u>Sum Sqs.</u>	<u>Variance Analysis</u>		<u>F Val.</u>	<u>F Vals. required for significance</u>
			<u>Mean Sqs.</u>	<u>St. Dev.</u>		
Variety	1	1,215.00	1,215.00		4.289	4.03 at 5%
Class	1	209.06	209.06			7.17 at 1%
Series	4	2,417.73	604.43			
Error	50	14,162.94	283.26	16.83	Other F values not significant.	
Total	56	18,004.73				

Number of fruits produced by polycotyledons and normal plants.

The numbers of fruits picked from the Marglobe and Rutgers plants in the field trial are given in TABLE V. The following were considered in the analysis of variance:

2 varieties	Interactions-	
2 classes (normal vs. polycot)	$c \times y$	$c \times d \times y$
5 series	$c \times d$	
3 dates of picking	$d \times y$	

Only varieties, class x date and date x varieties showed significant differences. Variance analysis data from these sources, omitting non-significant sources, follows:

Source	D.F.	Sum Sqs.	Mean Sqs.	St.Dev.	F Vals.	Signif. F Vals.	
						5%	1%
varieties	1	112.02	112.02		4.693	3.91	6.81
class x date	2	405.88	202.94		8.502	3.06	4.75
date x varieties	2	211.54	105.77		4.431	3.06	4.75
error	155	3700.61	23.87	4.885			
total	170	4643.98					

The variance due to cotyledon class was non-significant and indicated that the total number of fruits produced by normal plants did not differ significantly from that produced by polycots. On the other hand, the F value, 8.502, for class x date, indicated that plants from these two main seedling classes produced different proportions of their total fruit number at different times.

TABLE V

Number of fruits picked at three dates in normal and polycot plants of Marglobe and Rutgers. Charleston, S. C., Fall 1942

Series	Marglobe						Rutgers					
	Normal			Polycot			Normal			Polycot		
	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
I	14	14	3	14	5	4	18	6	2	18	5	2
	5	7	4	12	14	9	10	6	0	22	4	1
	16	16	12	7	5	18	10	9	3	6	3	3
II	7	16	16	5	7	13	16	6	4	4	6	12
	11	14	23	7	6	21	29	8	4	3	3	4
	14	16	9	9	6	22	(15	10	4) ¹	10	2	9
III	1	5	6	4	15	23	6	10	12	4	4	14
	9	7	6	8	9	16	4	5	9	3	14	13
	15	16	7	4	8	15	3	10	10	6	8	15
IV	15	6	8	12	8	5	14	9	5	(9	5	6)
	5	8	17	3	4	16	13	5	3	10	7	8
	(14	9	6)	14	10	10	14	16	4	15	12	4
V	17	8	4	10	8	4	13	5	7	10	7	13
	11	12	4	11	7	18	13	11	9	11	7	12
	<u>7</u>	<u>7</u>	<u>6</u>	<u>10</u>	<u>7</u>	<u>4</u>	<u>11</u>	<u>7</u>	<u>5</u>	<u>10</u>	<u>7</u>	<u>14</u>
	161	161	131	130	119	198	189	123	81	141	94	130

¹Numbers in parentheses calculated, 1 degree of freedom removed for each.

These relationships are indicated in the following values:

Totals, both varieties:

	Number of fruits from 30 plants			Differences ¹		
	Early	Mid	Late	Early-Mid.	Mid-Late	Early-Late
Normal	350	284	212	66	72	138
Polycot	<u>271</u>	<u>213</u>	<u>328</u>	58	-115	-57
Diff.	79	71	-116			

Totals, each variety:

<u>Marglobe</u>						
Normal	161	161	131	0	30	30
Polycot	<u>130</u>	<u>119</u>	<u>198</u>	11	-79	-68
Diff.	31	42	-67			
<u>Rutgers</u>						
Normal	189	123	81	66	42	108
Polycot	<u>141</u>	<u>94</u>	<u>130</u>	47	36	11
Diff.	48	29	-49			

In some of the comparisons above, significant differences were present between normal and polycot plants. In the totals, the early picking contained a significantly higher number of fruits from normal plants than from polycots and in the late picking, the reverse was true. In Marglobe, normal plants showed a relatively uniform production in the three pickings but the polycot plants produced a significantly higher number of fruits in the late picking than in the early or mid-season picking. In Rutgers, the polycot plants were relatively uniform but the normal plants produced a significantly higher number of fruits in the early picking than in the late picking. The principal observation was that polycot plants did not produce as high a proportion of their crop in the early picking as did normal plants from the same source.

¹In the totals of both varieties, a difference of 74.7 fruits was required for significance and in the totals of each variety, 52.8 at the 5% level.

Total fruit weight was recorded for the plants of the Marglobe and Rutgers experiment but no significant differences were found, other than those brought out by total fruit number. That is, individual fruit weights were essentially the same in comparable groups.

Increase in polycotyledony by selection. A. Selection in hybrids. Since the original observations of polycotyledony in the present study involved 4th generation plants, attempts were made to further increase the percentages of polycots by selection in the fifth and later generations. Most of the selection data with hybrids has been obtained from a hybrid, No. 244, involving the Red Currant tomato and the variety Marglobe. The cross was made at the U. S. Vegetable Breeding Laboratory primarily for disease resistance studies and the progenies selected for this purpose were examined as well as those set aside for polycotyledon analysis.

Several groups of seedlings, involving 2nd to 6th generation plants originating from single F₁ plants, were classified by cotyledon phenotypes. The results of the classification of a typical group are given in TABLE VI. In this table it is apparent that the later generations showed a marked increase in percentages of polycotyledons in individual progenies. Selecting one line for illustration, No. 244-2-7-3A-10-2 which is a sixth generation plant, it is found that the percentages (underlined) changed in the following series; 1.0, 5.9, 39.0, 94.6 and 42.8 %. The next to the last percentage, representing a line with 265 polycotyledons out of 280 seedlings selected at random, was the highest percentage observed in this study. It should be noted that the percentage did not go beyond 94.6% but dropped back to percentages approximating 50%.

TABLE VI

Seedling analysis of V.B.L. No. 244-2 and descendants

V.B.L. Number ¹	Seed- lings	Poly- cots	% Poly	V.B.L. Number	Seed- lings	Poly- cots	% Poly
<u>Second generation</u>							
244-2	400	4	1.0	244-2-6-A-15	23	15	65.2
<u>Third generation</u>				-16	20	10	50.0
244-2-1	136	0	0.0	-20	32	7	21.9
244-2-5	210	0	0.0	-21	62	21	33.9
244-2-2	160	4	2.5	244-2-7-2-3	87	0	0.0
244-2-3	390	2	0.5	-7	101	7	6.9
244-2-4	229	1	0.4	-6	149	22	14.8
244-2-6	174	15	8.6	-4	224	39	17.4
244-2-7	541	32	5.9	-5	210	40	19.0
<u>Fourth generation</u>				-1	200	46	23.0
244-2-1-4	116	5	4.3	-2	235	145	61.7
244-2-2-2	60	2	3.3	244-2-7-3A-B	106	31	29.2
244-2-6 (5 F ₄ lines)	576	0	0.0	244-2-7-3A-8	442	132	29.9
244-2-6-2	130	3	2.3	-15	58	19	32.8
244-2-6-4	117	3	2.6	-13	180	81	45.0
244-2-6-5	117	2	1.7	-17	170	91	53.5
244-2-6-A	401	168	41.8	-9	89	49	55.0
244-2-7-5	282	0	0.0	-14	83	48	57.8
244-2-7-(4 F ₄ lines)	1233	28	2.3	-16	37	23	62.2
244-2-7-1	352	78	22.1	-11	39	26	66.7
244-2-7-2	470	70	14.9	-12	129	78	60.5
244-2-7-3A	464	181	39.0	-10	280	265	94.6
244-2-7-3B	182	91	50.0	244-2-7-3B			
<u>Fifth generation</u>				(15 F ₅ lines)	1100	540	49.1
244-2-6-6-(5 F ₅ lines)	186	0	0.0	<u>Sixth generation</u>			
244-2-6-4-(2 F ₅ lines)	78	2	2.6	244-2-7-3A-8-NA	30	6	20.0
244-2-6-4-(2 F ₅ lines)	78	3	3.8	-5B	28	9	32.1
244-2-6-5-(3 F ₅ lines)	99	0	0.0	-9C	318	119	37.4
244-2-6-A-3	37	2	5.4	-5A	142	65	45.8
244-2-6-A-6	10	4	40.0	-4	34	17	50.0
244-2-6-A-7	30	4	13.3	-NB	33	21	63.6
244-2-6-A-11	12	5	41.7	-10	88	62	70.5
244-2-6-A-13	12	9	75.0	-NC	112	89	79.5
				244-2-7-3A-10-4	20	8	40.0
				-1	27	11	40.7
				-2	140	60	42.8
				-5	32	21	65.6
				-3	18	12	66.7

¹Accession number at the U. S. Regional Vegetable Breeding Laboratory, Charleston, S. C.

In this same series there was exhibited the typical behavior of the polycot producing line described in an earlier section. This is No. 244-2-7-3A shown in the fourth generation group, TABLE VI. It produced 39 polycots in each 100 seedlings, but all the 100 seedlings, including the 61 phenotypically normal, themselves produced more polycots. For example, 25 fifth generation plants from No. 244-2-7-3A, taken at random, all showed polycot production. Eleven of these are included in TABLE VI, numbers 244-2-7-3A-B through 244-2-7-3A-10 and the other 14 are in TABLE II. (The 15th plant in TABLE II is the same as the 94.6% line in TABLE VI). In addition, all the progenies in the sixth generation produced polycots, and as shown previously, seedlings with normal phenotypes produced polycots as abundantly as those with abnormal phenotypes.

A summary of the selection data from three separate first generation plants is given in TABLE VII. The percentages given in the last column confirmed the observations that increases could accompany selection in hybrid material.

The positive results obtained above were not realized in all selection from cross No. 244. Five other second generation populations and available 3rd and 4th generation families were classified by cotyledon phenotypes and in these only very low percentages were observed.

A summary of these follows:

Number of families	Generation	Number of seedlings	Number of polycots	% polycots
5	second	815	2	0.2
35	third	3,139	13	0.4
17	fourth	1,424	14	1.0

The low percentages were in sharp contrast to those of approximately 30% to 90% in the other series described. It was evident that

TABLE VII

Data from three sister F₂ populations and their descendants, showing increase in percentages of Polycots

Generation	No. of progenies	No. of seedlings examined	Polycots	% Polycots
F ₂	1	400	4	1.0
F ₃	7	1840	54	2.9
F ₄	20	4500	631	18.0
F ₅	68	6252	2758	44.1
F ₆	13	1020	500	49.0
F ₂	1	470	2	0.4
F ₃	3	859	12	1.4
F ₄	3	685	86	12.6
F ₅	29	2097	542	25.8
F ₂	1	210	0	0.0
F ₃	3	644	62	9.6
F ₄	9	869	232	26.7

both positive and negative results could be obtained in attempts to increase greatly the percentages of polycotyledons in hybrids.

B. Selection in varieties and species. It has been noted by other investigators that selection within commercial varieties of tomatoes produced negative results with regard to increasing polycot production. In the present study attempts at increasing polycot production percentages were made with certain varieties as well as selected lines and species of Lycopersicon. From these plants, seedlings with normal and polycot phenotypes were selected, grown to maturity and cotyledon classifications made of their progenies. The results of the classification are given in TABLE VIII.

In the varieties Pritchard and Rutgers, increases in percentages were observed. In Rutgers, it should be noted that polycots appeared in the progeny of a parent plant with phenotypically normal cotyledons.

In Bonny Best and Bounty, polycots appeared in some of the progenies and were not observed in others. The percentages produced, however, were low. Even in the second generation from the original Bounty plant, a tricot (class 7) produced only 1 tricot in 150 seedlings.

Number 625, which showed very marked increases in polycot percentage, is a line from an advanced generation hybrid selected at the U.S.D.A. Bureau of Plant Industry Station at Beltsville, Maryland. The hybrid originated from a cross involving a Red Currant tomato, P. I. No. 79,532, the same used at Charleston in producing hybrid No. 244.

In both of the lines of Lycopersicon peruvianum included in TABLE VIII, polycotyledons appeared in the progenies examined. In this species, as well as in L. esculentum, differences in the results of selection were apparent.

TABLE VIII

Selection experiments involving polycotyledony in commercial tomato varieties, selected lines and Lycopersicon peruvianum.

V.B.L. Number	Identification	Parental seedling phenotype ¹	Total seedlings	Poly-cots	% poly-cots
192	Fritchard	Original planting ----	237	6	2.5
	First derived generation	7	177	23	13.0
200	Rutgers	Original planting -	204	8	3.9
	First derived generation	N	97	1	1.0
		4	130	10	7.7
		7	146	2	1.4
		7	94	1	1.0
1046	Bounty	Original planting -	144	3	2.1
	First derived generation	N	152	3	2.0
		5	299	7	2.3
		7	150	1	0.7
	Second derived generation	N	40	1	2.5
		7	150	1	0.7
		7	100	0	0.0
243	Bonny Best	Original planting -	1362	14	1.0
	First derived generation	9	136	0	0.0
		9	202	1	0.5
625	U. S. 23W-3-1	Original planting -	129	11	8.5
	First derived generation	N	44	3	6.8
		N	31	11	35.5
		N	52	20	38.5
		N	135	53	39.2
		7	16	14	87.5
545	<u>Lycopersicon peruvianum</u>				
	Original planting	-	232	9	3.9
	First derived generation	N	243	8	3.3
		5	587	13	2.2
		7	531	29	5.5
631a	"	"			
	Original planting	-	66	4	6.1
	First derived generation	5	136	40	29.4

¹N equals normal cotyledons; number 4 and 5, hemitricotyledons; number 7, tricotyledons; and 9, tetracotyledon.

The above data show that selection for increased percentages of polycotyledons could bring both positive and negative results.

Inheritance studies with polycotyledony. From the original observations of the polycotyledons, their irregularity of appearance, and from the results of selection within hybrid material, it seemed probable that the inheritance was not due to a single factor pair as are most of the recorded characters in tomatoes. The failure of each cotyledon phenotype to reproduce itself when selfed also suggested some complicating factors. However, to test the assumption that a simple explanation of the inheritance was not in effect, several crosses were made which included plants of known and different phenotypes. These crosses between plants from one high polycot line and the first generation phenotypes follow:

<u>Female</u>	<u>Parents</u>		<u>Phenotypes in first generation</u>			
		<u>Male</u>	<u>normal</u>	<u>hemitricot</u>	<u>tricot</u>	<u>tetracot</u>
tetracot	x	tricot	x	x	x	x
normal	x	tricot	x	x	x	
tricot	x	normal	x	x	x	x
hemitricot	x	tricot	x	x	x	x
tricot	x	tricot	x	x	x	x

In the above results there were no indications that one phenotype was dominant over another and it was evident that phenotype segregation alone should not be used in estimating genetic ratios.

A second approach to the genetic situation involved consideration of production of polycots as an inherited character. In the selection studies and in the classification of varieties, there were observed three principal types of behavior in this respect. The three types were: First, normal lines or non-producing lines. In such lines no polycots appeared during any seeding or in any generation. Second,

low polycot-producing lines. In these, each plant produced polycots but only in relatively low percentages. Third, high polycot-producing lines. In these lines, every plant produced polycots in high but variable percentages.

Using appropriate combinations of parent lines from these three types, 16 crosses were made. Since the greatest contrast was shown by types one and three, crosses between the two were selected for critical analysis. The actual seedling classification observed in two of these crosses and the number of plants which were non-producing and producing are given in TABLE IX.

In the seedling phenotype classification, no polycots appeared in 13 first generation plants from the first cross and one out of a total of 87 from its reciprocal. Although practically all the first generation plants of the second cross (N x A) were normal in appearance, they all possessed factors for production of polycots since, of the 19 taken at random and grown to maturity, all produced polycots among the F₂ seedlings. This confirmed the validity of the cross.

Cross N x A was carried to the second and third generations. The polycot percentages from all seedlings of each generation showed an increase from 1.1 to 5.6%. In the second generation, the actual ratio of normal to polycot seedlings was 5,248 : 228 but as shown above, this could not be used in determining the number of factors involved. Instead, a random sample of plants from the F₂ had to be grown and the polycot production of each plant determined. From 175 second generation plants, seedling classifications were made and in 171 of these, polycotyledons were present.

TABLE IX

Seedling classification and polycot production data in a cross, normal
(parent A) x polycot (parent N) producing lines.

<u>Parents</u>		<u>Seedling pheno- type classification</u>			<u>Number of plants which produced-</u>		
		normal	polycot	%polycot	only normals	some polycots	
A	selfed	165	0	0.0	From parent A	6	0
N	selfed	25	22	46.8	From parent N	0	9
<u>Crosses</u>							
A x N	F ₁	13	0	0.0			
N x A	F ₁	86	1	1.1	From F ₁ (N x A)	0	19
"	F ₂	5,248	228	4.2	From F ₂ (N x A)	4	171
"	F ₃	26,872	1,591	5.6			
	(F ₃ from 175 F ₂ plants)						

Inspection of the ratio 171:4 indicated that it did not fit a Mendelian 3:1 ratio ($\chi^2 = 46.95$) but that it lay between a 15:1 and a 63:1 ratio. The χ^2 values for these two ratios are:

Ratio	χ^2	Values of significant differences	
		5%	1%
15:1	4.04	3.84	8.63
63:1	0.22	3.84	8.63

The extremely low χ^2 for the 63:1 ratio suggested that it might be the true one in this case. It would apply if there were three pairs of independent factors (triplicate factor pairs) all affecting polycot production. However, before accepting this interpretation the phenotype classification of the 175 F_3 families was examined. This information is given in Fig. 10, in which the parental phenotypes, F_1 , F_2 and F_3 populations or families are shown.

It is shown in this figure that parent A produced no polycots and that none of its progeny produced any. Parent N produced approximately 47 polycots in each 100 seedlings and all of its progeny showed similar production. The F_1 approached the percentage of the lower parent and the F_2 showed a range from 1 to 6%. In the F_3 families, however, the complete range of both parents was recovered, in fact, two families exceeded parent N in the percentage of polycots present. The mean of the F_3 percentages was 6.79 and the standard deviation 8.159.

A striking feature of the F_3 histogram was the strongly skewed distribution ($s = +1.02$). This feature resembled distributions obtained by other investigators dealing with size or weight inheritance and suggested that inheritance pattern of polycot production might be similar. Since such inheritance has involved geometric processes and the logarithmic values of the original data have been plotted, the latter

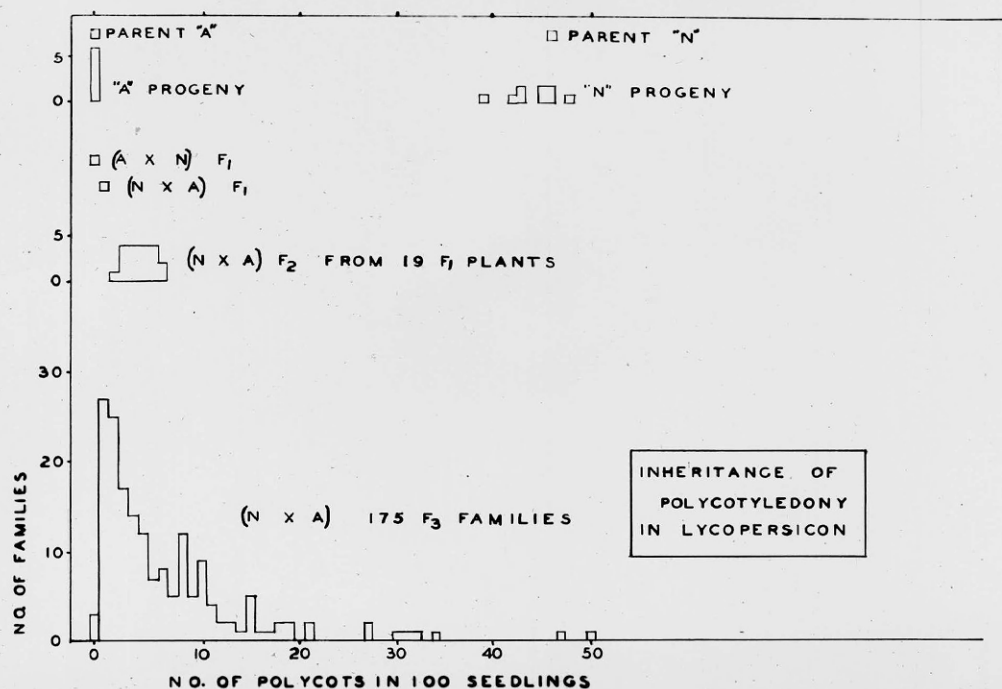


Figure 10. Polycot production in a normal line, a high polycot producing line, and their hybrids.

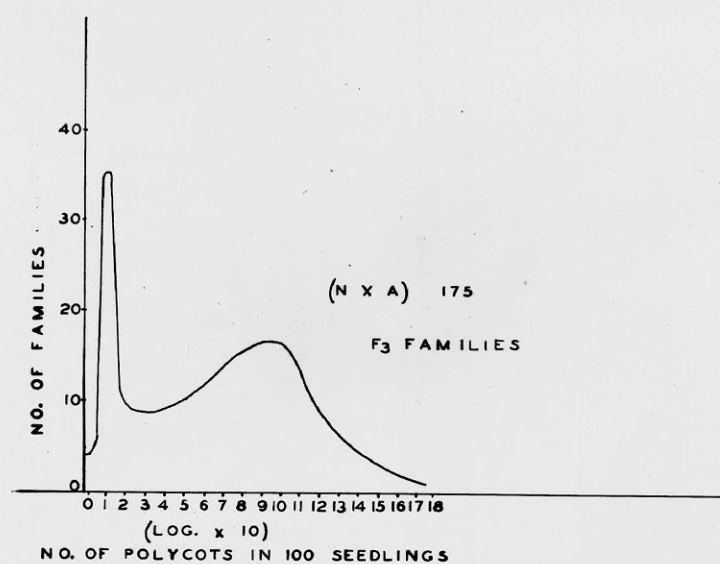


Figure 11. Distribution of 175 F₃ families from cross N x A, plotted on logarithmic values.

procedure was applied to the data at hand. Such treatment should cause the curve to assume a more normal shape. The curve obtained is given in Fig. 11.

In this figure the expected shift in the bulk of the curve toward the normal distribution was obtained. As shown in Fig. 10, the highest frequency was in the lowest polycot percentage group, but a second mode appeared. In the histogram based on actual polycot production numbers, there was a suggestion of a second mode at approximately 8 to 10 polycots in 100 seedlings, but this was emphasized in plotting the logarithmic values. The first mode was due to the large number of families in which there appeared only one polycot in 100 to 300 seedlings. The approximate modal value within this group was 0.8%, that of the second mode 10.0%. No certain explanation for the appearance of two modes was evident from the data obtained but it suggested that genes affecting polycot production differed in their individual effectiveness.

The data from the crosses above suggested multiple factor inheritance. As a further test of this, a comparison was made of the F_1 and parental means of some of the remaining crosses. This comparison is shown in TABLE X.

In the first two groups of crosses, involving parents with greatly different polycot production, the F_1 polycot percentages (third column of numbers) closely approximated the percentages of the low or normal parents. In addition, the F_1 values were much closer to the geometric means than to the arithmetic means. The F_2 percentages were in each case higher than their respective F_1 percentages. In group two, crosses $F \times L$ and $L \times H$ were carried past the second generation and the increases in the mean percentages from the first to the third generations were evident.

TABLE X

Classification of parental lines and crosses involving polycotyledony.

Type I. Normal				Type II. Low				Type III. High			
Parent symbol	Seedling phenotype			Parent symbol	Seedling phenotype			Parent symbol	Seedling phenotype		
	Norm	Poly	% poly		Norm	Poly	% poly		Norm	Poly	% poly
A	165	0	0.0	E	207	1	0.5	L	199	119	37.4
B	105	0	0.0	F	118	6	4.8	M	12	21	63.6
C	135	0	0.0	G	435	5	1.1	N	25	22	46.8
D	220	0	0.0	H	204	1	0.5	O	47	43	47.8
				I	52	2	3.7	P	69	43	38.4
				J	168	2	1.2	Q	75	31	29.2
				K	1439	18	1.2				
Crosses. Group I. Normal x High.				Means, polycot % of parents							
		Normal	Poly	% poly				Geometric ¹		Arithmetic	
C x P	F ₁	16	0	0.0				1.96		19.2	
	F ₂	1612	64	3.8							
P x C	F ₁	88	3	3.3				1.96		19.2	
	F ₂	722	97	11.8							
P x D	F ₁	24	0	0.0				1.96		19.2	
	F ₂	1271	112	8.1							
Group II. Low x High.											
E x L	F ₁	47	1	2.1				4.32		18.9	
F x L	F ₁	50	1	1.9				13.38		21.1	
	F ₂	1797	458	20.3							
	F ₃	3192	957	23.1							
L x H	F ₁	98	2	2.0				4.31		18.9	
	F ₂	1588	38	2.3							
	F ₃	870	83	8.8							
Q x J	F ₁	116	3	2.5				5.92		15.2	
	F ₂	309	33	9.6							
Group III. Normal x Low.											
H x B	F ₁	24	0	0.0				0.22		0.25	
Group IV. Low x Low.											
G x I	F ₁	61	0	0.0				2.02		2.40	
G x K	F ₁	27	0	0.0				1.15		1.15	
	F ₂	419	8	1.8							
Group V. High x High											
M x L	F ₁	6	5	45.4				47.9		50.5	
	F ₂	11	9	45.0							
L x M	F ₁	16	32	66.7				47.6		50.5	
O x L	F ₁	43	21	32.8				42.2		42.6	
N x P	F ₁	17	5	22.7				42.4		42.6	

¹ Geometric means involving Type I parents estimated by using 1% as approximation of 0%.

The range of values exhibited in these two crosses was also of importance and was as follows:

Range of polycot percentages exhibited in crosses F x L and L x H
Number of polycots in 100 seedlings

0	5	10	15	20	25	30	35	40	45	50	55	60
x-x Parent F												
x-x Parent L												
x (F x L) first generation												
x-----x (F x L) second generation, from 17 F ₁ plants												
x-----x (F x L) third generation, from 27 F ₂ plants												
x Parent H												
x (L x H) first generation												
x--x (L x H) second generation, from 5 F ₁ plants												
x-----x (L x H) third generation, from 8 F ₂ plants												

The ranges in the incidence of polycots in the first, second and third generations showed increases in both crosses. Since both parents were polycot producing, no normal producing plants would be expected to appear in the second generation. No normal producing F₂ plants did appear since none of the F₃ families from 35 plants taken at random were found in the "0" polycot column.

In TABLE X, the third, fourth and fifth groups of crosses involved sets of parents with approximately equal polycot production. In groups three and four, the F₁ means were 0% or low, just as were the parents involved. In these groups it was evident that the geometric means and arithmetic means did not differ widely from the F₁ means, the equality resulting from the relatively uniform percentages shown by the parents.

Group V, involving high polycot producing parents, showed that high production was maintained in the first generation. In the first

cross of this group, M x L, the F_2 generation also showed a similarly high percentage.

It should be pointed out that the high polycot producing parents, Type III at the top of TABLE X, have shown partial sterility, often producing only three or four fruits. In addition, crosses involving them frequently failed. It is not known whether this was due to factors associated with polycotyledony or to other factors in themselves detrimental, which have been recombined during selection for polycot production.

From several attempts to make backcrosses to Type III parents, only two were successful. One backcross to a normal parent succeeded. The seedling classification of the first generation from these follows:

	Seedling classification		
	Normal	Polycot	% polycot
Q x (Q x J) F_1	28	7	20.0
(P x C) F_1 x P	37	10	20.6
(C x P) F_1 x C	14	0	0.0

In the first of the three backcrosses above, both parents were polycot producing and the backcross to the higher producing parent, Q, resulted in a relatively high first generation phenotype. The second backcross involved a normal and high producing parent. The F_1 shown in TABLE X, Group I, exhibited polycot production and this crossed with parent P also resulted in polycot production. In the third backcross, the F_1 which had shown no polycots in 16 seedlings, resulted also in no polycots when crossed with the normal parent C. Only the first generation from the backcrosses could be examined, and the results could not be used to confirm or deny estimates of the number of factors involved. However, the results confirmed the presence of the factors in the F_1

and showed differences in crosses involving parents of Types 1 and 3.

From all of the 16 crosses described above, there were 68 F_1 plants grown to maturity. All of these produced polycots among the F_2 seedlings.

DISCUSSION

Polycotyledony is a phenomenon about which very few investigations are being made today. Because of this fact there was available no complete review of the literature of this subject more recent than that of Duchartre in 1848 (58). However, the extensive nature of the occurrence of these seedling forms among Dicotyledonous plants was surprising. It was found that there were at least 295 species in 68 families which had been described as producing polycotyledons. This is far over the total of 145 listed by Penzig (156, 157) and that of approximately 50 suggested by Litovchenko (119). The latter author also stated that such families as the Chenopodiaceae and Polygonaceae most frequently showed these forms. In the present study it was found that Compositae and Leguminosae were first and second in rank, respectively, in the number of species reported with polycotyledons. This is, of course, the same order in which these two families stand in total number of species. Several other families in which nine or more polycotyledonous species have been observed, are relatively large families with 1,000 or more species, excepting the Ranunculaceae, with at least twelve polycotyledons in a family of some 680 species.

The phenomenon is apparently widespread among Dicotyledons. In view of the fact that seedlings are not usually observed as carefully as mature plants, and that there are also many unrecorded observations of polycotyledony, it seems quite probable that dozens if not hundreds of other species actually contain these abnormal seedlings.

The forms assumed by the cotyledons in the polycot seedlings consisted of a continuous series and followed a definite pattern regardless of the species, genus, or even family to which the individual plants

belonged. This similarity was so striking that the polycotyledons of a maple (Acer Pseudoplatanus) might well be taken for those of a hollyhock (Althea rosea) or even of tomato.

The phenotypic expression of the condition in Lycopersicon has been fully described here and it has been found to follow closely the range exhibited by other genera previously reported. DeVries (198), in addition to other investigators, has pointed out that polycotyledons may have simply notched cotyledons, or the division may be such that three, four or even five cotyledons are formed. In the present case, judging from the examination of over 100,000 tomato seedlings, the range in Lycopersicon extends from the normal condition through tricotyledons to tetracotyledons, the latter with four entire cotyledons being the absolute maximum. The fact that the tomatoes examined in the present study came from dozens of sources scattered throughout the world, and showed the same forms of polycotyledony, indicated that the condition was common to the genus Lycopersicon.

It has been pointed out that polycotyledony is widespread among Dicotyledons and that the expression of the condition is same in all recorded occurrences. These facts are suggested here as further evidence of the generally accepted fact that the Dicotyledon group has a common ancestry. This is especially so because the observations deal with such a basic morphological stage of the plants, the embryo.

The studies of the gross vascular supply to the cotyledons confirmed the fact, pointed out by Woodcock (210) that two principal veins supply a cotyledon making a total supply of four veins. His study concerned only normal plants but it was established here that regardless of the division or multiplication of the cotyledons, the total supply

of veins was the same. For example, in a tricotyledon, with three separate members, one cotyledon contained two veins and the other two cotyledons contained one vein each. At first, this observation would seem to be at variance with a statement of Coulter and Land (50), who pointed out that growing primordia determine the number of vascular strands, the latter structures being secondary in nature, and their appearance dependent on the character of the primary structure. The authors gave further information, however, which may throw some light on the cotyledon situation in tomatoes. In describing the embryo of Cyrtanthus sanguineus, it was shown that four cotyledonary primordia began development separately, but that they soon "grew together" in pairs, so that two cotyledons, each with two points, were for a time evident. They inferred from this evidence that the possibility of polycotyledony in Cyrtanthus seemed plain.

It is not known at the present whether there are four original cotyledonary primordia in Lycopersicon, and no information on this point was given by Smith (173) who studied embryogeny in this genus. It seems highly probable, however, since the maximum number of cotyledons observed was four and the constant number of cotyledon veins was four. It also seems possible that the maximum number of cotyledons found in polycotyledonous seedlings of any given species may indicate the vascular situation in the cotyledons of such a plant.

A feature of polycotyledony which has not been fully explained is that of inheritance. The indications were plain from the attempts of others to explain this feature that it was certainly not due to a single factor pair. In the present study, the problem was approached by the establishment of lines which differed in their production of polycotyledons. In this way, crosses were analyzed between lines pure for the

production of normal seedlings and those pure for the production of polycotyledons. In the latter, the percentages of the forms produced varied but every plant in these lines gave rise to some polycotyledons, indicating the presence of genes associated with the character. The results obtained gave every indication that a form of quantitative inheritance was in effect. Several features pointing to this conclusion were the lack of true dominance, the approach of the first generation mean to mean of the parental classes and the recovery of polycot producing genotype in 171 and the normal genotype in only 4 out of 175 second generation plants. The ratio 171:4 resembled a 63:1 ratio and suggested that there were at least three independent factor pairs affecting polycot production.

In quantitative inheritance it was pointed out by Sinnott (171), MacArthur and Butler (127) and others that the second generation distribution curve would be positively skew as a result of the geometric, cumulative action of the genes involved. The studies with which the authors dealt were those of size or weight inheritance and the values plotted were calculated on both an arithmetic and logarithmic basis. The latter was found to shift the curves from positive skewness to approximate normality. In the present studies with tomatoes a strongly positive skewed curve was obtained in plotting arithmetic values of polycot incidence in the F_2 but plotting logarithmic values produced a more nearly normal curve, and revealed the presence of two modes. The original positively skewed curve and the shift obtained supported the hypothesis that quantitative inheritance was in effect. The bimodality could not be fully interpreted from the data obtained but suggested that the genes controlling polycot production were not equal in their

effectiveness. Such unequal effects would not be unusual (171).

Previous investigators have shown that in certain genera, selection could bring the incidence of polycotyledony up to nearly 100% but that no lines could be established in which every plant was phenotypically a polycot. In two of the studies in which reference was made to polycotyledons in tomatoes (76, 124), the attempts to increase percentages of these forms were unsuccessful. In the present study, such attempts were successful in certain lines and unsuccessful in others. In hybrids from cross No. 244, L. pimpinellifolium x L. esculentum var. Marglobe, it was possible to increase the percentages up to 94.6%, but not beyond. The actual percentages obtained in successive generations of selection in these hybrids closely approximated ones obtained by DeVries (198) and others working with other genera. The experience with tomatoes supports the view expressed by DeVries that attempts to establish lines with 100% polycotyledons are futile. It was pointed out here, however, that lines of tomatoes could be readily established in which 100% of the plants produced such forms.

In the light of the data presented above, a logical explanation may be given for the conflicting results obtained in selection. In races or lines such as the Halbrasse of DeVries or certain tomato varieties, only a limited number of genes for polycot production were present, and when these became homozygous, no further change was possible. In the Mittelrasse or cross No. 244, additional genes belonging to the series of multiple factors were present and selection made it possible to establish lines with a larger number of genes, maintaining polycot production on a higher level.

It was shown that individual phenotypes, found in the series of

forms collectively called polycotyledons, did not reproduce themselves exclusively. A tricotyledon, for example, could produce not only tricotyledons but phenotypically normal plants, tetracotyledons and any of the other steps in the series. The explanation for the presence of the continuous series of forms found among polycotyledons was not apparent in the observations made here. There was no indication that normally formed cotyledons were later split. On the contrary, the shape of the cotyledons must have been determined at the time of their inception in the embryo, and any forces influencing the degree of division would have acted at that time. Since the final form of the cotyledons was the only stage examined, no positive interpretation of this feature can be given, but it seems possible that there are modifying genes which influence the degree to which polycotyledons are divided.

In certain populations of tomato hybrids in which high percentages of these forms appeared, partial sterility was found. This was manifested not only in their meager fruit production but often in the inability to effect crosses with them. This was not apparent, however, in the occasional polycot seedlings which were to be found in commercial varieties. It was pointed out by Tukey (192) that in seedlings of many varieties of cherries and peaches, presence of polycotyledons indicated heterozygous breeding material. It may be said that in tomatoes, the presence of high percentages of these forms in any line indicated that the line had been inbred for several generations.

When the possible practical advantages of polycotyledony were suggested by Litovchenko (119), who found increased yields in beet (Beta vulgaris) as well as in other plants, it seemed possible that beneficial changes might be found in these forms in tomatoes. The tests reported

here indicated that tomato seedlings showing polycotyledony often had abnormal leaf placements which resulted in higher numbers of leaves in plants up to four or five weeks of age. By the time of the maturity of the plants, however, the two groups had approximately the same total number of leaves. Any changes were thus effective only in the young plants.

In comparisons of normal and polycotyledonous plants in a field trial it was found that the total number of fruits produced by the two groups of plants did not differ significantly, but that the time of peak production was different. Plants of Marglobe and Rutgers from seedlings possessing the abnormal cotyledons were found to be later in fruit production than normal plants from the same seed supply. The significance of this finding is apparent, in that the total early crop would be significantly lower if these forms were included with the normal plants. If the early crop is of importance in any given planting it would be advantageous to discard all seedlings showing cotyledon division or multiplication. This would not be difficult since the forms are readily distinguishable within 3 to 10 days after emergence from the soil of the seed flat or field.

Seedling classification of several hundred lines of tomatoes revealed that the polycotyledons were quite common, and occurred in many commercial varieties. As a general rule, such seedlings have been found to be identical with normal ones in horticultural characteristics such as bush habit, fruit type and all characters with the exception of time of maturity cited above.

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SUMMARY

A literature survey revealed that polycotyledony was much more frequent than recent investigators had reported. At least 295 species in 68 families contained these forms. The two largest Dicotyledonous families, Compositae and Leguminosae, contained the largest numbers of polycot species according to published reports.

In numerous commercial varieties and foreign accessions polycotyledons were observed. First reports were given of their occurrence in Lycopersicon pimpinellifolium, L. peruvianum, L. peruvianum var. dentatum and L. glandulosum.

The complete range of expression of the polycotyledonous condition in Lycopersicon was presented. Cotyledon variations followed a continuous series from normal through notching and division to the extreme form with four separate, entire cotyledons. The variations were strikingly similar to all such series reported for numerous other species and genera.

The total number of veins supplying the cotyledons was shown to be four in both normal and polycotyledonous seedlings.

Selection within varieties to increase the incidence of the forms gave both positive and negative results, depending on the lines tested. In hybrid populations from a cross, L. pimpinellifolium x L. esculentum var. Marglobe, selection increased the incidence from 1% in the first generation to 94.6% in the fifth.

Three types of polycot lines were isolated; the first invariably produced normal seedlings, the second invariably produced polycotyledons in low percentages, and the third polycotyledons in high percentages.

Cotyledon analysis of appropriate crosses between these types revealed that quantitative inheritance was operating. At least three pairs of genes, probably differing in their effectiveness, controlled polycot production. Several reciprocal crosses revealed no differences due to the direction of the cross.

The various forms of polycotyledons did not reproduce their own phenotype exclusively but in addition, gave rise to all other forms. The tricotyledon appeared most frequently. The wide variation shown suggested that several modifying genes were affecting the expression of the polycotyledonous condition.

As a result of altered leaf placement at the lower nodes, polycot plants often had higher numbers of leaves than normal plants up to four or five weeks of age. At maturity, the total leaf numbers were essentially the same.

Total fruit production was found to be the same in normal and polycot plants. However, the time of peak production differed in that polycot plants were later. This fact suggested that such forms should be discarded in any planting in which earliness was a beneficial economic factor.

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Publications:

Bamford, R., G. B. Reynard and J. M. Bellows, Jr. Chromosome number in some Tulip hybrids. Bot. Gaz., Vol. 101, Dec., 1939, pp. 482-490.

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