DELTA-CAROTENE IN THE TOMATO[1]

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DELTA-carotene was found in quantity in certain selections from crosses of *Lycopersicon esculentum* Mill. × *L. hirsutum* Humb. and Bonpl. (PORTER and ZSCHEILE 1946; PORTER and LINCOLN 1950). It was reported by SOOST (1956) in derivatives of the cross *L. chilense* Dun. × *L. esculentum*. *Delta*-carotene is not a normal constituent of the ripe flesh of the commercial tomato. At maturity, the standard red tomato contains three carotenoids in more than trace quantities. The major pigment is lycopene and it is largely responsible for the red color. There is some *beta*-carotene, and a small quantity of *gamma*-carotene. Red fleshed tomatoes contain traces of neurosporene, *zeta*-carotene, and *alpha*-carotene, but rarely in excess of 1 μg/g fresh weight. The *delta*-carotene producing selections contain the same pigments, but produce *delta*-carotene in addition, and have enhanced *alpha*-carotene fractions (KARGL, QUACKENBUSH, and TOMES 1960; TOMES 1963). *Delta*-carotene differs from *gamma*-carotene in the position of one double bond in the ring structure on one end of the molecule. Thus, *delta*-carotene contains an *alpha*-ionone rather than a *beta*-ionone ring. No ring is present on the other end of the molecule in *gamma*- or *delta*-carotene. *Alpha*-carotene differs from *beta*-carotene in having an *alpha*- rather than a *beta*-ionone ring at one end of the molecule. Both *alpha*- and *beta*-carotene have a *beta*-ionone ring at the other end of the molecule. Single factor control of this ability to produce *delta*-carotene has been reported, but without detail (SOOST 1956; TOMES 1963). The symbol *Del* (*delta*-carotene) was assigned by TOMES (1963). Data pertinent to the interaction between gene *B* (*beta*-carotene) and *Del* have been reported (TOMES 1967). I now report genetic and biochemical studies of *Del* in crosses with normal red, yellow (*r*), apricot (*at*), and tangerine (*t*).

MATERIALS AND METHODS

The *delta*-carotene parent had a complex origin. The pedigree includes the varieties Indiana Baltimore, Rutgers, and Marglobe, as well as the green fruited wild species *L. hirsutum* (PI 126445) and *L. hirsutum* (PI 127827). The *delta*-carotene parent has fruit with orange-red flesh. Sib selections differ in *delta*-carotene content, but the parent is fairly consistent. In the crosses reported, the normal red parent was Rutgers. The yellow parent was a standard *r r* line which has been used in other pigment studies (TOMES *et al.* 1953). The apricot parent (*at at*) came from the late DR. J. A. JENKINS, and the tangerine parent (*t t*) was Golden Jubilee. Genes *r*, *t*, and *at* are recessive and various genetic and biochemical studies have been reported (JENKINS and MACKINNEY 1953, 1955; TOMES *et al.* 1953, 1958).

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TABLE 1

Average pigment and polyene content of tomato fruit from five parent strains and six F_1 hybrids

Parent or F_1	Number of plants sampled	μg/g fresh weight ± standard deviation										
		phytoene	phyto-fluene	alpha-carotene	beta-carotene	zeta-carotene	proneuro-sporene	delta-carotene	prolyco-pene	gamma-carotene	neuro-sporene	lycopene
Rutgers (red)	8	9.5±2.4	4.1±0.8	tr†	4.7±0.8	tr	..	..	..	0.9±0.2	tr	65.5±7.7
Del Del (orange-red)	11	10.6±5.6	3.4±1.6	2.4±0.4	5.0±0.9	tr	..	31.5±8.5	..	4.8±1.2	tr	16.3±6.9
r r (yellow)	6	2.8±0.4	..*	..	1.4±0.3	..	..	..	..	tr	..	0.2±0.2
at at (apricot)	12	2.8±0.7	..	..	6.3±1.8	..	..	..	..	0.9±0.6	..	1.8±0.9
t t (tangerine)	12	45.9±11.2	15.6±2.7	..	1.2±0.6	39.1±9.8	18.1±4.8	..	25.6±8.6	..	tr	3.4±0.4‡
F_1–Rutgers × *Del Del*	8	8.1±2.4	1.9±0.9	0.3±0.4	4.5±1.0	..	..	16.9±1.6	..	4.5±1.0	..	57.0±18.4
F_1–*Del Del* × Rutgers	13	N.D.§	N.D.	0.3±0.9	4.4±0.8	..	..	16.4±2.7	..	3.7±0.3	..	44.6±11.4
F_1–*r r* × *Del Del*	8	N.D.	N.D.	0.7±0.3	5.4±3.3	..	..	18.7±2.8	..	4.1±0.8	..	19.8±8.1
F_1–*Del Del* × *r r*	6	3.0±0.3	0.4±0.1	0.8±0.5	5.0±0.8	..	..	17.4±2.1	..	3.9±0.4	..	20.0±9.1
F_1–*Del Del* × *at at*	3	11.8±3.0	3.5±0.8	1.6±0.9	5.8±1.1	..	..	9.3±2.0	..	2.6±0.5	..	30.0±4.4
F_1–*Del Del* × *t t*	16	10.8±3.4	3.4±1.0	0.9±0.6	5.4±0.9	..	..	15.0±5.4	..	3.9±1.5	..	31.8±10.0

* .. = not detected.
† tr = trace (less than 1 μg/g).
‡ lycopene isomers–above prolycopene on the column-read as lycopene.
§ N.D. = not determined.

The methods are those summarized by TOMES (1963). Briefly, ripe fruits (several per sample) were deep frozen until analyzed. Fruits were thawed in sealed containers and homogenized. A 25g sample was extracted, washed, saponified, rewashed, dried, and made up to volume. One fourth of the extract was chromatographed and the quantities of individual pigments and polyenes were determined spectrophotometrically. The progenies and parents were grown and classified in the field at the Purdue University O'Neall Farm over a period of years.

RESULTS

Pigment and polyene analyses for the various parents and F_1's are summarized in Table 1. Phytoene and phytofluene are colorless polyenes structurally related to the carotenes. They are more saturated than the carotene pigments and are presumed by many to be pigment precursors. Lycopene is the major pigment in the red fleshed variety Rutgers, averaging 65.5 μg/g fresh weight in these samples. A small quantity of *gamma*-carotene is present, and 4.7 μg of *beta*-carotene. The *delta*-carotene parent (*Del Del*) produces the same pigments and polyenes, and *delta*-carotene, averaging 31.5 μg/g. The *alpha*- and *gamma*-carotene fractions are also enhanced. *Delta*-carotene is the major fraction. As compared with Rutgers, lycopene is reduced.

The yellow parent (*r r*) is distinguished primarily by the gross restriction of almost all pigment synthesis during maturation. The major pigment is *beta*-carotene which causes the yellow flesh color. Even this small *beta*-carotene fraction may not be formed during maturation, however, since *beta*-carotene is present in immature tomatoes in similar quantities.

The apricot parent (*at at*) represents a restriction of pigment synthesis. Lycopene, and the polyene fractions are greatly reduced, while *beta*-carotene is not. The 6.3 μg average for the *beta*-carotene fraction is comparable to that found in many red fleshed varieties. Because *beta*-carotene is the predominant pigment, the flesh is yellow and somewhat more intense than in the *r r* type. Traces of lycopene occur in some *at at* genotypes giving a pinkish tinge; hence the name apricot.

The tangerine (*t t*) orange flesh of the Golden Jubilee parent is qualitatively different. Here prolycopene, *zeta*-carotene, and proneurosporene are the major pigments. In Table 1, the lycopene fraction for *t t* is a complex of lycopene isomers. These analyses of parent pigment types are in line with previous reports for *r*, *t*, and *at* (JENKINS and MACKINNEY 1953, 1955; TOMES *et al.* 1953, 1958).

Pigment and polyene contents of all four F_1's between *Del Del* and the other pigment types are summarized in Table 1, along with values for reciprocal F_1's for *Del Del* × Rutgers and *Del Del* × *r r*. All F_1's produced *delta*-carotene, and all produced detectable *alpha*-carotene, thus inferring dominance of *Del* in the ability to produce *delta*- and *alpha*-carotene. In the F_1 hybrids, *gamma*-carotene was enhanced, as in the *Del Del* parent. Most F_1 *delta*-carotene values were about half the average of the *delta*-parent, suggesting incomplete dominance of *Del*. The lower value for the *delta*-carotene fraction of *Del Del* × *at at* may be spurious, since only 3 samples were analyzed. Each F_1 had less lycopene than Rutgers, but more than the *delta*- parent.

The reciprocal F_1's involving *Del Del* and *r r* gave like values. Those for Rutgers and *Del Del* were also similar with the possible exception of the lycopene fraction. These two F_1's were grown and assayed at different times. Since environmental factors affect pigment synthesis, this difference is not surprising. There is no reason to suspect a maternal effect.

Rutgers × Del Del: F_1's were grown several times and were classified as having red-orange flesh. The fruits were redder than the orange-red *delta* parent, but could be distinguished from the red flesh typical of Rutgers. These observations reflect the pigment analyses reported in Table 1. The lycopene content of the F_1 was less than that of Rutgers, but well above that in the *delta* parent. F_2 progenies were grown several times, but considerable inviability was always encountered. Only 68 of 210 seeds were recovered the first time and these were classified as 49 red-orange: 19 red ($\chi^2 = .31$, P = .50–.70 for a 3:1 ratio). Another planting yielded 21 plants of 105 seeds (13 red-orange: 8 red. $\chi^2 = 1.92$, P = .10–.20). A third attempt yielded 81 of 210 (57 red-orange: 24 red. $\chi^2 = .93$, P = .30–.50). These data and the pooled data ($\chi^2 = 2.26$, P = .10–.20) suggest that *Del* is a single gene. There was plant to plant variation in the red-orange class, but it was apparent that further separation visually would be extremely difficult. A backcross of the F_1 to the *Del Del* parent yielded 56 plants of 70 seeds, classified with difficulty as 33 red-orange and 23 orange-red. A small backcross progeny to Rutgers yielded only red-orange and red in about equal numbers. This cross was not pursued because of the inviability, although there was no indication that any class was eliminated or reduced.

r r × Del Del: F_1 progenies of this cross or its reciprocal were grown on 4 occasions. They had orange-red flesh, like the *delta* parent, or a little redder. The lycopene content of the F_1 was only slightly higher than in the *delta* parent (Table 1). The total amount of pigment produced was less than in the prior cross so that both the ratio of red to yellow and the smaller quantity of pigment yielded a lighter, more orange-red appearance.

Much less inviability was encountered here. The first F_2 progeny yielded 195 plants of 210 seeds. These were classified as 40 red: 54 red-orange: 53 orange-red: 48 yellow. With incomplete dominance one would expect a 3:6:3:4 ratio ($\chi^2 = 127.32$, $P \ll .01$). The 48 yellow fleshed plants were typical of the *r r* type. This represents almost a perfect one-fourth of the population ($\chi^2 = .15$ for a 1:3, P = .50–.70), so the segregation of *r* is not responsible for the discrepancy. Of the remaining 147 plants which produced pigment in quantity, red flesh should constitute one-fourth ($\chi^2 = 3.84$, P = .05 for 1:3). This appears to be a questionable fit but subsequent analyses showed these to lack *alpha-* and *delta*-carotene and they bred true for the Del^+ allele in subsequent generations. Thus, the discrepancy must be in the classification of the red-orange and orange-red classes.

Of the 195 plants in this F_2, 190 were analyzed for pigment content. Of these, 45 gave pigment values similar to the yellow (*r r*) parent in which pigment synthesis is limited. These were all classified as yellow in the field. Thirty-nine gave pigment values which are typical of the red fleshed type. These lacked *alpha* and *delta*-carotene and were classified as red in the field. The remaining 106

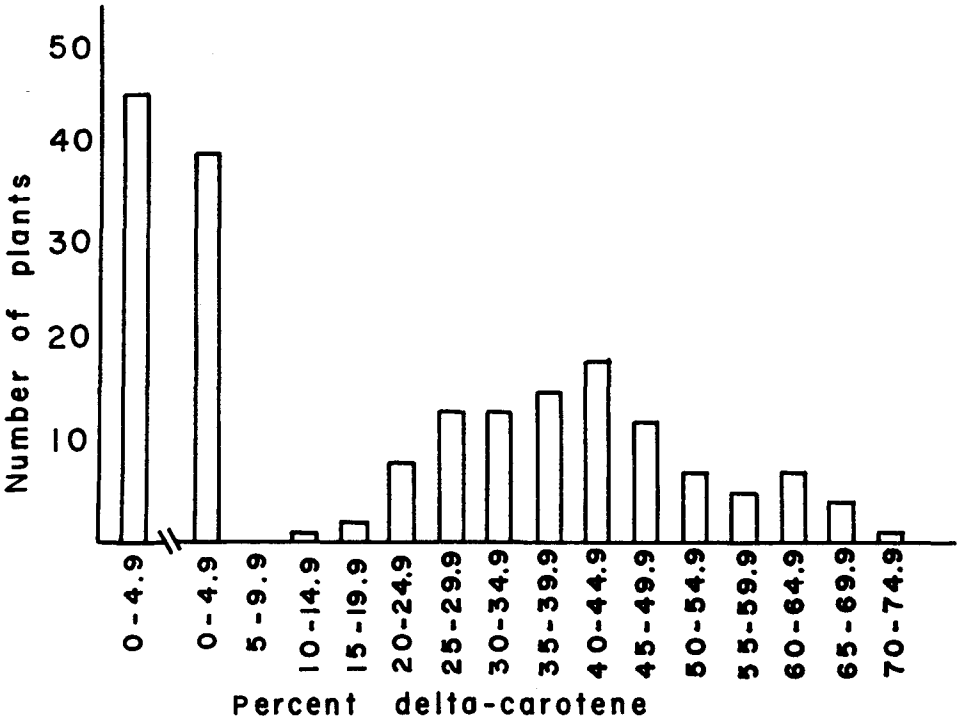

FIGURE 1.—The *delta*-carotene content (expressed as percent of total pigment) of F_2 plants from the cross, *r r* × *Del Del*. Those in the 0–4.9% class to the left of the break in the abscissa were low in total pigment (yellow fleshed) plants. All to the right of the break were normally pigmented. In this group the 0–4.9% plants were red, the remainder red-orange or orange-red.

plants produced fruits containing both *alpha*- and *delta*-carotene. When the pigments were analyzed, an array of *delta*-carotene values was found which, in terms of percent of pigment (i.e. excluding polyenes), ranged from 14 to 71. The distribution (Figure 1) was not normal. A somewhat bimodal distribution was found, which might correspond to *Del/Del*$^+$ and *Del/Del* with a dosage effect. Were this true, it is obvious that there is considerable overlap between the two classes where either chemical or visual classification would leave doubt as to homozygosity.

From the distribution, and from the fact that the *Del/Del* parent contained 50% of the pigment as *delta*-carotene, the class break was arbitrarily set at 50%. (Some plants in the 50–54.9 class subsequently bred true; others in the 45–49.5 class produced progenies which segregated.) On the basis of this chemical classification, the F_2 contained the following:

39 *r*$^+$-*Del*$^+$*Del*$^+$—red, no *delta*.

82 *r*$^+$-*Del Del*$^+$—red-orange, less than 50% *delta*.

24 *r*$^+$-*Del Del*—orange-red, more than 50% *delta*.

45 *r r* - - —yellow, very little pigment.

This is an acceptable fit for a 3:6:3:4 ratio ($\chi^2 = 5.79$. P = .05–.10). The aver-

TABLE 2

Average tomato fruit pigment content of F_2 plants from the cross of r r × Del Del

F_2 class	Number of plants sampled	μg/g fresh weight ± standard deviation					
		alpha-carotene	beta-carotene	delta-carotene	gamma-carotene	lycopene	Total
r+-Del+ Del+ (red)	39	..*	6.5±1.8	tr†	1.1±0.4	47.7±17.0	55.5±17.6
r+-Del Del+ (red-orange)	82	1.1±0.5	4.5±1.0	16.8±7.5	2.1±0.9	24.1±13.0	48.6±18.6
r+-Del Del (orange-red)	24	1.4±0.4	4.1±1.1	28.0±9.3	2.5±1.1	11.8±8.0	47.7±18.0
r r - - (yellow)	45	..	1.2±0.4	..	..	0.1±0.1	1.3±0.4

* .. = not detected.
† tr = trace (less than 1 μg/g).

age pigment contents are summarized in Table 2. The similarity in pigment content and pattern of the various classes with comparable parent or F_1 types is obvious. There was variation in the *delta*-carotene and lycopene classes, some of which arose from the variation in the amount of total pigment produced.

Small F_3 progenies from 35 of these F_2 plants were grown. They were classified visually to determine the accuracy of prediction of the basis of pigment content. All progenies behaved as predicted on the basis of the genotypes assigned allowing, of course, for some visual misclassification of *delta*-containing plants as orange-red or red-orange. Only 1 other exceptional plant was found. This was a red-orange plant in the progeny from a red F_2 selection. Since these progenies were from uncontrolled field selfed F_2 plants, this may have been an outcross.

From the visual classification of the F_2, and the classification on the basis of pigment determination, it is obvious that considerable discrepancy in visual classification occurred. The distinction between red-orange and orange-red was difficult, and often arbitrary. This discrepancy caused the aberrant classification of the original F_2. F_4 and a few F_5 progenies were later grown and classified visually. Within the limits of error in visual classification, these behaved as predicted.

In the F_2 (Table 2), where modifying genes were segregating at random, the dosage effect of *Del/Del+* versus *Del/Del* may be noted. Also of interest, where *delta*-carotene was formed, less lycopene was synthesized, i.e. *delta*-carotene was formed at the expense of lycopene.

Two more F_2 progenies were later grown and classified visually with extra care. Ripe fruit from each plant were cut and compared side by side. In one F_2, 117 of 140 possible were classified 21 red: 45 red-orange: 21 orange-red: 30 yellow ($\chi^2 = 0.13$, P = .98–.99). Another F_2 yielded 23 red: 46 red-orange: 15 orange-red: 23 yellow ($\chi^2 = 3.09$, P = .30–.50). The pooled data gave an acceptable fit ($\chi^2 = 1.68$, P = .50–.95). With special care a reasonable classification can be made. These were not progeny tested for accuracy, however.

I conclude that *Del* is a single gene, with incomplete dominance. A dosage effect can be demonstrated, and there is considerable overlap between *Del/Del*

and *Del/Del*$^+$. Visual distinction is sometimes difficult. Chemical separations are more accurate.

Since one-fourth of the population was yellow and produced very little pigment, it is obvious that *r* must be r^+ before *delta*-carotene can be produced in quantity. This is consistent with earlier work on the action of *r* suggesting that *r* is non-specific, and results in gross limitation of all pigment and polyene synthesis.

Del Del × at at: This F_1 was grown 4 different times. The flesh was red-orange, as expected from the F_1 values in Table 1. The F_2 was classified visually in 2 different years. In the first case 181 of 210 seeds were recovered and these were classified as 34 red: 96 red-orange: 51 apricot ($\chi^2 = 1.07$, P = .50–.70 for a 3:9:4). No distinction was made between plants in the red-orange class and even the red *versus* red-orange distinction was difficult at times. The apricot group ranged from straight yellow, through yellow with a pinkish tinge, to a very pale pinkish, indicating considerable modification. As in the *r* cross, there was variation in the amount of pigment produced in different plants. The second F_2 produced 226 plants of 280; 42 red: 138 red-orange: 46 apricot ($\chi^2 = 2.88$, P = .20–.30 for a 3:9:4; for both F_2 progenies, $\chi^2 = 0.32$, P = .95–.99).

Pigment and polyene fractions from a few plants in each class were separated. Plants in the red and the apricot class gave pigment values and patterns typical of the red and the apricot types and, where tested, subsequent progenies bred as predicted. The red-orange plants produced *alpha-*, *beta-*, *delta-*, *gamma*-carotene, and lycopene. In some, *delta*-carotene was the predominant pigment; in others lycopene, suggesting again that the quantitative distribution reflects the dosage effect. Several of these were progeny tested with predictable results.

Because of the variation in the apricot class, and because variation in total pigment production resulted in some paler red and red-orange plants, some 22 F_3 progenies, 26 F_4, and 13 F_5's were grown and classified visually. The results were acceptable within the limits of error already noted.

Since apricot produces some pigment during maturation, the question of whether any *delta*-carotene is produced in *at at Del Del* plants arises. Progenies were grown from apricot plants in progenies which segregated only apricot and red-orange. Fruit extracts were prepared and double the usual quantity of extract was chromatographed. An array of pigments was found in these *at at Del Del* fruits (Table 3) including *alpha-* and *delta*-carotene, and an unknown pigment with an absorption curve similar to *alpha*-carotene. This pigment adsorbs near the top of the chromatographic column. An hydroxy derivative of *alpha*-carotene is suggested. The *at at* plants from which progenies were assayed were *at at Del Del* as shown by crossing each with Rutgers. Ten plants in one such cross and 7 in another produced *alpha-* and *delta*-carotene in quantity. Average contents are listed in Table 3. These should be similar to the *Del Del* × *at at* F_1's listed in Table 1. Note that the *delta*-carotene values more nearly approach those other F_1's involving *Del*.

The action of *at at* alone is primarily the restriction of lycopene synthesis (Table 1, and JENKINS and MACKINNEY 1955; TOMES *et al.* 1958). About the

TABLE 3

Average tomato fruit pigment or polyene content in at at Del Del *plants, and in the* F_1*'s of* at at Del Del × *Rutgers and the reciprocal*

Selection or cross	Number of plants sampled	μg /gr fresh weight ± standard deviation								
		phytoene	phyto-fluene	alpha-carotene	beta-carotene	delta-carotene	gamma-carotene	unknown pigment	neuros-porene	lycopene
at at Del Del (62–3–40)	4	1.1±0.4	. .*	0.7±0.2	3.1±0.9	2.6±1.5	tr†	N.D.‡	tr	tr
at at Del Del (62–3–41)	4	2.4±1.5	. .	0.8±0.1	3.9±0.4	1.2±0.2	0.5±0.2	1.5±0.6§	1.2±0.9	. .
Rutgers (*at*+*at*+*Del*+*Del*+) × *at at Del Del* (62–3–37)	10	8.0±2.6	2.3±0.7	0.9±0.2	4.5±0.8	14.0±1.8	3.3±0.7	. .	0.4±0.4	18.1±5.5
at at Del Del × Rutgers (*at*+*at*+*Del*+*Del*+) (62–3–36)	7	9.0±2.3	1.6±0.5	0.9±0.1	4.9±0.4	13.5±4.5	3.6±0.9	. .	0.4±0.3	23.8±10.2

* . . = not detected.
† tr = trace (less than 1 μ/g).
‡ N.D. = not determined.
§ Estimated as alpha-carotene, since the absorption curve is similar.

normal amount of *beta*-carotene is synthesized. In *at at Del Del* (Table 3) little or no lycopene is synthesized. Though no direct comparison can be made, there appears to be less *beta*-carotene than in *at at* alone, and some *alpha*- and *delta*-carotene is produced. Other studies (TOMES 1967) in strains with enhanced *beta*-carotene fractions suggest that when *Del* is present, *alpha*- and *delta*-carotenes are synthesized in competition with *beta*-carotene.

Del Del × t t: The F_1 of this cross was grown 6 different times. The flesh was red-orange, in line with the pigment values (Table 1). An F_2 progeny of 166 plants of 210 seeded was grown. These were classified as 42 red: 83 red-orange: 41 tangerine ($\chi^2 = 4.96$, P = .05–.10 for a 3:9:4). Visual differences were noted among the red-orange plants, some being paler or more orange than others, but no clear cut distinction was made.

The first 30 plants in this progeny were analyzed. This included 9 tangerine fleshed plants (*t t* — —), 6 red fleshed plants (t^+ — *Del*$^+$ *Del*$^+$), and 15 red-orange (t^+ — *Del* —). A small F_3 progeny was later grown from each of the F_2 plants. The 9 tangerine plants bred true for tangerine. These 9 F_2 plants produced pigments typical of the tangerine complex (Table 4) but 5 of them produced an additional small *alpha*-carotene band. The 6 F_2 red plants either bred true for red flesh, or segregated red and tangerine. These F_2 plants lacked *alpha*- and *delta*-carotene and gave typical red fleshed values (Table 4). The 15 F_2 red-orange plants contained *alpha*- and *delta*-carotene. Five of these either bred true for red-orange or segregated red-orange and tangerine. The remaining 10 yielded red and red-orange plants, or red, red-orange, and tangerine. Mean pigment contents for those F_2 plants shown to be *Del/Del* and *Del/Del*$^+$ are in Table 4. There were 2 discrepancies among the 15 red-orange plants. In plant 11, *delta*-carotene was the predominant pigment, but this plant proved to be *Del/Del*$^+$. Plant 12 gave pigment values typical of a heterozygote, but proved to be *Del/Del*. I believe that the two samples were interchanged. These values are not reported in Table 4.

In the *r r* × *Del Del* cross, distinction between *Del/Del* and *Del/Del*$^+$ was set arbitrarily where 50% of the total pigment was *delta*-carotene. With the 2 exceptions noted, among the 15 red-orange plants in this F_2, those in which *delta*-carotene was the largest fraction bred true for *Del/Del*. In the remaining *Del/Del*$^+$ plants, lycopene was the largest fraction. Again the dosage effect was obvious.

Certain of the tangerine fleshed F_2 plants contained *alpha*-carotene. That these plants were *t t Del* — is suggested, and the question of whether they also contain undetected *delta*-carotene arises. Tangerine plants in F_3 progenies that segregated only tangerine and red (i.e. *t t Del*$^+$*Del*$^+$ plants) lacked the *alpha*-carotene band, and samples from each of 3 such progenies gave typical tangerine pigments with quantities similar to the parent. In like manner, *t t* samples from progenies segregating only tangerine and red-orange (i.e. *t t Del Del* plants) always contained a small *alpha*-carotene band. The remaining pigments approached the quantities typical of the tangerine parent. No *delta*-carotene band was noted. Since *delta*-carotene should adsorb on the column in the area around proneuro-

TABLE 4

Average tomato fruit pigment or polyene content of F_2 plants from the cross Del Del × t t

F_2 Class	Number of plants sampled	μg/gr fresh weight ± standard deviation									
		phytoene	phytofluene	alpha-carotene	beta-carotene	zeta-carotene	proneuro-sporene	delta-carotene	prolycopene	gamma-carotene	lycopene
t+–*Del*+*Del*+ (red)	6	18.0±4.6	7.5±1.4	. .†	7.2±1.8	. .	. .	. .	. .	1.2±0.1	56.0±21.7
t+–*Del Del*+ (red-orange)	9	10.2±2.2	3.4±1.0	1.6±0.7	5.4±0.9	. .	. .	9.7±1.8	. .	2.7±0.3	20.3±5.4
t+–*Del Del* (red-orange)	4	9.2±2.8	3.1±0.7	1.5±0.4	4.9±0.7	. .	. .	24.1±7.3	. .	4.2±0.8	18.0±1.6
t t–— — (tangerine)	9	38.4±16.5	13.8±6.0	. .*	3.2±0.7	21.1±13.8	7.7±3.4	. .	35.7±5.1	. .	2.8±0.3‡

* Of the 9 plants, 5 had detectable alpha-carotene bands—these 5 averaged 1.0±0.3 μg.
† . . = not detected.
‡ Lycopene isomers-above prolycopene on the column-read as lycopene.

sporene, or prolycopene, absorption curves for these fractions from *t t Del Del* and *t t* Del^+Del^+ plants were examined. The proneurosporene band from *t t Del Del* plants contained a contaminant. The contaminated absorption curve could be simulated by adding a small quantity of *delta*-carotene to the proneurosporene fraction from a *t t* Del^+Del^+ extract. Further, the discrepancy in the contaminated proneurosporene curve corresponded to that to be expected by such an addition. Thus, *t t Del Del* plants produce both *alpha* and *delta*-carotene in small quantities, in addition to the pigments typical of the tangerine complex. No further effort to separate the proneurosporene and *delta*-carotene was made. From the absorption curves it appeared that *delta*-carotene was a minor contaminant and that *delta*-carotene was not produced in major quantities in *t t Del Del* types.

DISCUSSION

Certain similarities between the action of gene *B* (*beta*-carotene) and *Del* in tomato pigment synthesis have been noted (TOMES 1963). The insertion of *B* into an otherwise normal system enhances the ring-containing *beta*-carotene fraction and, to a lesser extent, *gamma*-carotene, at the expense of lycopene. In the *Del* types, *delta*-carotene and *alpha*-carotene, and to a small extent *gamma*-carotene, form at the expense of lycopene. In *r r* strains, where little or no synthesis occurs, both *B* (TOMES *et al.* 1953) and *Del* are ineffective. In *at at* types where lycopene synthesis is restricted, both *B* (TOMES *et al.* 1958) and *Del* cannot produce large quantities of cyclic carotenes, and where the type of pigment formed is disrupted qualitatively as in tangerine (*t t*), both *B* (TOMES *et al.* 1953) and *Del* cannot produce quantities of cyclic carotenes. In short, *B* and *Del* are effective only in systems which would otherwise produce the "normal" pigment complex. The enhanced *beta*-carotene formed with *B*, the *delta*-carotene formed with *Del*, and lycopene all share a common synthetic path, either by conversion of one to the other, or by synthesis from a common pool. Studies on the interaction of *B* and *Del* (TOMES 1967) suggest that these genes compete for a common precursor rather than guiding a sequential conversion consisting of cyclization to a *beta*-ionone ring followed by shifting the double bond in the ring to form a *alpha*-ionone as was suggested earlier (PORTER and LINCOLN 1950; PORTER and ANDERSON 1962). A similar conclusion has been drawn from labeling experiments with this *delta*-carotene producing tomato (WILLIAMS, BRITTON and GOODWIN 1967).

SUMMARY

Lycopene is the major flesh pigment in the standard red tomato. *Beta*-carotene and to a lesser extent, *gamma*-carotene, are also formed during maturation. Crosses between strains which produce *delta*- and *alpha*-carotene, in addition to the normal pigments, with normal red, yellow (*r r*), apricot (*at at*), and tangerine (*t t*) were studied. The ability to produce *delta*-carotene in quantity depends on a single gene which lacks dominance. A dosage effect between *Del/Del* and *Del/*Del^+ was shown. *Del* was without effect in *r r* types. In *at at* and *t t* types,

Del resulted in the production of small quantities of *alpha-* and *delta*-carotene, but *Del* produced appreciable quantities of *delta*-carotene only in genotypes which were otherwise "normal." In these "normal" types, *delta*-carotene was produced at the expense of lycopene. Pigment synthesis was discussed briefly in view of these results.

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