THE INHERITANCE OF CAROTENOID PIGMENT SYSTEMS IN THE TOMATO[1]

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IN the tomato three types of fruit flesh color have long been known. The red flesh (*RRTT*) of normal canning tomatoes is due to the presence of major quantities of the pigment lycopene. A minor quantity of beta-carotene is also present, as are traces of certain other carotenoid pigments. Yellow-fleshed tomatoes (*rrTT*) are characterized by the lack of pigment in major quantities. Orange tomatoes (*RRtt*) of the Jubilee or Tangerine varieties, on the other hand, contain a mixture of carotenoids of which prolycopene and zeta-carotene are the principal components. Recently a new pigment type, orange in color, has been isolated (LINCOLN and PORTER 1950). Unlike the orange Tangerine type, this tomato contains largely beta-carotene with minor quantities of lycopene. LINCOLN and PORTER postulate that in beta-orange tomatoes the shift from red (lycopene) to orange (beta-carotene) depends primarily upon a single gene *B* which lacks dominance.

When the present study was initiated the monohybrid segregations of *R/r* and of *T/t* were well established on a visual basis (MACARTHUR 1931, 1934). Moreover, considerable analytical information was available concerning the parent pigment types (LEROSEN, WENT and ZECHMEISTER 1941; ZECHMEISTER, LEROSEN, WENT and PAULING 1941; LEROSEN and ZECHMEISTER 1942; NASH and ZSCHEILE 1945; PORTER and ZSCHEILE 1946a, 1946b). Crosses between *r* and *t*, however, had not been thoroughly analyzed, and crosses involving *B* and either *r* or *t* had not been reported. The possibility existed that *B* might be an allele of either *r* or *t*. FLEMING and MYERS (1937) cite correspondence with MACARTHUR in which the latter suggested that crosses involving Tangerine orange (*RRtt*) and yellow (*rrTT*) produce a 9 red : 3 yellow : 4 orange (3 orange and 1 light orange) F_2 ratio. From their own data, however, these authors suggested that the inheritance was considerably more complicated. Recently JENKINS and MACKINNEY (1951) have confirmed MACARTHUR's prediction. Moreover, MACKINNEY and JENKINS (1949, 1952) have extended the analytical information with regard to parent types and have included an analysis of the segregants involving these two genes. The present work supports the data reported by MACKINNEY and JENKINS with respect to *R* and *T*, and in addition extends the analysis to include the gene *B*.

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METHODS

The characterization of the four parental pigment types, characterization of the six F_1 hybrids produced by crossing these parents in all combinations, and an analysis of the F_2 populations were undertaken in the present study. The variety Rutgers was chosen as a representative red type (*RRTT*). Jubilee, a Tangerine derivative, was chosen as representative of the Tangerine orange group (*RRtt*). For the yellow (*rrTT*) parent, a selection of PI 91458 was used. This line is characterized by the greatly reduced production of carotenoids. We have accordingly called this strain " low total." The identity of the *r* locus was proven by test crosses. For the beta-orange (*BB*) parent an advanced selection of the parent strain used by LINCOLN and PORTER (1950) in determining the inheritance of beta-carotene in crosses with the red variety Indiana Baltimore was used.

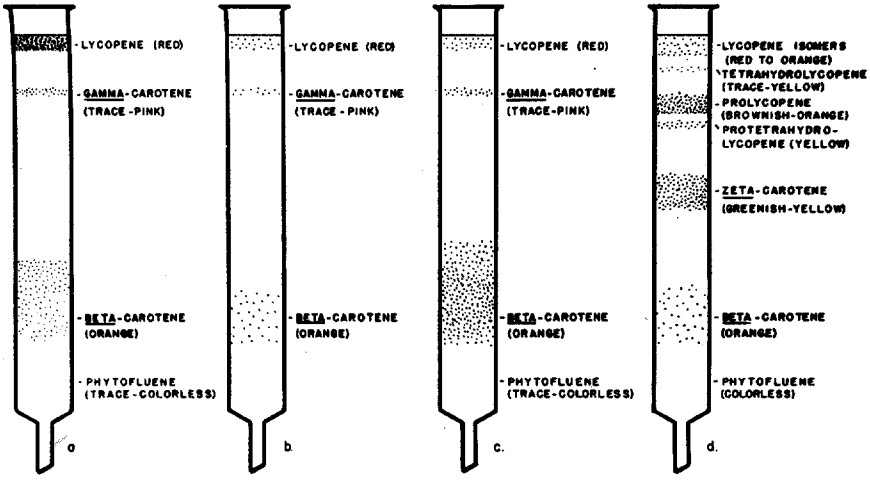

FIGURE 1.—Chromatograms of the four parent pigment complexes. a. Rutgers (red); b. low total (yellow); c. beta-orange; d. Jubilee orange.

Note: Under ultra-violet light the bands of phytofluene appear fluorescent.

Certain methods of chemical analysis used in the present work have been described in detail by ZSCHEILE and PORTER (1947), PORTER and ZSCHEILE (1946a) and PORTER and LINCOLN (1950). In brief the method was as follows:

The homogenized fruits were extracted with a mixture of acetone and hexane, the xanthophylls and esters removed, and a 20 to 25 gm aliquot of the remaining carotene solution chromatographed on magnesia. The analyst recorded the pigments present and the approximate width of each band. These data were sufficient to classify the pigment system in most cases. However, when quantitative data were desired, either of two procedures was used, depending on the complexity of the pigment system. When the chromatogram showed lycopene and beta-carotene predominating to the near exclusion of all

other pigments, direct spectrophotometric readings were made on the carotene solution and the amounts calculated. When more precise information was required or more complex pigment systems were encountered the individual pigments were eluted from the chromatogram and quantitatively determined.

It should be noted that in the method described xanthophylls and esters were discarded in the phasic separation involved in extraction. The small quantity of fruit extracted in the individual samples may also account for the fact that pigments present in extremely small quantities may escape detection entirely on the chromatographic columns.

All crosses and selfs were produced under controlled conditions in the greenhouse. In characterizing the parental strains, selfed progenies of the original plants used in the crosses were analyzed. In the F_2 populations every plant was analyzed when the original cross involved the high beta-carotene parent. In crosses involving Jubilee orange and high beta, for example, chemical characterization was the only method available for separating the two types. In populations involving segregations of the genes *R* and *T* only, the number of samples analyzed was sufficient to detect any aberrant types which visual classification might fail to detect.

THE PARENT PIGMENT TYPES

The pigment system which was typical of each of the four parent strains is illustrated in the chromatograms sketched in figure 1. (In this paper we have followed the nomenclature used by PORTER and LINCOLN 1950. Protetrahydrolycopene has been designated as psi-carotene, and tetrahydrolycopene as neurosporene by other authors.) Three of the types, red, yellow and beta-orange were differentiated by quantitative shifts involving the same pigments. Jubilee orange, on the other hand, was distinguished from the other three by possessing a number of different pigments, several of which could not be detected in any of the other parent types.

TABLE 1

Major carotenes of the fruit of 16 Jubilee orange (RRttbb)[1] tomatoes.

Pigment[2]	Mean % s
Lycopene isomers	4.2 ± 1.6
Prolycopene	36.2 ± 7.7
Protetrahydrolycopene	17.6 ± 2.7
Zeta-carotene	40.5 ± 6.8
Beta-carotene	1.8 ± 1.1

[1]This genotype was assigned after the subsequent analyses of the F_2 progenies reported in the present paper.

[2]These fruits contained a mean total carotene content of 100.1 ± 26.2 micrograms per gram fresh weight. Total carotene for Jubilee orange was calculated by the addition of the quantities obtained for the five major pigment components. Trace pigments were not included in the calculation. In addition to the pigments recorded the fruits contained 24.3 ± 10.1 micrograms/gm fresh weight of the colorless polyene phytofluene.

The quantitative relationship between the various pigments of the Jubilee complex was determined by chromatographic separation of each of the major pigment components. Table 1 presents the mean proportion of each pigment and the total pigment content as determined by addition of the quantities determined for each fraction.

In addition to the pigments assayed, Jubilee orange tomatoes contained an average of 24.3 micrograms per gram fresh weight of the colorless polyene

TABLE 2

The major carotene content of the fruit of three parent tomato strains and six F_1 hybrids.

Progeny	Year	Number of plants sampled	Mean total carotene content		Mean lycopene content		Mean beta-carotene content	
			micrograms/gm fresh wt.	s	%	s	%	s
Rutgers (red)	1949[2]	9	70.8	± 9.2	91.8	± 2.2	8.2	± 2.2
RRTTbb[1]	1950	20	88.4	± 17.0	97.0	± 2.4	3.0	± 2.4
Low total (yellow)	1949	11	1.4	± 0.2	19.7	± 12.3	80.3	± 12.3
rrTTbb	1950	20	2.2	± 0.6	38.6	± 19.3	61.4	± 19.3
Beta-orange	1949	11	71.3	± 14.6	10.5	± 2.0	89.5	± 2.0
RRTTBB	1950	19	83.6	± 16.2	6.9	± 1.8	93.1	± 1.8
F_1 Rutgers × low total	1949	10	78.0	± 19.8	98.1	± 1.9	1.9	± 1.9
RrTTbb (red)	1950	11	75.6	± 12.9	93.1	± 3.9	6.9	± 3.9
F_1 Rutgers × Jubilee	1949	10	84.4	± 21.9	95.7	± 2.3	4.3	± 2.3
RRTtbb (red)	1950	5	70.9	± 14.9	92.4	± 2.5	7.6	± 2.5
F_1 Rutgers × beta	1949	5	66.8	± 12.7	51.3	± 4.8	48.7	± 4.8
RRTTBb (orange-red)	1950	10	82.3	± 15.0	52.8	± 3.8	47.2	± 3.8
F_1 Jubilee × low total	1949	11	81.3	± 13.2	96.3	± 2.1	3.7	± 2.1
RrTtbb (red)	1950	10	97.9	± 18.1	95.3	± 2.8	4.7	± 2.8
F_1 beta × low total	1949	17	39.6	± 5.5	32.3	± 6.6	67.7	± 6.6
RrTTBb (orange-red)	1950	11	66.6	± 10.8	41.3	± 1.7	58.7	± 1.7
F_1 Jubilee × beta	1949	11	61.7	± 10.3	46.1	± 3.8	53.9	± 3.8
RRTtBb (orange-red)	1950	10	72.4	± 9.2	44.8	± 7.8	55.2	± 7.8

[1]The genotypes assigned to the various progenies are those shown to be correct by the subsequent analyses of the F_2 progenies reported in the present paper.

[2]The plots were located on the Agronomy Farm in 1949 and on the O'Neall Farm in 1950 (Lafayette, Indiana).

phytofluene. Red, and beta-orange tomatoes contained only traces of this colorless polyene. Phytofluene was present in such small quantities in yellow tomatoes that it remained undetected when small individual samples were assayed.

Red, yellow and beta-orange tomatoes contained lycopene, gamma-carotene and beta-carotene. Lycopene and beta-carotene were the two major pigment components in each system. Gamma-carotene, a structural intermediate between lycopene and beta-carotene, was present only in trace quantities in each of the three types. Table 2 presents the mean total carotene content and the

relative proportions of lycopene and beta-carotene in these three parent types and in the six F_1 hybrids produced by all possible combinations of the four parents.

The data reported in table 2 were derived by direct readings on the crude pigment extract. However, more than half of the samples were also analyzed by separation of the beta-carotene fraction. Reasonable agreement was observed between the two methods. The genotypes shown to be correct by subsequent analyses of the F_2 progenies have been supplied in tables 1 and 2.

The low total parent differed from the red and the beta-orange largely in the gross restriction of total pigment production. Both lycopene and beta-carotene were present in the yellow strain, and in the majority of cases the beta-carotene content predominated. These observations are in line with those reported by MACKINNEY and JENKINS (1949) in which, on the basis of bulk samples, yellow lines were shown to contain both lycopene and beta-carotene, with beta-carotene representing the major fraction.

A consideration of the data presented in tables 1 and 2 shows that the substitution of the genes *rr* in place of *RR* resulted in the restriction of pigment production. The substitution of *tt* for *TT* resulted in the production of pigments of the Jubilee complex, principally zeta-carotene and prolycopene. *TT* plants produced mainly lycopene and beta-carotene. In a lycopene, beta-carotene system, the substitution of *BB* for *bb* reversed the relative proportions of lycopene and beta-carotene resulting in a plant which produced major proportions of beta-carotene.

THE PIGMENT SYSTEMS OF THE F_1 HYBRIDS

With respect to the six F_1 hybrids, all produced a pigment system containing lycopene, traces of gamma-carotene, and beta-carotene. In addition to these

TABLE 3

The F_2 populations derived from crosses involving the four parent pigment types.

Cross	Total no. of plants	Chemical classification number of plants						Chemical ratio	χ^2
		Beta-orange	Orange-red	Red	Jubilee-orange	Yellow	Pale orange		
F_2-Rutgers × low total *RRTTbb* × *rrTTbb* (red × yellow)	273			196		77		3:1	1.4957
F_2-Rutgers × Jubilee *RRTTbb* × *RRttbb* (red × orange)	191			150	41			3:1	1.2722
F_2-Jubilee × low total *RRttbb* × *rrTTbb* (orange × yellow)	147			84	25	30	8	9:3:3:1	.6337
F_2-beta × low total *RRTTBB* × *rrTTbb* (orange × yellow)	200	40	70	36		54		3:6:3:4	.880
F_2-Jubilee × beta *RRttbb* × *RRTTBB* (orange × orange)	237	45	85	42	65			3:6:3:4	.949

pigments, all produced traces of phytofluene. Three of the F_1 hybrids produced chromatograms which were indistinguishable from that produced by the red parent. The remaining three produced chromatograms which were intermediate between those produced by the red parent and the beta-orange parent.

A comparison of the quantitative data (table 2) for the Rutgers parent (*RRTTbb*) and the F_1 hybrid of Rutgers × low total (*RrTTbb*) shows that each produced comparable quantities of total carotene and each contained approximately 95% lycopene. From this we may deduce that *R* is dominant to *r* chemically as well as visually. Comparing Rutgers with the F_1 of Rutgers × Jubilee (*RRTtbb*) shows a comparable situation and leads to the conclusion that *T* is strictly dominant to *t* both chemically and visually.

A comparison between the F_1 of Rutgers × beta (*RRTTBb*) and either the Rutgers parent (*RRTTbb*), or the beta parent (*RRTTBB*), suggests that the gene *B* lacks dominance. The heterozygote produced quantities of lycopene and beta-carotene intermediate between those produced by the two parents. The visual appearance of such fruit was also intermediate between the two parents, the flesh color being orange-red.

THE F_2 POPULATIONS

The analyses of the F_2 populations are summarized in table 3. From the standpoint of new pigment types, only one system was found which has not been discussed under the parent and F_1 types. This new type, a pale orange, was typical of the *rrtt* genotype (see below).

The F_2's of the crosses of Rutgers (*RRTTbb*) × low total (*rrTTbb*) and of Rutgers × Jubilee (*RRttbb*) yielded the 3 to 1 ratios expected. Chemically the plants in the progenies were shown to produce pigment systems identical with the parent types.

The one new pigment system produced was the result of recombination of *r* and *t* in the F_2 of the cross of Jubilee (*RRttbb*) × low total (*rrTTbb*). Chemically this cross produced the four classes expected in a dihybrid ratio. The double recessive *rrtt* produced a pigment system in which the amount of pigment was restricted, as might be expected on the basis of *rr*. The pigments which were produced were of the Jubilee type, as might be expected on the basis of *tt*. Unlike the Jubilee parent, however, zeta-carotene was produced in only limited quantities. Prolycopene was by far the major constituent. Table 4 presents a detailed analysis of bulk samples of three *rrtt* plants. As has been recently reported by MACKINNEY and JENKINS (1952), the *rrtt* genotype produced more total carotene than did *rrTT* plants, although the total carotene production was still quite limited as compared with any genotype carrying dominant *R*. The genotypes of the three plants on which data were collected were proven by test crosses to both the low total and the Jubilee parent.

In table 3 it may be noted that the F_2 of the cross of Rutgers (*RRTTbb*) × beta (*RRTTBB*) is not given. This progeny was not analyzed in the present study. The original report by LINCOLN and PORTER (1950) was a product of this laboratory. Moreover, careful consideration of the segregations in the

remaining two crosses in table 3 lends support to their data. In the F_2 of the cross of beta (*RRTTBB*) × low total (*rrTTbb*) the ratio obtained was 3 orange : 6 orange-red : 3 red : 4 yellow. Of the yellow plants in the F_2 population, those carrying *BB*, *Bb* or *bb* could not be distinguished phenotypically. Nor was any chemical distinction observable with small individual samples. That certain of these yellow fleshed plants actually contained *B* in a masked condition was shown by crossing 10 of the F_2 yellows by the beta parent (*BB*). Among the 10 crossed, progenies of the three types expected were obtained proving that certain F_2 yellows were *BB*, *Bb* and *bb* respectively.

In the highly pigmented portion of the population (*R*–), the plants fell into the 1 : 2 : 1 ratio typical of the F_2 segregation of *Bb*. The class limits used were those proposed by LINCOLN and PORTER (1950). The 146 highly pigmented plants gave a complete range of beta-carotene values. The distribution curve showed three distinct peaks corresponding to values typical of a red, a beta

TABLE 4

The quantities and relative proportions of pigments and phytofluene in bulk samples of three plants of the rrtt genotype.

Plant No.	23		44		50	
Pigment or polyene	Micrograms/gm fresh wt.	Pigment %	Micrograms/gm fresh wt.	Pigment %	Micrograms/gm fresh wt.	Pigment %
Lycopene isomers	2.72	23.3	2.27	24.6	1.62	29.6
Prolycopene	7.73	66.2	5.92	64.1	2.72	49.7
Protetrahydro-lycopene	.48	4.1	.39	4.2	.38	6.9
Zeta-carotene	.34	2.9	.47	5.1	.32	5.9
Beta-carotene	.40	3.4	.19	2.1	.43	7.8
Phytofluene	.48		.30		.39	
Total carotene[1]	11.67		9.24		5.47	

[1]Derived by addition of pigment fractions.

parent, and the F_1 of a cross between these two types. The low points on the distribution curve corresponded to the low points reported by LINCOLN and PORTER in their report of a cross involving a red variety with a beta type.

We may deduce from this cross that *B* is not an allele of *R*. Dominant *R* is required for the production of pigment in quantity regardless of the constitution with respect to *B*. In the presence of *R*–, the gene *B* appears to behave as originally postulated. In the presence of *rr*, the gene *B* is without apparent effect.

A somewhat comparable situation holds for the last F_2 reported in table 3. The ratio chemically was 3 orange, beta : 6 orange-red, intermediate : 3 red, lycopene : 4 orange, Jubilee. In this case, however, the beta-orange type could not be distinguished visually from the Jubilee orange type. The visual ratio thus became 7 orange : 6 orange-red : 3 red. Plants carrying *tt* produced pigment systems comparable to the Jubilee parent regardless of the genotype with respect to *B*. In the presence of *T*–, again we obtained the 1 : 2 : 1 segregation of *Bb*,

yielding the orange, beta type; the orange-red, intermediate type; and the red, lycopene type. From these F_2 data we may conclude that *B* is not an allele of *T*. *T* must be dominant before *B* can be expressed and *tt* produces pigments of the Jubilee complex regardless of the genotype at the *B* locus.

DISCUSSION

It is apparent that the major pigment shifts reported above depend upon the action and interaction of at least three independent loci, *R*, *T* and *B*. Since these genes control radically different pigment systems, they merit consideration as to their probable role in pigment synthesis.

Those who have investigated plants carrying *rr* from a chemical standpoint have agreed that *R* favors pigment synthesis, while *rr* produces only a limited amount of pigment. Beyond this point, however, several suggestions have been made regarding the role of *R*. LEROSEN et al. (1941) reported that *rr* genotypes produced no lycopene. They suggested that *R* determined first the presence of this pigment. ZECHMEISTER et al. (1941) suggested that the gene *R* might be involved in the synthesis of prolycopene in both Tangerine orange and red tomatoes and that the gene *T* might be responsible for the conversion of prolycopene to lycopene in red tomatoes. LINCOLN and PORTER (1950) apparently believed that *R* possessed a certain specificity for lycopene formation for they placed *R* in their synthetic scheme between zeta-carotene and lycopene.

With the knowledge of the *rrtt* genotype, MACKINNEY and JENKINS (1952) state that *R* clearly favors carotenoid synthesis, and that when *T* is recessive, prolycopene is synthesized regardless of *R*. From this, and from the present work, it is clear that *R* has no specificity for lycopene production, or for prolycopene or zeta-carotene production. *R–T–* produces a lycopene, beta-carotene system; *rrT–* produces the same qualitative system in limited quantity. *R–tt* produces the Jubilee or Tangerine system; *rrtt* produces the same qualitative system in limited quantity. The simplest explanation of the role of *R* would place *R* early in the sequence of synthesis. *R* appears to be responsible for the production of an unknown precursor (or precursors) in quantity.

Two difficulties are encountered with this view. The data suggest that *rrtt* produced more pigment than *rrTT*. MACKINNEY and JENKINS (1952) have reported a similar situation in unrelated material. Thus, if *rr* were responsible for the production of a limited amount of precursor, the end products of which were determined by the alternate alleles at the *T/t* locus, it would be reasonable to expect that the total carotene production in each case should be similar. Since we have discarded the oxygen derivatives in the extraction procedure, it is possible that both might produce comparable yields if all carotenoid derivatives were taken into consideration.

The second difficulty encountered with the view that *R* and *r* control merely quantitative reactions is the fact that the relative proportions of lycopene and beta-carotene were altered in the *rrT–* genotypes as compared with the *R–T–* genotypes. Similarly, the relative proportions of zeta-carotene and prolycopene

were altered in the *rrtt* genotypes as compared with the *R–tt* genotypes. The significance of these pigment shifts, however, is obscured by the fact that the primary action of *rr* appears to be the gross restriction of pigment synthesis. In view of this, the most plausible role of *R* and *r* would seem to be purely quantitative as regards precursors. This view is strengthened by the fact that neither *rrTT* nor *rrtt* fruits contained known polyene components which distinguished them from plants carrying dominant *R*, nor was any component produced in greater quantity in the recessive *r* genotypes.

With regard to the action of gene *T*, it seems to be generally agreed that *T* converts pigments of the Jubilee complex into a lycopene, beta-carotene system. There is a question as to which pigment is typical of the Jubilee complex, or which pigment serves as an immediate precursor for lycopene. ZECHMEISTER and WENT (1948) favor prolycopene. PORTER and LINCOLN (1950) favor zeta-carotene. If the proposed structures of zeta-carotene and prolycopene are correct, it is incompatible with modern genetic theory to assume that a single gene *T* may mediate the conversion of both zeta-carotene and prolycopene to lycopene. In the case of zeta-carotene a dehydrogenation is required to produce lycopene. With prolycopene a shift of bonds from the cis to trans configuration is required.

The above-mentioned authors lacked a knowledge of the *rrtt* genotype when these opinions were expressed. Plants of this genotype produced prolycopene in fair quantity (table 4), but the relative proportion of zeta-carotene was decreased as compared with *RRtt* plants (table 1). This may suggest that prolycopene rather than zeta-carotene is the key compound in *tt* genotypes. If ZECHMEISTER and WENT'S (1948) contention that the action of the gene *T* is one of stereochemical guidance is correct, *T* determines the spatial configuration of the molecule with respect to cis and trans bonds. On this basis *T* is not responsible for a dehydrogenation process which converts zeta-carotene to lycopene as postulated by PORTER and LINCOLN (1950). The saturated carotenes and polyenes might result from side reactions in which carotene acts as a suitable hydrogen acceptor.

The dominance relation of the gene *T* would seem to infer that some component of the Jubilee complex is converted into either lycopene or beta-carotene. Whether this step is one of dehydrogenation or of spatial direction cannot be answered at the present time. Moreover, in the tomato, the fact that phytofluene is present in much larger quantities in the Jubilee system than in the red, yellow or beta-orange types fails to prove more than coexistence of phytofluene with the more saturated carotene pigments. From a genetic standpoint, proof is still lacking that phytofluene is an immediate precursor for carotene, as has been suggested by ZECHMEISTER (1948) and PORTER and LINCOLN (1950).

Where lycopene and beta-carotene are present in quantity, the relative proportion of lycopene or beta-carotene is determined by the alternate states of *B/b*. The fact that gamma-carotene is always present in trace amounts in these systems suggests an interconversion of lycopene to beta-carotene, or *vice versa,*

mediated by the action of *B* or *b*. If, as is suggested by the data, *B* lacks dominance, this gene is of little assistance in determining the direction of synthesis. Lycopene may be formed first as PORTER and LINCOLN have suggested, or beta-carotene may appear first in the sequence.

Before concluding the discussion it should be noted that there is considerable evidence from advanced breeding lines that the *B* gene may be modified by a dominant inhibitor contributed by certain other tomato strains. While the hypothesis remains to be proven, certain aberrant results suggest that *B* may actually be a dominant gene and that the intermediate nature of the F_1, as well as the F_2 segregations of *Bb*, might be accounted for if the beta-orange parent lacked a dominant inhibitor of *B* contributed by the other parent. Among the progenies derived from crosses involving orange (beta-carotene) selections and red varieties are certain lines which breed true for orange-red color and consistently yield intermediate beta-carotene values. Moreover, some advanced selections which are high in beta-carotene content yield progenies of two types, those breeding true for high beta-carotene content, and those segregating both orange (beta) and red (lycopene), but lacking intermediate orange-red plants. A further analysis of the *B* gene is in progress.

SUMMARY

Four true breeding types of tomatoes are known which differ with respect to the carotenoid pigments produced in the flesh of the fruit. Three of these, the red (*RRTTbb*), the yellow (*rrTTbb*) and the beta-orange (*RRTTBB*), are characterized by quantitative shifts which involve the pigments lycopene and beta-carotene. The fourth type, Jubilee orange (*RRttbb*), possesses a different pigment system in which zeta-carotene and prolycopene are the major components. By analyzing the four parent types, the six F_1 hybrids produced by crossing these parents in all combinations, and the F_2 progenies derived therefrom, it is shown that these pigment systems depend upon the action of three independent genes *R*, *T* and *B*. *R* and *T* are shown to be dominant chemically as well as visually. The data presented with regard to *B* suggest that this gene lacks dominance. The primary action of gene *R* appears to be the production of an unknown precursor in quantity. *T* converts pigments of the Jubilee system into a lycopene–beta-carotene system, and *B* determines the relative proportions of lycopene and beta-carotene in the presence of *R* and *T*. Certain difficulties encountered in accepting this view with regard to the action of *R* are noted. These arise primarily from the consideration of the quantities of pigments and the relative proportions of certain pigments produced by the genotypes *rrTT* and *rrtt* as compared with *RRTT* and *RRtt*.

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