INHERITANCE OF CAROTENOID DIFFERENCES IN THE TOMATO HYBRID YELLOW × TANGERINE

J. A. JENKINS AND G. MACKINNEY
Divisions of Genetics and Food Technology, University of California, Berkeley

Received June 30, 1952

YELLOW varieties of tomatoes have been known since the crop was first introduced into Europe shortly after the discovery of America, and were probably to be found in Mexico before the conquest (JENKINS 1949). HALSTED et al. (1905) reported on the red × yellow hybrid, establishing the fact that the color difference was due to segregation at a single locus, a conclusion that has been confirmed repeatedly by subsequent workers. Presumably, the yellow arose as a mutant from the red, and probably the mutation occurred on several occasions. RICK (private communication) has recently found a yellow mutant in the variety Pearson.

The tangerine or orange tomato has a more obscure history. MACARTHUR (1934) lists, red fruit flesh (*T*) *v.* tangerine (*t*) in his table to tomato character contrasts (p. 124). He also states, " The monofactorial inheritance of the characters [listed in the table] has been definitely proven with adequate numbers and suitable tests." He refers to an earlier paper (1931) which contains data on the segregation of most characters listed in his 1934 paper. However, we found no reference to the tangerine tomato in his 1931 paper.

Apparently, MACARTHUR (1934) was the first to study segregation in the yellow × tangerine hybrid, but his report on this hybrid is incidental to a presentation of the linkage relations between various loci, and consists of three brief references. First, " The factor interactions of the two types of dwarfness lead to 12:3:1 ratios in F_2; those between the two forms of green stem and the two flesh colors produce 9:3:4 ratios " (p. 125). Secondly, in table III (p. 128) the crossover value between the yellow and tangerine loci is given as 52.1 ± 2.5, which indicates that he made the yellow-tangerine hybrid. Finally, in tables IX and X (p. 130) he gives additional crossover data from which he concludes that the tangerine locus is in linkage group VII with the two loci, uniform fruit and hairy stem, both of which show independent assortment with yellow in linkage group II.

FLEMING and MYERS (1938) through correspondence with MACARTHUR, were able to establish the latter's F_2 ratio as 9 red : 3 yellow : 4 orange (3 orange and 1 light orange). However, in their own data on the yellow-tangerine hybrid they obtained results which they interpreted in a somewhat more complicated manner. In backcrosses between the F_1 and the parents of the yellow × tangerine hybrid, they obtained the expected 1 : 1 ratios. In F_2, on the other hand, they report 459 red : 134 yellow : 179 orange. The significant excess of reds and deficiencies of yellows and oranges are not in accord with MACARTHUR's hy-

pothesis. Furthermore, the latter hypothesis, as the authors express it, " [does not] account for the presence of red-orange and orange-yellow combinations in the same fruit." Consequently, FLEMING and MYERS proposed a much more elaborate hypothesis to account for their backcross and F_2 segregations. They postulated in addition to the two basic color genes, tangerine and yellow, two modifying factors and two specific inhibitors.

In a chemical analysis by means of the chromatographic technique, LEROSEN et al. (1941) compared red (*RR*) and yellow (*rr*) tomatoes. They concluded that the *R* gene is responsible for an increase in red and yellow plastid pigments, chiefly lycopene and, to a much lesser extent, carotenes and xanthophylls. ZECHMEISTER et al. (1941) in their study of the tangerine tomato (*RRtt*) found a series of lycopene isomers, the most prominent of which was a new pigment, prolycopene.

MACKINNEY and JENKINS (1949) in reporting on the carotenoids of several strains of red, yellow and tangerine tomatoes found that some strains of yellow tomatoes did produce small amounts of lycopene, and also pointed out that while prolycopene determines the color of the tangerine tomato, its absorption spectrum is dominated by pigments with maxima between 430 and 400 mμ, which is accounted for by two pigments, all-trans zeta-carotene and a carotenoid which they designated as poly-cis psi-carotene. This latter pigment (which bears some relationship to the unidentified carotene I of PORTER and ZSCHEILE (1946) and to zone 16 of LEROSEN and ZECHMEISTER (1942)), and prolycopene are unique to the tangerine tomato. Zeta-carotene as a major component is also restricted to the tangerine.

A study of the yellow x tangerine hybrid was begun in 1947, and a partial account of the yellow x tangerine hybrid, stressing the biochemical aspects, was given by MACKINNEY and JENKINS (1952). The present paper will deal in greater detail with the genetic aspects of the study, but will also include sufficient biochemical data to discuss the role of the yellow and tangerine loci in carotenogenesis.

MATERIALS AND METHODS

The female parent (*rrTT*) of the original hybrid was an inbred tester line developed by E. W. LINDSTROM, which in addition to being homozygous at the yellow locus, contained the following recessive genes in the homozygous condition: $dwarf_1$, peach, oval, compound inflorescence. The male parent (*RRtt*) was the commercial variety Jubilee, which in addition to being tangerine had uniform and colorless fruit-skin. The yellow parent had small, two-loculed fruits ranging from 15 to 50 grams in weight. The tangerine, on the other hand, had much larger multilocular fruits ranging up to 250 grams. In order to avoid contamination, all of the hybridizations were carried out in an insect-free greenhouse. In fact, most of the segregating generations were grown in six- or eight-inch pots in the same greenhouse.

Details of the methods used in determining the carotenoid content of the fruits are given by MACKINNEY and JENKINS (1949, 1952).

EXPERIMENTAL RESULTS

As was to be expected from the fact that MACARTHUR had placed the yellow and tangerine loci on different chromosomes, the fruit color in the F_1 generation of the yellow-tangerine hybrid was red. This result was also in conformity with the data of FLEMING and MYERS. Furthermore, these F_1 fruits could not be distinguished from those of typical red varieties either from their phenotypic appearance or on the basis of their carotenoid content.

The classification of the F_2 phenotypes, on the other hand, presented several difficulties, and it was not until data from chemical analysis were obtained that a satisfactory classification of the F_2 could be made. It is clear from the last line of table 1 that the F_2 segregated in the ratio of 9 red : 3 yellow : 4 orange.

TABLE 1

Segregation of fruit colors in the F_2 of the Yellow × Tangerine hybrid.

Culture		Red	Yellow	Orange	Total	Tangerine	Yellow-tangerine
		9	3	4		3	1
1	Obs.	14	1	5	20	5	0
	Calc.	11.25	3.75	5.00	20	3.75	1.25
2	Obs.	7	5	4	16	4	0
	Calc.	9.00	3.00	4.00	16	3.00	1.00
3	Obs.	11	1	8	20	4	4*
	Calc.	11.25	3.75	5.00	20	3.75	1.25
4	Obs.	10	2	2	14	1	1
	Calc.	7.88-	2.62	3.50	14	2.62	0.88
5	Obs.	8	8*	5	21	4	1
	Calc.	11.81	3.94	5.25	21	3.94	1.31
Total	Obs.	50	17	24	91	18	6
	Calc.	51.19	17.06	22.75	91	17.06	5.69

*Large deviations from expectation.

Furthermore, the orange class could be further subdivided into two classes: a tangerine class, which had the same carotenoid content as the tangerine parent and a yellow-tangerine class, which had a distinctly different carotenoid content. Thus we were able to confirm MACARTHUR'S ratio of 9 red : 3 yellow : 3 tangerine : 1 light tangerine (yellow-tangerine).

Since it was planned to analyze the carotenoid content of the segregating generations on an individual plant basis, the F_2 were grown in small cultures of about twenty plants each. The first difficulty that arose was that the yellow-tangerine (*rrtt*) did not appear until the third of these cultures had been grown (table 1). This late appearance as well as the sporadic occurrence of other non-red segregates in the various cultures has been attributed to chance. The totals fit MACARTHUR'S ratio and, in addition, there is no evidence of heterogeneity between cultures ($\chi^2 = 14.99$ with 8 d.f., $P = 0.10$–0.05). However, in testing

the homogeneity of the cultures on the basis of a 9:3:3:1 ratio, there is some evidence against the hypothesis that all cultures come from the same population ($\chi^2 = 22.49$ with 12 d.f., P = 0.05–0.02). But, the deviations are not large, with two exceptions which are indicated by an asterisk in table 1.

The second and most serious difficulty that arose in classifying the F_2 generation was due to environmental variability. Because the cultures were not all grown simultaneously but scattered throughout the year, there was considerable variability in the color of the tangerine fruits and more particularly in the yellow-tangerines. Plants grown during the winter season had a somewhat higher carotenoid content, a slightly different distribution of pigments and a darker color than those grown during the summer. In fact, cuttings from the same plant grown at different seasons often had quite distinct fruit colors. Some of the yellow-tangerines were so light that they could easily be mistaken for yellows and others were so dark that without chemical analysis they could easily be considered as tangerines. Even some of the tangerines were sufficiently dark to be mistaken for reds.

Finally, segregation at other loci, principally the colorless-skin locus, was responsible for variability in genotype both within and between cultures. As pointed out by SMITH and SMITH (1931) high temperatures and high light intensity either inhibit the production or hasten the destruction of carotenoid pigments. Plants homozygous for the colorless skin gene had greater variation in fruit color. There was often less intense pigmentation immediately under the skin in various parts of the fruit, which often resulted in a mottled appearance. Furthermore, in the F_2 generation there was a great range of fruit size which also led to considerable difficulty in classification because, as a rule, small fruits are more intensely pigmented than large fruits.

Due to environmental variability and to segregation at other loci, the phenotypic appearance was not always a reliable indicator of the genotype. Consequently, in order to confirm the F_2 classification, individual F_2 plants were selfed for the purpose of studying segregation in their progeny. In addition, several tangerine and yellow-tangerine plants were crossed to the yellow parent to determine whether or not they contained the recessive allele *r*. Similarly, a yellow was crossed with the tangerine parent in order to test for the presence of the *t* allele (table 3).

In all cases F_3 cultures from individual F_2 plants segregated as expected on the basis of their F_2 classification (table 2). The progenies from red-fruited F_2 plants were of different types, and together they segregated all four phenotypes: red, yellow, tangerine and yellow-tangerine. The single yellow F_2 tested gave only yellow F_3 progeny. Tangerines as a group segregated both tangerines and yellow-tangerines. It is possible that the two cultures which had only tangerine progeny were of the parental genotype (*RRtt*). However, the numbers are too small to draw definite conclusions. Finally, the yellow-tangerines had only yellow-tangerine progeny.

Similarly, the test crosses (table 3) behaved as predicted on the basis of their F_2 classification. The tangerines were of two types, *RRtt*, which only

gave red progeny on crossing with the yellow parent, and *Rrtt,* which gave half red and half yellow when crossed with the yellow parent. The yellow-tangerines *rrtt* gave only yellow progeny when crossed with the yellow parent. The only yellow F_2 tested by crossing with the tangerine parent, gave all red progeny indicating that it had the genotype *rrTT*.

In conclusion, all of the data conform to MACARTHUR'S 9 red : 3 yellow : 4 tangerine (orange). If the yellow-tangerine, which may at times be as highly colored as the tangerine, is considered to be identical with MACARTHUR'S light tangerine (light orange), there is complete agreement with the latter's

TABLE 2

Segregation of fruit colors in F_3 progenies from F_2 selfed plants.

F_2 parent	F_3 progenies							
Phenotype	Red		Yellow		Orange			Total
	Anal.	Not anal.	Anal.	Not anal.	Analyzed		Not anal.	
					Tang.	Y-tang.		
Red	2	2	1	3				8
"		1						1
"		6		1	1		2	10
"		5		2	1	1		9
"		6		1	1	1		9
"		6		1			1	8
Yellow			2	1				3
Tangerine					1	2	4	7
"					2	1	4	7
"					2		2	4
"					2		2	4
"					1	1	5	7
"					2	1	5	8
"					1	3	1	5
Yellow-Tang.						9	1	10
"						6	1	7
"						3	6	9
"						6	3	9
						7		7

9 : 3 : 3 : 1 ratio. The failure of FLEMING and MYERS (1938) to confirm MACARTHUR'S results in their F_2 generation could very well be due to a combination of variability of the environment and to segregation at genes at other loci, especially since they obtained the expected 1 : 1 ratios in their backcross generations. In any case, their elaborate explanation does not apply to the present data.

The distribution of the analyzed carotenoids in the various phenotypes has been reported already (MACKINNEY and JENKINS 1952). As far as our observations go there is complete dominance of the *T* and *R* alleles; in other words, we could detect no difference between the various red genotypes and similarly

for the two genotypes within the yellow and tangerine phenotypes. The variability within phenotypes is due to other causes, such as environment, genetic background and experimental error. The most surprising result of the analysis was the high total carotenoid content of the yellow-tangerine. That is, the double recessive has a higher content than the yellow. This indicates that the low production of total carotenoid associated with *rr* does not affect all carotenoids equally. All-trans lycopene, in particular, is strikingly reduced in amount by the substitution of *rr* for *RR* or *Rr*.

Red. The predominant pigment of red tomatoes, and this applies to red varieties generally as well as to the red segregates in this hybrid, is all-trans lycopene and lesser amounts of beta-carotene and phytofluene respectively, as well as trace amounts of other carotenoids.

TABLE 3

Segregation of fruit colors in test crosses.

F_2 parent		Test progenies		
Phenotype	Genotype	Red	Yellow	Total
Tangerine[1]	*RRtt*	10	....	10
"	"	6	....	6
"	"	10	....	10
"	*Rrtt*	2	4	6
"	"	5	5	10
Yellow-Tang.[1]	*rrtt*	....	10	10
"	"	....	10	10
Yellow[2]	*rrTT*	9	....	9

[1]The tangerine and yellow-tangerine F_2 plants were crossed with the yellow parent (*rrTT*).

[2]The yellow F_2 plant was crossed with the tangerine parent (*RRtt*).

Yellow. The most striking feature of the yellow tomato is its very low total carotenoid content; and the reduction is most pronounced in the case of all-trans lycopene.

Tangerine. The characteristic pigment in the tangerine tomato is prolycopene, which gives the peculiar orange color to this phenotype. In addition to prolycopene there are varying amounts of mono-cis lycopenes. Since these have a red color, they are largely responsible for the variability in color of the tangerine tomato, which in extreme cases makes it almost indistinguishable from a red tomato. In addition to differences in the lycopene set (the absence of all-trans lycopene and the presence of prolycopene and mono-cis isomers), the tangerine differs from the red most strikingly in its content of psi-carotene and zeta-carotene. The content of beta-carotene and phytofluene does not differ markedly between the two. Thus *tt* does not alter the total content, but has a marked effect on several different carotenoids.

Yellow-tangerine. The double recessive is essentially a tangerine, since, like the latter, it contains prolycopene and mono-cis isomers. However, unlike the

tangerine it contains no psi-carotene and only a trace of zeta-carotene. The reduction in carotenoid production associated with *rr* is obvious, although the total reduction is not so great as in the case of the yellow. Nevertheless the latter has a higher content of beta-carotene, so that *rr* interferes with the production of all carotenoids, but the interference is selective in that some carotenoids are affected more than others.

DISCUSSION

The obvious first approach in determining the role of mutant genes is to look for specific blocks in the biosynthetic chain, which are usually detected by the accumulation of an intermediate. ZECHMEISTER et al. (1941) suggested that prolycopene was such an intermediate and further suggested that the *R* allele is involved in the synthesis of prolycopene and that the *T* allele is responsible for the conversion of prolycopene to lycopene in red tomatoes. However, the tangerine tomato has large amounts of mono-cis lycopene and poly-cis psi-carotene (which we have not been able to detect in the red tomato), as well as considerably larger amounts of zeta-carotene. Consequently, there seems to be no reason to single out prolycopene as the specific precusor of lycopene. WENT et al. (1942) demonstrated that high temperature (33°C) inhibits the formation of lycopene in red tomatoes but they did not report any accumulation of prolycopene. Of course, it is possible that the biosynthesis of lycopene may have been inhibited farther back in the chain. More convincing evidence against the hypothesis is our observation that the double recessive (*rrtt*) is capable of synthesizing considerable quantities of prolycopene in the absence of *R*.

From a study of the hybrid between a typical red tomato (*Lycopersicon esculentum*) and a selection with a high beta-carotene content, LINCOLN and PORTER (1950) came to the conclusion that lycopene was a precursor of beta-carotene. The high beta-carotene selection had been obtained from the interspecific hybrid between *L. esculentum* and the related green-fruited wild species *L. hirsutum* (KOHLER et al. 1947). A single gene (*B*), derived from *hirsutum,* when segregating with its *esculentum* allele (*b*) gave the following percentages of beta-carotene in F_2: *bb* 0–24, *Bb,* 25–74.9, *BB* 75–100. The increase in beta-carotene content was accompanied by a corresponding decrease in lycopene. Since beta-carotene is isomeric with lycopene and differs from the latter in having ring structures at both ends, LINCOLN and PORTER assumed that lycopene was a precursor of beta-carotene.

Largely on the basis of its formula and its widespread occurrence in association with carotenoids, ZECHMEISTER and SANDOVAL (1946) concluded that phytofluene could be an intermediate in carotenogenesis. However, they were careful to point out that phytofluene and the carotenoid pigments may be derived independently from a common precursor.

PORTER and LINCOLN (1950) in summarizing work on the carotenoids presented a formal scheme for the biosynthesis of the carotenes. Starting with a nearly-saturated 40-carbon chain ($C_{40}H_{76}$), a stepwise removal of four hydro-

gen atoms at a time would lead to lycopene ($C_{40}H_{56}$). Lycopene could then be transformed to gamma-carotene by ring closure at one end and the latter into beta-carotene by ring closure at the other end. The chain up to lycopene appears logical from a chemical point of view. However, the mere presence of these supposed intermediates in many tomatoes does not demonstrate that they are in fact intermediates, since they could just as well be derived independently from common precursors. In fact their presence in ripe tomatoes, in some cases in substantial amounts, is puzzling if they are true intermediates.

On the other hand, GOODWIN and his coworkers (GARTON et al. 1951; GLOVER et al. 1951; GOODWIN and LIJINSKY 1951; GOODWIN 1952), on the basis of extensive experiments on growing *Phycomyces blakesleeanus* on media containing amino acids and sugar, have concluded that there is dehydrogenation of five-carbon units, most probably isovaleraldehyde, prior or subsequent to formation of the C_{40} polyene. Thus the carotenoids could be formed in parallel or in sequence. We ourselves favor the view that there is little or no conversion of many of the carotenoids one to another. The varying proportions of the different carotenoids would thus be due to the presence and availability of the various repeating units. MACKINNEY et al. recently obtained supporting evidence for this hypothesis. They demonstrated that it was possible to increase greatly the production of beta-carotene in a short period (5 to 20 hours) and of lycopene to a very minor extent by providing *P. blakesleeanus* with compounds theoretically capable of providing the terminal groups of the carotenoid molecule.

Since there is no good evidence that the recessive alleles at the yellow and tangerine loci block specific reactions towards the ends of the biosynthetic chain, they must either block reactions far back in the chain or in some other way influence the availability of early precursors. Of course, this assumes that each allele has a single primary action. GOODWIN'S hypothesis has opened up a whole new set of possibilities. However, until we have more precise knowledge of carotenogenesis than we have at present, it seems more profitable to consider the role of these two loci in general terms. Homozygous yellow (*rr*) interferes with carotenoid biosynthesis and the interference is greater with some carotenoids than with others. Homozygous tangerine (*tt*), on the other hand, has no effect on the total carotenoid content but does alter the pathways and end products of synthesis.

SUMMARY AND CONCLUSIONS

The F_1 hybrid between yellow (*rrTT*) and tangerine (*RRtt*) tomatoes was red and the F_2 segregated 9 red : 3 yellow : 3 tangerine : 1 yellow-tangerine (*rrtt*). Dominance at both loci was considered as complete, since we could detect no difference in carotenoid content within the various classes. That is, all of the reds in the F_1 and F_2 (*RRTT, RrRR, RRTt, RrTt*) had the same carotenoids as typical red varieties; similarly the yellow (*rrTT, rrTt*), and the tangerine (*RRtt, Rrtt*) could not be distinguished from the parental types.

Substitution of *tt* in an otherwise red genotype had no effect on the total

carotenoid content but did markedly alter the individual components. Thus *tt* alters the pathway and products of synthesis.

On the other hand, *rr* interferes with the total carotenoid production. In an otherwise red background *rr* only produced about five percent of the total carotenoids characteristic of the red. Contrary to expectation the double recessive (*rrtt*) had three to four times as much total carotenoid as the yellow. As in the case of the yellow, *rr* interfered with the production of all carotenoids in the yellow-tangerine, but again the individual pigments were affected differently. Thus, the interaction at the two loci are nonadditive, both in regard to the total content and to the constituent pigments. Further data will be required before the primary action of the alleles at the yellow and tangerine loci can be determined with greater specificity.

In conclusion, all of the data conform to MACARTHUR'S 9 red : 3 yellow : 4 tangerine (orange). If the yellow-tangerine, which may at times be as highly colored as the tangerine, is considered to be identical with MACARTHUR'S light tangerine (light orange), there is complete agreement with the latter's 9 : 3 : 3 : 1 ratio. The failure of FLEMING and MYERS (1938) to confirm MACARTHUR'S results in their F_2 generation could very well be due to a combination of variability of the environment and to segregation at genes at other loci, especially since they obtained the expected 1 : 1 ratios in their backcross generations. In any case, their elaborate explanation does not apply to the present data.

LITERATURE CITED

FLEMING, H. K., and C. E. MYERS, 1938 Tomato inheritance, with special reference to skin and flesh color in the orange variety. Amer. Soc. Hort. Sci. Proc. **35:** 609–624.

GARTON, G. A., T. W. GOODWIN and W. LIJINSKY, 1951 Studies in carotenogenesis 1. General conditions governing β-carotene synthesis by the fungus *Phycomyces blakesleeanus* Burgeff. Biochem. J. **48:** 154–163.

GLOVER, J., T. W. GOODWIN and W. LIJINSKY, 1951 Further observations on carotenogenesis by *Phycomyces blakesleeanus*. Biochem. J. **50**(2) : x.

GOODWIN, T. W., 1952 Studies in carotenogenesis 3. Identification of the minor polyene components of the fungus *Phycomyces blakesleeanus* and a study of their synthesis under various cultural conditions. Biochem. J. **50:** 550–558.

GOODWIN, T. W., and W. LIJINSKY, 1951 Studies in carotenogenesis 2. Carotene production by *Phycomyces blakesleeanus*: The effect of different amino-acids when used in media containing low concentrations of glucose. Biochem. J. **50:** 268–273.

HALSTED, B. D., E. J. OWEN and J. K. SHAW, 1905 Experiments with tomatoes. N. J. Agr. Exp. Sta. Ann. Rept. **26:** 447–477.

JENKINS, J. A., 1948 The origin of the cultivated tomato. Econ. Bot. **2:** 379–392.

KOHLER, G. W., R. E. LINCOLN, J. W. PORTER, F. P. ZSCHEILE, R. M. CALDWELL, R. H. HARPER and W. SILVER, 1947 Selection and breeding for high β-carotene content (provitamin A) in tomato. Bot. Gaz. **109:** 219–225.

LEROSEN, A. L., and L. ZECHMEISTER, 1942 Prolycopene. J. Amer. Chem. Soc. **64:** 1075–1079.

LEROSEN, A. L., F. W. WENT and L. ZECHMEISTER, 1941 Relation between genes and carotenoids of the tomato. Proc. Nat. Acad Sci. **27:** 236–242.

LINCOLN, R. E., and J. W. PORTER, 1950 Inheritance of beta-carotene in tomatoes. Genetics **35:** 206–211.

MACARTHUR, J. W., 1931 Linkage studies with the tomato. III. Fifteen factors in six groups. Roy. Canad. Inst. Trans. **18:** 1–19.

1934 Linkage groups in the tomato. J. Genet. **29:** 123–133.

MACKINNEY, G., and J. A. JENKINS, 1949 Inheritance of carotenoid differences in *Lycopersicon esculentum* strains. Proc. Nat. Acad. Sci. **35:** 284–291.

1952 Carotenoid differences in tomatoes. Proc. Nat. Acad. Sci. **38:** 48–52.

MACKINNEY, G., T. NAKAYAMA, C. D. BUSS and C. O. CHICHESTER, 1953 Carotenoid production in *Phycomyces*. J. Amer. Chem. Soc. **75:** 236–238.

PORTER, J. S., and R. E. LINCOLN, 1950 I. *Lycopersicon* selections containing a high content of carotenes and colorless polyenes. II. The mechanism of carotene biosynthesis. Arch. Biochem. **27:** 390–403.

PORTER, J. W., and F. P. ZSCHEILE, 1946 Carotenes of *Lycopersicon* species and strains. Arch. Biochem. **10:** 537–545.

SMITH, LAURA LEE W., and O. SMITH, 1931 Light and carotenoid content of certain fruits, and vegetables. Plant Physiol. **6:** 265–275.

WENT, F. W., A. L. LEROSEN and L. ZECHMEISTER, 1942 Effect of external factors on tomato pigments as studied by chromatographic methods. Plant Physiol. **17:** 91–100.

ZECHMEISTER, L., A. L. LEROSEN, W. A. SCHROEDER, A. POLGÁR and L. PAULING, 1943 Spectral characteristics and configuration of some stereoisometric carotenoids including prolycopene and pro-γ-carotene. J. Amer. Chem. Soc. **65:** 1940–1951.

ZECHMEISTER, L., A. L. LEROSEN, F. W. WENT and L. PAULING, 1941 Prolycopene, a naturally occurring stereoisomer of lycopene. Proc. Nat. Acad. Sci. **27:** 468–474.

ZECHMEISTER, L., and A. SANDOVAL, 1945 Phytofluene. J. Amer. Chem. Soc. **68:** 197–201.