Genes for long shelf-life in tomato[1]

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ABSTRACT

One hundred eighty-four red-fruited tomato accessions from various origins were screened in Puerto Rico in 1981 for shelf-life of ripened fruit; 13 were found to have exceptionally long life (16 weeks or more). From these, six lines were selected and crossed with Kewalo from Hawaii and F_1, F_2 and F_3 generations as well as BC_1 and F_2 of BC_1, were grown. Long shelf-life was controlled by several genes in these crosses, and discrete ratios were not obtained. Among the hybrids longest shelf-life was found in individuals of F_2 families. Both recessive and dominant genes were segregating. Individual plants with fruit of exceptional shelf-life were obtained even in the most advanced generations. Pedigree selection is suggested as a useful technique for concentrating the genes for long shelf-life in a standard variety. Pure lines can then be crossed to combine genes from different sources. Minor genes for long shelf-life in homozygous pure lines may prove more useful than simple dominant genes in hybrids.

INTRODUCTION

As a tomato fruit ripens, it loses chlorophyll, synthesizes carotenoids, reduces its content of sugars and acids, softens, and shrinks (6). Respiration reaches a peak, the climacteric (4), and then declines. The useful life of the fruit is that stage at which the fruit can be used as food. However, the shelf-life, as defined here, is that stage when the tomato is suitable for table use, that is, from the appearance of red until disease, softening, or shriveling becomes excessive and the fruit becomes useless for table purposes.

Tomato fruits differ in their shelf-life. Growing conditions, state of maturity, and postharvest treatment all affect shelf-life; nevertheless, probably genetic constitution is the single most important factor. At the present time, there is considerable interest in recently discovered tomato mutants (table 1), which impede ripening and extend shelf-life (1, 9). In the homozygous state, these genes inhibit the fruit from ever ripening adequately for fresh consumption. Their use in the heterozygous state (in hybrids, for example), is most likely to be useful as a commercial technique (2, 8).

From an *a priori* standpoint, it can be postulated that there exist still other undiscovered genes that affect the ripening process, and that some of the genes might be milder in their effect on ripening than the current

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TABLE 1.—*Major genes affecting tomato fruit ripening*

Gene symbol	Source	Color of mature fruit	Shelf-life of Fruit[1] Homozygote	Heterozygote	Reference
NR (Neverripe)	Mutant	Yellow green	3	2	10
rin (ripening inhibitor)	Mutant	Yellow	4	2	10
nor (non ripening)	Mutant	Yellow to orange	5	2–3	8
alc (alcobaca)	Portugal France	Yellow to orange	5	2–3	7
GR (Green-ripe)	Mutant	Green to yellow	5	4	5
l (lutescent)	Mutant	Cream	4	2	This paper

[1] Rated from 1 (normal, 2 weeks) to 5 (4–6 months).

ripening mutants, and thus more useful. Genes that extend the shelf-life of red fruit would be very valuable in homozygous or pure lines.

The studies reported here were made to discover such genes, to transfer them to large-fruited lines, to learn something of their inheritance, and thus to develop a strategy for breeding tomatoes with long shelf-life.

MATERIALS AND METHODS

One hundred eighty-four red-fruited tomato varieties were studied. The collection included standard and primitive cultivars of *Lycopersicon esculentum* and gene stocks, varieties of *L. esculentum* f. *cerasiforme*, *L. pimpinellifolium*, and hybrids of *L. pimpinellifolium* with *L. esculentum*. These were grown in the greenhouse or field at the Tropical Agriculture Research Station, Mayagüez, Puerto Rico.

Fruits that were orange, with only a small residue of green, were harvested and placed on the laboratory bench with ambient temperatures of 24 to 28° C. Fruits were observed weekly and rated from 1 to 5 for three causes of deterioration: disease, softness and shriveling. The scale for disease: 1, free of disease; 2, very minor spots; 3, some definite rotting; 4, rotting but diseased spots could still be removed; 5, inedible because of rotting. For softness: 1, hard; 2, slightly yielding; 3, slightly soft; 4, soft and yielding but recovering; 5, so soft that shape is not recovered. For shriveling: 1, none; 2, slight wrinkles; 3, definite wrinkles; 4, severe wrinkles but still judged edible; 5, judged inedible because of shriveling. Shelf-lives were compared by analysis of variance.

Six lines were selected for further testing of shelf-life. Shelf-life of each was measured on three occasions from fruits produced in separate greenhouse plantings. One tomato cultivar, Kewalo, bred in Hawaii and resistant to several diseases, with an average shelf-life of 7.5 weeks, was selected for crossing. The six lines were crossed as males to Kewalo, and the F_1 hybrids were backcrossed to Kewalo. F_2 generations were produced from F_1's and BC_1's. The shelf-life of the F_1, F_2, BC_1 and F_2 of BC_1 hybrids and of F_3's from plants with outstanding shelf-life were tested.

RESULTS

Figure 1 gives the frequency distribution of varieties with shelf-life from 0 to 23 weeks. The majority of the varieties had shelf-lives of 3 to 8 weeks (mean=5.4). The least significant difference ($p=0.05$) in shelf-life was 2.9 weeks. The fruits of a few varieties kept for double or even triple the mean time. Table 2 gives thirteen lines with exceptional shelf-life, and their identification by class of tomato. Only 4 of these lines were *L. esculentum*. The long shelf-life of 2 of these was associated with a single previously known gene, lutescent, *l* (3), revealed here to have major effects on shelf-life. The other two varieties were small-fruited primitive tomatoes. No modern large-fruited variety showed exceptional shelf-life, but the best was cultivar Pope, a plum-shaped tomato, with an average shelf-life of 13 weeks. A small-fruited line identified as Burdick-038, collected in Morocco, had a shelf-life of 15 weeks.

Table 3 gives shelf-lives of the 6 chosen lines, as compared to the control. All lines had shelf-lives much longer than that of the control. When hybridized, progeny shelf-life values ranged widely in each cross from short (3 to 4 weeks) to moderately long (12 to 15 weeks). Table 4 gives the shelf-lives of the parents, F_1, F_2, selected F_3, and BC_1 plants. In three F_1's the shelf-life was longer and in the other 3 it was shorter than that of the long-lived male parent, but in all cases shelf-life was equal to or longer than the mean of the shelf-lives of the two parents.

Almost all shelf-lives in the F_2 were shorter than the shelf-life of the original male parent (table 4). The mean shelf-lives of the F_2's were shorter than the mean of the parents, except in one case. Mean shelf-life of all F_2's was 9.4 weeks.

Figure 2 shows the frequency distribution of F_2 shelf-lives. The mean of the original male parent is indicated on the bar graph (single arrow). Average of the means of the two parents is also shown (double arrow). The majority of the F_2's had shorter shelf-lives than the average of the parents. In each F_2 population a few segregants demonstrated shelf-lives almost as long as those of the original long-lived parent.

These F_3 families were small, 6 to 24 plants (table 4). The range in shelf-life of the F_3's was somewhat longer than the mean shelf-life of the F_2's. In the BC_1, F_1 plants had been crossed to the original female Kewalo. Small families of 6 to 22 plants were grown (table 4). Shelf-life of the BC hybrids ranged from 2 to 13 weeks, but the mean shelf-life was reduced in every family to less than that of F_1, F_2 or F_3 generations. In

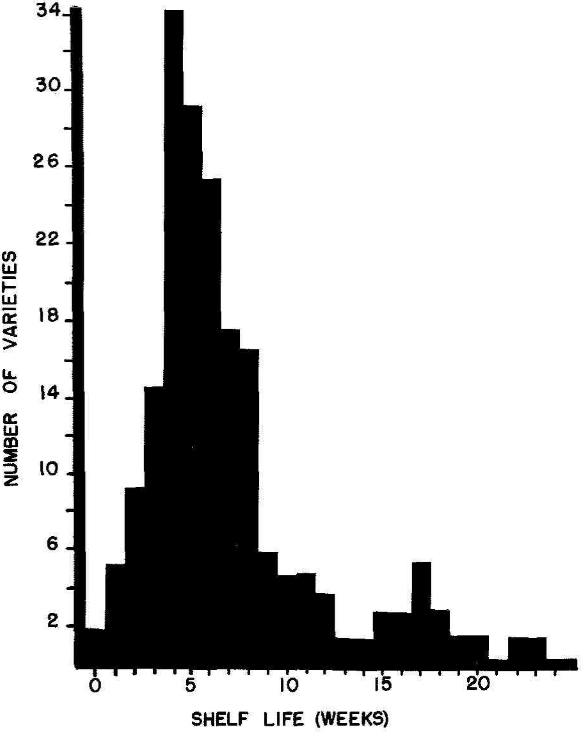

FIG. 1.—Frequency distribution of shelf-life in weeks of 184 tomato varieties.

the F_2's of the BC_1's no plants with shelf-life approaching that of the original parents were found. The suggestion is that some genes were lost during the backcrossing.

DISCUSSION

Current emphasis on major genes affecting fruit ripening has been useful in understanding the ripening process. Furthermore, some of

TABLE 2.—*Red fruited tomatoes with exceptional shelf-life*

Tars No.	PI No.	Species	Shelf-life (weeks)	Sources
TA 185	144955	*L. pimpinellifolium*	23.2	Fr. Peru
TA 181	129097	f. *cerasiforme*	22.0	Fr. Colombia
TA 194	212409	*L. pimpinellifolium*	20.7	Fr. Venezuela
TA 75	212429	*L. esculentum*	19.7	Gene, Lutescent
TA 162	118790	f. *cerasiforme*	18.5	Fr. Venezuela
TA 273	205011	*L. esc.* × *L. pimp.*	18.2	Hybrid from USA
TA 309	128277	*L. esculentum*	17.6	Fr. Argentina
TA 326	204980	*L. esc.* × *L. pimp.*	17.3	Hybrid from USA
TA 276	205020	*L. esc.* × *L. pimp.*	17.5	Hybrid from USA
TA 285	286098	*L. esculentum*	17.5	Fr. Nigeria
TA 325	204978	*L. esc.* × *L. pimp.*	17.1	Hybrid from USA
TA 159	100697	f. *cerasiforme*	17.0	Fr. Peru
TA 68	193399	*L. esculentum*	16.1	Gene, lutescent

these major genes may play a role in the development of long-lasting hybrid tomatoes. However, the effects of these genes are too drastic for use in commercial tomato varieties, which are mostly pure lines (homozygous for all genes).

As revealed by these studies, long-lasting tomatoes from six cultivars appeared to be controlled by minor genes. In F_1 hybrids with a normal tomato, these genes are expressed, and thus at least some must be dominant in effect. In F_2, F_3 and BC_1 generations considerable segregation occurred for shelf-life; this finding suggests that several genes control this characteristic, both dominant and recessive. Although segregating populations were small, plants with better than mean shelf-life were recovered from most populations. Thus, the number of genes affecting shelf-life appears to be small and manageable. Whereas some of the differences among generations could be due to testing during different seasons, the differences within generations appear genuine and useful.

TABLE 3.—*Shelf-life in weeks of selected red fruited tomato cultivars as compared to that of a standard variety, in three trials*

Tomato line	Species or variety	Fruit size		Greenhouse		
		Length	Diameter	1981	1982	1983
		mm	*mm*			
TA 10	*L. esculentum* (Pope)	48	35	10.1	8.2	21.0
TA 162	*f. cerasiforme*	15	18	18.5	10.2	8.4
TA 181	*f. cerasiforme*	22	23	22.0	13.4	14.2
TA 194	*L. pimpinellifolium*	10	10	20.7	11.8	14.6
TA 273	Hybrid, *L. esculentum* × *L. cerasiforme*	15	19	11.2	8.0	15
TA 277	*L. esculentum*	15	16	14.8	14.8	14.4
TA 8	*L. esculentum* (Kewalo)	51	62	7.1	8.0	7.4

TABLE 4.—*Shelf-life of fruits in weeks of six tomato F_1, F_2, F_3 and BC hybrids, as compared to shelf-life of parent lines*

Original parents and shelf-life	F_1	F_2 No. of plants	F_2 Range	F_2 Mean	Selected F_3 No. of plants	Selected F_3 Range	Selected F_3 Mean	BC_1 No. of plants	BC_1 Range	BC_1 Mean
Kewalo, 7.5 × TA 110, 13.1	18.6	18	7–13	8.1	17	8–13	11.1	11	4–6	5.4
Kewalo, 7.5 × TA 162, 12.4	17.8	17	3–13	7.6	17	5–14	10.0	6	6–12	7.6
Kewalo, 7.5 × TA 181, 16.6	13.4	17	6–15	11.2	24	5–17	10.4	16	6–13	9.1
Kewalo, 7.5 × TA 194, 16.5	12.2	18	4–15	9.6	6	7–13	10.6	13	3–13	6.4
Kewalo, 7.5 × TA 273, 12.5	10.8	14	3–12	9.0	16	7–13	10.5	22	2–13	5.8
Kewalo, 7.5 × TA 277, 14.7	18.8	16	9–14	11.0	13	6–15	12.1	18	5–12	9.2

[1] Shelf-life of parents follows the name or number.

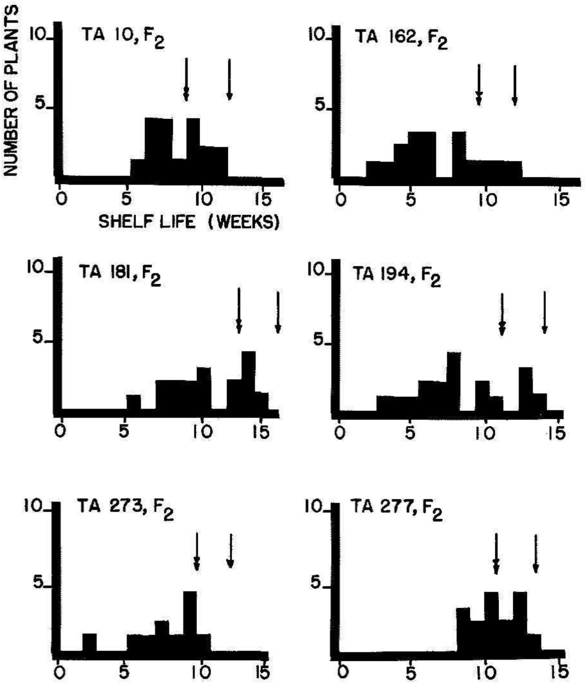

FIG. 2.—Frequency distribution of shelf-life in weeks of F_2 families from six parental combinations. The single arrow represents mean shelf-life of the original male parent. The double arrow represents mean shelf-life of the two parents.

During the course of these investigations many individual plants were found with fruits of outstanding shelf-lives. The fruits of these plants lasted for 4 months or more, and during that time they remained red, they did not soften, and they did not shrivel excessively. The few fruits tested remained edible, but a thorough study of edibility and quality would be desirable.

There is now a question of how the minor genes might be used in developing tomatoes with longer shelf-life. It is suggested that these genes might be tranferred to lines with larger fruits and other improved horticultural characteristics first.

Therefore, it appears that a useful strategy for the development of tomatoes with long shelf-life would be the use of the minor genes transferred to suitable lines combining other characteristics of value. Because the individual lines do not necessarily contain the same minor genes for improved shelf-life, combinations of genes from different sources might further increase shelf life. It would be desirable, however, to transfer the genes by continued pedigree selection in the Kewalo background until pure lines with larger fruits are achieved. The lines developed in this fashion as pure lines would have fruits that are normal in all aspects, and also have outstanding keeping quality. The interactions of minor genes for long shelf life from different sources could then be studied efficiently. Tomato germplasm could be improved so that long shelf life would be routinely incorporated into new varieties.

RESUMEN

Genes para que el tomate dure más después de cosecharlo

En 184 variedades de tomates de frutas rojas de diversas fuentes se estudió el estado útil de la fruta; 13 se encontraron en estado útil por 16 semanas o más. Seis variedades se cruzaron con 'Kewalo' (de Hawaii) y se produjeron generaciones F_1, F_2, F_3, retrocruces y F_2 de retrocruces. La longevidad de las frutas está controlada por varios genes, pero no se encontraron razones géneticas exactas. En los híbridos, el estado útil más largo se encontró en la segunda generación. Se segregaron genes recesivos y dominantes. Se encontraron plantas individuales, con frutas de longevidad excepcional aun en las generaciones más avanzadas. Se sugiere la selección por genealogía como técnica útil para concentrar los genes correspondientes en una útil longevidad en una sola variedad. El cruce entre tales líneas puras podría hacerse para combinar genes de fuentas distintas. Tales genes menores en líneas homozigóticas pueden ser más útiles que genes sencillos dominantes en híbridos.

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