CAROTENOIDS OF THE APRICOT TOMATO AND ITS HYBRIDS WITH YELLOW AND TANGERINE

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THE red color of the cultivated tomato, *Lycopersicon esculentum* Mill. is due to the carotenoid lycopene. LEROSEN *et al.* (1941) and ZECHMEISTER *et al.* (1941) first analyzed the carotenoids of yellow (*rr*) and tangerine (*tt*) strains, each of which differs from the red by a single recessive gene. MACKINNEY and JENKINS (1952), JENKINS and MACKINNEY (1953), and TOMES *et al.* (1953) have examined the yellow-tangerine double recessive. LINCOLN and PORTER (1950) transferred from *L. hirsutum* a gene (*B*), which, when homozygous in *L. esculentum*, resulted in a type described as beta orange. TOMES *et al.* (1953) reported further on hybrids involving beta orange. More recently TOMES and QUACKENBUSH (1953) have suggested that the intermediate appearance of the B^+B heterozygotes is really due to the presence of a dominant inhibitor derived from the red-fruited parent. That is, *B* is completely dominant to its allele (B^+) in cultivated tomatoes. MACKINNEY, RICK and JENKINS (1954) reported a gene similar to *B* in a variety of *L. pimpinellifolium* from the Galapagos Islands.

In this paper we discuss the effects of a new recessive gene, apricot (*at*), which is involved in the biosynthesis of carotenoids. In particular, we describe the carotenoids of the apricot homozygote (*atat*) together with the two double recessives, yellow-apricot (*rr atat*) and tangerine-apricot (*tt atat*).

MATERIAL AND METHODS

The apricot tomato was found in the Tehuacan market, State of Puebla, Mexico in December 1945. It was somewhat more orange in color than a typical yellow acquired on the same day. The line established from the original apricot tomato has oval-shaped two-loculed fruits averaging about 45g in weight. Characteristically the flesh has a few small red spots visible from the surface as well as a pink blush in the interior locular walls near the placenta. Because yellow tomatoes vary considerably in color, the overall appearance of some yellows and apricots may be quite similar. However, the yellows never have the small islands of sharply defined red tissue nor do they have the pink locular wall. Where pinkish regions occur in yellow tomatoes, they are confined to the outer walls and, for the most part, toward the base of the fruit.

Apricot was hybridized with all of the lines listed in table 1. All crosses were made in an insect-free greenhouse where all F_1 cultures were grown to maturity. For the most part, F_2 and all other segregating generations were started in the greenhouse and transferred to the field. Where technical color names were used they were taken from RIDGWAY (1912). Carotenoid analyses were made from fruits of individual plants according to methods described earlier (MACKINNEY and JENKINS 1949, 1952).

TABLE 1

Description of the tomato lines

Line	Genotype	Source
Red	Colorless skin (*yy*).	JENKINS
Yellow	Dwarf (*dd*), Pubescent fruits (*pp*), Ovate fruits (*oo*), Compound inflorescence (*ss*), Yellow flesh (*rr*).	LINDSTROM *via* RICK
Tangerine	Colorless skin (*yy*), Uniform fruit (*uu*), Tangerine flesh (*tt*).	MACARTHUR *via* LESLEY
Beta Orange	High β-carotene (BB)	PORTER
Apricot	Colorless skin (*yy*), Apricot flesh (*atat*).	JENKINS
Yellow-tangerine	Yellow flesh (*rr*), Tangerine flesh (*tt*)	JENKINS

TABLE 2

Carotenoid contents of homozygous lines, in micrograms per gram of fresh fruit

Line	Xanthophylls	Lycopene* Isomers	ζ-carotene	β-carotene	Phytofluene
Yellow	3–5	0–1	—	1–3	0.1
Apricot	3–7	2–5**	—	6–10	0.2
Yellow-apricot	6.2	—	—	1.2	trace
	5.4	—	—	0.4	0.5
	5.7	—	—	0.4	trace
Tangerine-apricot	negligible	15.0	0.7	1.8	0.5
	negligible	6.5	1.0	1.0	0.6
	negligible	14.0	0.8	0.7	0.7
	negligible	21.4	0.6	2.1	1.1
Yellow-tangerine	negligible	10–15	0.1	0.5–1.0	0.7–1.0

* All-*trans* lycopene for yellow and apricot, mostly prolycopene for tangerine-apricot and yellow-tangerine.

** In a seedless specimen, this rose to 23 μg.

RESULTS

Carotenoids of apricot

The apricot line not only resembles many yellows in general appearance but has very nearly the same carotenoids (table 2). Both have essentially the same content of xanthophylls and of phytofluene. Though apricot has a somewhat higher lycopene content, the major difference between the two lies in the higher content of β-carotene of the apricot, which is at a level typical of normal red-fruited tomatoes.

First generation hybrids

The F_1 hybrids red × apricot, yellow × apricot, yellow-tangerine × apricot and tangerine × apricot were red in color, but as can be seen from table 3, the lycopene content was not always within the range of a typical red, which normally has 70 to

TABLE 3

*Carotenoid contents of the F_1 hybrids with Apricot, in micrograms per gram of fresh fruit**

F_1 Hybrid	Lycopene	β-carotene	Phytofluene
Apricot × red	67.5	8.0	6.8
Yellow × apricot	73.9	8.7	4.6
Yellow-tangerine × apricot**	61.0	7.6	4.7
Tangerine × apricot	67.0	7.0	not determined
Beta Orange × Apricot	50.0	54.6	15.4

* All hybrids had in addition to the listed carotenoids traces of γ-carotene.

** traces of ζ-carotene.

130 μg of lycopene per gram of fresh fruit. However, these small deviations from the normal red carotenoid content could very well have been due to environmental effects, since data obtained in 1953 varied somewhat from the analyses of 1954. In the case of beta orange × apricot the F_1 color was red-orange (grenadine red to flame scarlet) and had about equal proportions of lycopene and β-carotene together with a high phytofluene content (table 3). In its ratio of β-carotene to lycopene our beta orange × apricot F_1 was similar to the F_1 red × beta orange reported by LINCOLN and PORTER (1950). That is, the characteristic carotenoid content of F_1 beta orange × apricot apparently depends upon heterozygosity at the *B* locus rather than heterozygosity at the *at* locus. Data from all of the F_1 hybrids consistently show that apricot is a new recessive gene that is not allelic to any of the carotenoid genes already described.

Segregating generations of the yellow × apricot hybrid

In a total of 139 F_2 plants, belonging to 4 different cultures, 80 were red and 59 non-red, which does not differ significantly from a 9:7 ratio expected from segregation of two independent loci. Data from backcrosses of F_1 to both parents were in full agreement. The backcross to yellow had 32 red and 26 yellow, while the backcross to apricot gave 42 red and 27 apricot. Neither of the backcross ratios differ significantly from the 1:1 expectation.

The non-red plants obtained in the F_2 ranged continuously from a fully colored apricot to a light yellow. Since the double recessive yellow-apricot (*rr atat*) could not be recognized in F_2, selfed progeny of non-red plants in the F_2 as well as in both backcrosses were grown. In order to avoid contamination from foreign pollen only plants growing in the greenhouse were chosen as parents of the selfed progenies.

One F_3 culture (534H129) was obtained that segregated 14 apricot plants to 4 plants with lighter colored fruits that lacked the red areas near the placenta, which are characteristic of apricot. The F_4 progenies that were grown from these four F_3 plants likewise were lighter in color and lacked the red placental areas. One of the F_3 plants (534H129.1) when test-crossed with yellow gave only yellow progeny, indicating that the F_3 plant was homozygous for yellow. In addition, two of its F_4 progeny were test-crossed with apricot and the test-cross progeny were all apricot. Consequently the line established from 534H129.1 was the double recessive yellow-apricot.

The yellow-apricot was also recovered from selfed progeny of the F_1 backcrossed to apricot. Progenies were grown from 5 apricot plants, which were expected to be r^+r^+ *atat* or r^+r *atat*. One progeny gave only pure apricot plants, while four of them segregated giving a total of 26 apricot to 8 yellow-apricot. The latter were classified as the double recessive because they lacked the pink blush on the transverse locular walls adjacent to the placenta, which is characteristic of apricot fruit. Furthermore, one of the 26 apricot plants was test-crossed with both parents: with apricot the progeny were all apricot and with yellow the test-cross progeny had 5 red and 5 yellow plants. Therefore the tested plant had the constitution r^+r *atat*. On selfing it gave 7 apricot to 3 yellow-apricot.

Recognition of the yellow-apricot in the selfed progenies of the backcross of F_1 to yellow was much more difficult. However, of the 4 yellow plants of the first backcross generation that were progeny tested, one gave progeny that segregated (2 yellow : 4 yellow-apricot). On the other hand, another of the first backcross yellow plants was shown to have the genotype *rr* at^+at by testcrosses yet no yellow-apricot plants were detected in a selfed progeny of 10 individuals.

The pigment contents of 3 yellow-apricot (*rr atat*) plants are given in table 2; the first two are F_4 while the last is a third generation of the backcross to apricot. As was to be expected from their light color, they contained very little pigment, mostly xanthophylls, while no lycopene was detected and the β-carotene content was frequently somewhat lower than in a typical yellow. In other words, the yellow-apricot might be characterized as a weakly-pigmented yellow.

Segregating generations of the tangerine × apricot hybrid

The F_2 tangerine × apricot segregated 41 red to 34 non-red, which does not differ significantly from a 9:7 expectation on the basis of two independently segregating genes. However, as in the case of the yellow × apricot, the non-red plants could not be further classified with any degree of certainty. The main difficulty was due to environmental variability which tended to obliterate discontinuities between the various color classes. Even in F_3 cultures from individual non-red F_2 plants, classification was not satisfactory. A further complication arose. Since nearly 3 percent of the F_3 plants were red, these undoubtedly arose from natural crossing between F_2 plants, which were grown in the field.

A careful comparison of cut fruits of F_3 plants showed that there was a type that did not resemble either tangerine or apricot. This intermediate type had a more pinkish color in the central part of the fruit and the outer wall was less pigmented than in the tangerine. The cut section of the outer wall was not very different from apricot. Selfed progenies were grown in the greenhouse from individual F_3 plants of the various color types including the new intermediate. At least one plant in each F_4 progeny was test-crossed to both parents, also selfed seeds (F_5) were collected from each of the test-crossed F_4 plants. Eight of the latter gave only all tangerine or all apricot progeny depending upon the parent used. Therefore, these 8 F_4 plants were tangerine-apricot (*tt atat*).

The carotenoid contents of four different tangerine-apricot plants are given in table 2 together with that of the yellow-tangerine. Tangerine-apricot is intermediate

between tangerine and apricot in its total content, but in characteristic constituents, principally prolycopene, it may be regarded as a weak tangerine. However, the decrease in the various pigments has not been proportional. Of the various carotenoids of tangerine, poly-*cis* ψ-carotene was not detected in tangerine-apricot, ζ-carotene showed the most marked decrease, followed in order by phytofluene, β-carotene and finally the lycopene set.

DISCUSSION

The apricot locus does not appear to be closely linked with any of the major carotenoid loci, nor were there any close linkages between apricot and any of the marker genes segregating in the various stocks. However, with the large number of small cultures examined, other than close linkages could be easily overlooked.

In its main effect on the suppression of lycopene, apricot acts very much like the yellow gene. Both have a very similar effect when they are crossed with tangerine, the carotenoids of the lycopene set are decreased in amount and the main constituent is prolycopene, the characteristic carotenoid of the tangerine. In the yellow-apricot, where both genes are homozygous, their separate actions on the suppression of lycopene are reinforced—we did not detect lycopene in yellow-apricot. On the other hand, the lycopene that is formed in yellow and in apricot is found in quite different regions of the fruit.

The action of the yellow and apricot genes on β-carotene synthesis is also quite different. Using the red as a standard, *at* does not have any effect on β-carotene, while yellow does. When the two are together in yellow-apricot, the inhibiting effect of *r* is enhanced. Again using the red as a standard, neigher *t* nor *at* by themselves have any appreciable effect on β-carotene, but when together in the tangerine-apricot, they have nearly as marked effect in reducing β-carotene as does the combination yellow-apricot.

Thus, while the apricot and yellow genes have many points of similarity in their action, they are distinct both in location and in their effect on carotenoid synthesis. Unfortunately at this time we cannot do more than describe the effects of these genes in their various combinations on the many carotenoid pigments. With the possible exception of the *B* gene, the effects are manifold in that each gene alters the content of more than one pigment and in a complex fashion.

SUMMARY

A new recessive gene apricot affecting the carotenoids of the tomato is described. The carotenoid contents of homozygous apricot (*atat*) and the two double recessives yellow-apricot (*rr atat*) and tangerine-apricot (*tt atat*) are given. The effects of the apricot gene are similar to those of yellow but there are distinct differences.

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