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GENETIC STRATEGIES FOR BREEDING LONG LASTING TOMATOES

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ABSTRACT

Tomatoes that will last for one month or more at tropical temperatures, without refrigeration, are now feasible. Attention has been given to major genes which drastically modify the ripening process. When these genes are homozygous, tomatoes do not develop full color and may not soften for months. In the heterozygous state, as would be found in hybrid tomatoes, these genes result in red tomatoes with extended shelf life. A search was made for genes that increase shelf life without drastic effects. Six sources of long-life were crossed to a conventional tomato cultivar and shelf life was measured in F_1, F_2, F_3 and BC generations. In each generation shelf lives were shorter than those of the long-lived parent, and usually as short or shorter than the mean of the two parents. A few segregants with exceptionally long shelf life were obtained. The results suggest that a relatively few genes are segragating and that these can be transferred to more suitable varieties to achieve long lasting tomatoes in pure lines.

RESUMEN

Ya es factible lograr tomates que puedon dura un mes o más a unas temperaturas tropicales, sin refrigeración. Se ha enfocados en algunos genes principales que modifican radicalmente el proceso de maduración. Cuando estos genes son homocigóticos, el color de los tombtes no se desarrolla plenamente y los frutos pueden tardar unos moses en ablandarse. En el estado heterocigótico, como el que puede observarso en los tomates híbridos, estos genes producen tomates rojos con una vida de almaconaje más extendida. Se buscó los genes que extiendon la vida de almacenajo sin producir otros efectas graves. Se cruzó seis especies duraderas con un cultivar de tomate tradicional y se calculó la vida de almacenaje para las generaciones F_1, F_2, F_3 y BC. Para cada generación, la vida de almacenaje era más corta que la de la planta madre más duradera; en la mayoría de los casos, era tan codta o más corta que la vida promedia de las dos plantas madres. Se obtuvo algunos elementos segregados con una vida de almacenaje excepcionalmente larga. Los resultados hacen creer que existen unos pocos genes segregantes y que éstos se pueden trasladar a unas especies más convenientes, afin de lograr tomates duraderas en las especies puras.

Keywords: Tomato, *Lycopersicum esculentum,* Breeding, Shelf life, Puerto Rico. Hot humid tropics.

The tomato, *Lycopersicum esculentum* Mill., is probably the most common and most highly acceptable fresh vegetable of the world. In addition to its many uses in processed form, it is part of the green salad that is considered essential in a balanced diet. The tomato production industry is enormous, with technology ranging from the primitive to the most advanced, complemented by systems of transportation and marketing, equally varied and complex. Yet the tomato is one of the most perishable vegetables. Its highest quality is seen when it is red-ripe, an ephimeral condition. Extensive refrigeration before or after ripening reduces quality.

It is desirable to have longer lasting tomatoes in the tropics. Tomatoes that reach a deep red color, and that retain their firmness and flavor for several weeks to a month, even without refrigeration, would result in greater flexibility in marketing and in convenience in the kitchen. Whether produced at home, in small farms, or in large commercial fields, such tomatoes would improve the conservation of the fruit and thus make usage more versatile.

The tomato fruit passes through a ripening process referred to as the climacteric (Khudairi, 1972). After a relatively long initial period of development as a green fruit, when physiological processes are fairly stable, the mature green fruit begins to ripen, a rapid process that will bring the tomato into an optimum state for consumption, and will then rapidly carry it beyond that stage to an unacceptable softness and off-flavor.

Some of the processes that occur before, during or after the climacteric include the following (Khudairi, 1972):

1. A synthesis of a series of carotenoids seen as progressive of yellow, orange and red color development, culminating in the production of lycopene. Meanwhile chorophyll degenerates.
2. The production of ethylene, which has hormonal effects on the process of ripening.
3. An increase in respiration, reaching a peak, the climateric, followed by a rapid decrease.
4. An increase in the action of certain enzymes, especially polygalacturonase, pectin esterase, and cellulase and the resultant softening of the fruit.
5. A decrease of acidity, dry matter, and sugars.
6. Other changes in flavor more difficult to define but of great importance.

An examination of fruits of the family Solanaceae shows that long-lasting fruits are not rare. The ornamental fruits of *Solanum mammosum* can last a year. Eggplant fruits are very slow in spoiling. The fruits of numerous red peppers may be stored for months. Even the common bell pepper fruit, when red ripe, can last a month or more. Thus, there is a suggestion that genes already exist in the family for long lived fruits. But can such genes be found in, or be incorporated in the tomato so that useful life is increased without loss of quality? In this paper I would like to stress that they can be found, and I would like to suggest a strategy for breeding long lasting tomatoes.

Major genes

Major genes with drastic effects on the ripening of the tomato have come from two sources, primitive varieties of tomatoes that were preserved in Europe because the fruits could be harvested and saved for the winter, and mutations that have been found by genetists and studied for their interesting characteristics. The major genes known are summarized in Table 1.

The five major genes have various aspects in common. First, they all have drastic effects. By drastic I mean to say that the homozygous plants produce fruits that ripen so poorly that they never become as good as normal tomatoes. Furthermore even if ethylene is used to stimulate ripening of mature green tomatoes, only slight improvements in ripening occur.

Table 1. Major genes affecting tomato fruit ripening

Gene Symbol and name	Source	Color of mature fruit	Shelf life of fruit* Homozygote	Heterozygote	Reference
Nr (Neverripe)	Mutant	Yellow green	3	2	Tigchelaar, *et al.*, (1978).
rin (ripening inhibitor)	Mutant	Yellow	4	2	Tigchelaar, *et al.*, (1978).
nor (non-ripening)	Mutant	Yellow to orange	5	2–3	Ng & Tigchelaar, (1977).
alc (alcobaca)	Portugal France	Yellow to orange	5	2–3	Lobo, *et al.*, (1984).
Gr (Greenripe)	Mutant	Green to Yellow	5	4	Jarret, *et al.*, (1984).

* Rated from 1 (normal, 2 weeks) to 5 (4 – 6 months)

Various salt solutions in the soil can increase ripening, however, and indeed there appear to be other responses as well (Arad and Mizraki, 1983). Because these tomatoes do not ripen well, they are resistant to postharvest diseases.

The heterozygous condition of these five genes is about the same as the homozygous in the case of the dominant genes *Neverripe*, and *Greenripe* (Jarrett, *et al.*, 1984) but quite different for the other three genes. In the heterozygous condition of the latter, fruits ripen slowly to a normal level of color. They also remain firm longer, resist postharvest diseases, and have a longer storage life. These genes are, therefore, best used in the heterozygous form, in suitable F_1 hybrids. One commercial hybrid variety known as 'Long Keeper' is based on one such gene. Fruits of F_1 hybrids based on the gene *nor* ripened late, held longer in storage, but firmness varied, and appeared to depend more on the particular parents in the cross (McGlassen *et al.*, 1983). *Nor* did not affect fruit size, soluble solids, pH, titratable acids, or total ascorbic acid.

The mechanisms of physiological control of these major genes are not well known, but all lack the full polygalacturonase enzyme activity of normal tomato fruits. This is the chief enzyme responsible for softening of the fruit. There is currently great interest in working out the mechanisms of control.

In the mutant genes the climacteric tends to occur but later than normal and in a much reduced fashion. Ethylene gas is produced in lesser quantities. The respiration is lower. Chlorophyll may begin to break down, and carotenoid pigments may begin to form. Softening is delayed and may be reduced to a minimum (Ng and Tigchelaar, 1977).

It appears that other commercial hybrids will be developed from these genes, and these may change the entire pattern of production and marketing of tomatoes.

Minor genes

If genes are found with major effects on the ripening process, genes with lesser effects might also occur. These genes might make it possible to extend shelf life in normal varieties, that is, in pure lines that are homozygous for these genes. Such tomato cultivars might be more useful than hybrid varieties based on heterozygosity of a major shelf life gene.

With this in mind, we studied the shelf life of tomato fruits from 184 red fruited cultivars. These included *Lycopersicum esculentum, L. esculentum F. cerasiforme, L. pimpinellifolium,* and suspected hybrids. Five fruits that were just beginning to ripen, called in the trade "breakers" were harvested, from each plant, held at room temperature (26 – 28 °C) and observed for shelf life. The fruits were examined weekly and were discarded when diseased or excessively soft or shrivelled. Shelf life was noted as the number of weeks from harvest to discard.

The frequency distribution of varieties with shelf life from 0 to 23 weeks are given in Fig. 1. The majority of the varieties had shelf lives of 3 – 8 weeks. However, the fruits of a few varieties kept for double or even triple this time. Thirteen lines with exceptional shelf life are given in Table 2 with their identification by class of tomato. Only four of these lines were *L. esculentum*. The long shelf life of two of these was associated with a single previously known gene, *lutescens,* 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 the cultivar 'Pope', a plum-shaped tomato, with an average shelf life of 13 weeks. A line known as Burdick-038, collected in Morocco, had a shelf life of 15 weeks, but small fruits.

Table 2 Tomatoes with exceptional shelf life

TARS NO.	PI No.	Species	Shelf life (weeks)	Source
TA185	144955	*L. pimpinellifolium*	23.2	Peru
TA181	129097	f *cerasiforme*	22.0	Colombia
TA194	212409	*L. pimpinellifolium*	20.7	Venezuela
TA75	212429	*L. esculentum*	19.7	USA
TA162	118790	f. *cerasiforme*	18.5	Venezuela
TA273	205011	*L. esc.* × *L. pimp.*	18.2	USA
TA309	128277	*L. esculentum*	17.6	Argentina
TA326	204980	*L. esc.* × *L. pimp*	17.3	USA
TA276	205020	*L. esc.* × *L. pimp*	17.5	USA
TA285	286098	*L. esculentum*	17.5	Nigeria
TA325	204978	*L. esc.* × *L. pimp.*	17.1	USA
TA159	100697	f. *cerasiforme*	17.0	Peru
TA68	193399	*L. esculentum*	16.1	USA

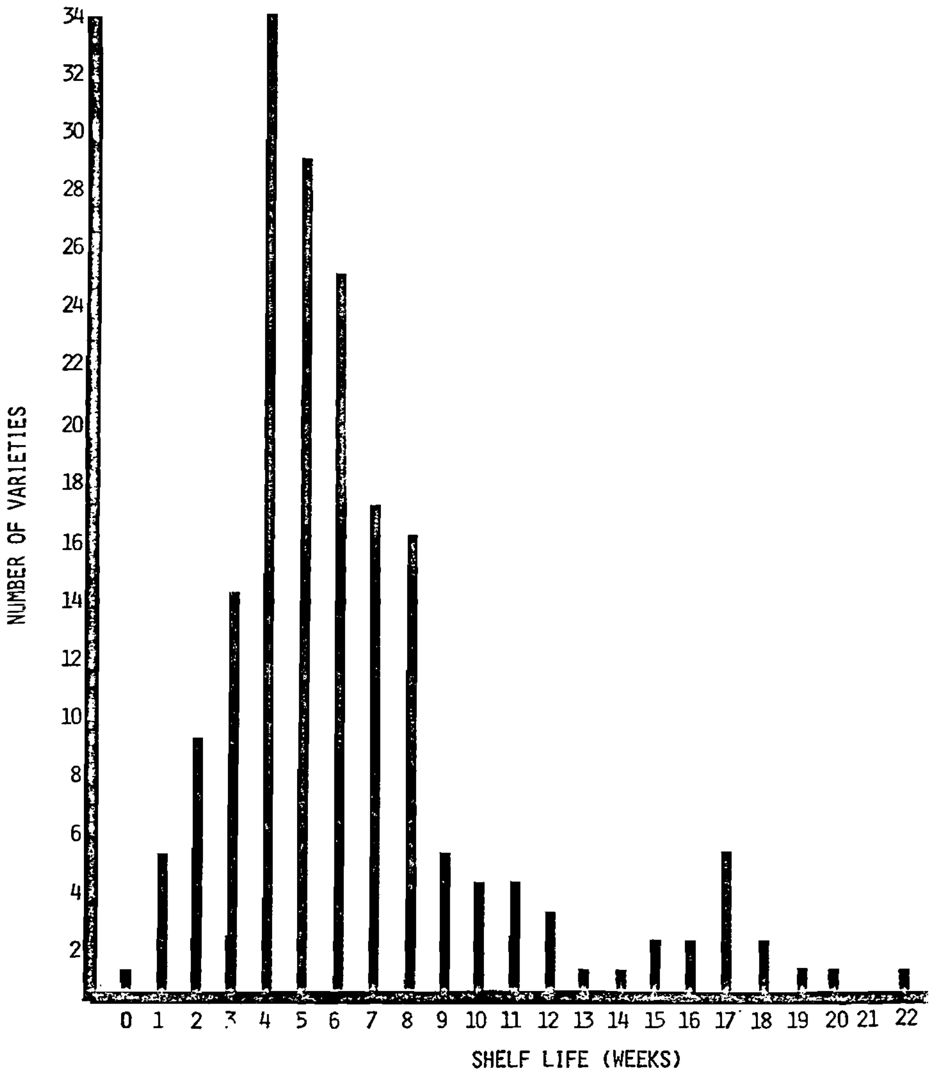

Fig. 1: Frequency distribution of tomato varieties with a shelf-life of 0 - 23 weeks.

Six of the lines were selected for further testing. Shelf life of each was measured three times from fruits produced in separate greenhouse plantings (Table 3). One tomato cultivar, 'Kewalo', bred in Hawaii and resistant to several diseases, with average shelf life of 75 weeks, was selected for crossing. The six lines were crossed as males to 'Kewalo', and the F_1 hybrids were backcrossed to 'Kewalo'. The shelf life of the F_1, F_2, and BC_1 hybrids and selected F_3's are given in Table 4, as compared to the shelf life of the original parents. In three F_1's the shelf life was longer and in the other three it was shorter than that of the male parent, but in all cases shelf life was equal to or greater than the mean of the shelf lives of the two parents.

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		Shelf life (weeks)		
		Length (mm)	Diameter (mm)	1981	1982	1983
TA 10	*L. esculentum* (Pope)	48	35	10.0	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
TA194	*L.pimpinellifolium*	10	10	20.7	11.8	14.6
TA 273	Hybrid, *L. esculentum* x *L. cerasiforme*	15	19	11.2	8.0	15.0
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 varieties as F_1, F_2, F_3, and BC hybrids, as compared to shelf life of parent lines.

Orginal parents and[1] shelf life	F_1	F_2			Selected F_3			BC	
		No of plants	Range	Mean	No of plants	Range	Mean	No of plants	Range
Kewalo, 7.5 x TA 110,13.1	18.6	18	7-13	8.1	17	8-13	11.1	11	4-6
Kewalo, 7.5 x TA 162,12.4	17.8	17	3-13	7.6	17	5-14	10.0	6	6-12
Kewalo, 7.5 x TA 181,16.6	13.4	17	6-15	11.2	24	5-17	10.4	16	6-13
Kewalo, 7.5 x TA 194,16.5	12.2	18	4-15	9.6	6	7-13	10.6	13	3-13
Kewalo, 7.5 x TA 273,12.5	10.8	14	3-12	9.0	16	7-13	10.5	22	2-13
Kewalo,7.5 x TA 277,14.7	18.8	16	9-14	11.0	13	6-15	12.1	18	5-12

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

From each of the six crosses, 14 – 18 plants of the F_2 were tested for shelf life. The shelf life values ranged widely in each cross from short (3 – 4 weeks) to moderately long (12 – 15 weeks). Almost all shelf lives in the F_2 were less than the shelf life of the original male parent (Table 4). The mean shelf lives of the F_2's were lower, (except in one case), than the mean of the parents. Mean shelf life of all F_2's was 9.4 weeks.

The frequency distributions of the F_2's are shown in Fig. 2. The mean of the original male parent is indicated on the bar graph by a single arrow. The average of the mean of the two parents is shown by a double arrow. The majority had shorter shelf lives than the average of the mean of the parents. In each F_2 population a few segregants demonstrated shelf lives almost as great as those of the original long-lived parent.

One outstanding F_2 plant was selected from each family and self pollinated. The shelf lives in F_3 families are given in Table 4. The F_3 families were small, six to 24 plants. The range in shelf lives were very similar to the ranges found in the F_2's. This signifies that there was considerable segregation in F_3's for the genes affecting shelf life. The mean shelf life of the F_3's was somewhat larger that the mean shelf life of the F_2's, which suggests progress due to selection.

In the BC (backcross generation) 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 mean shelf life was reduced in every family to less than the mean of the F_1, F_2, or F_3 generations. This suggests a continued segregation for genes affecting shelf life, and the presence of fewer genes that increase shelf life.

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. During that time they remained red, did not soften, or shrivel excessively. The few fruits tasted had remained edible.

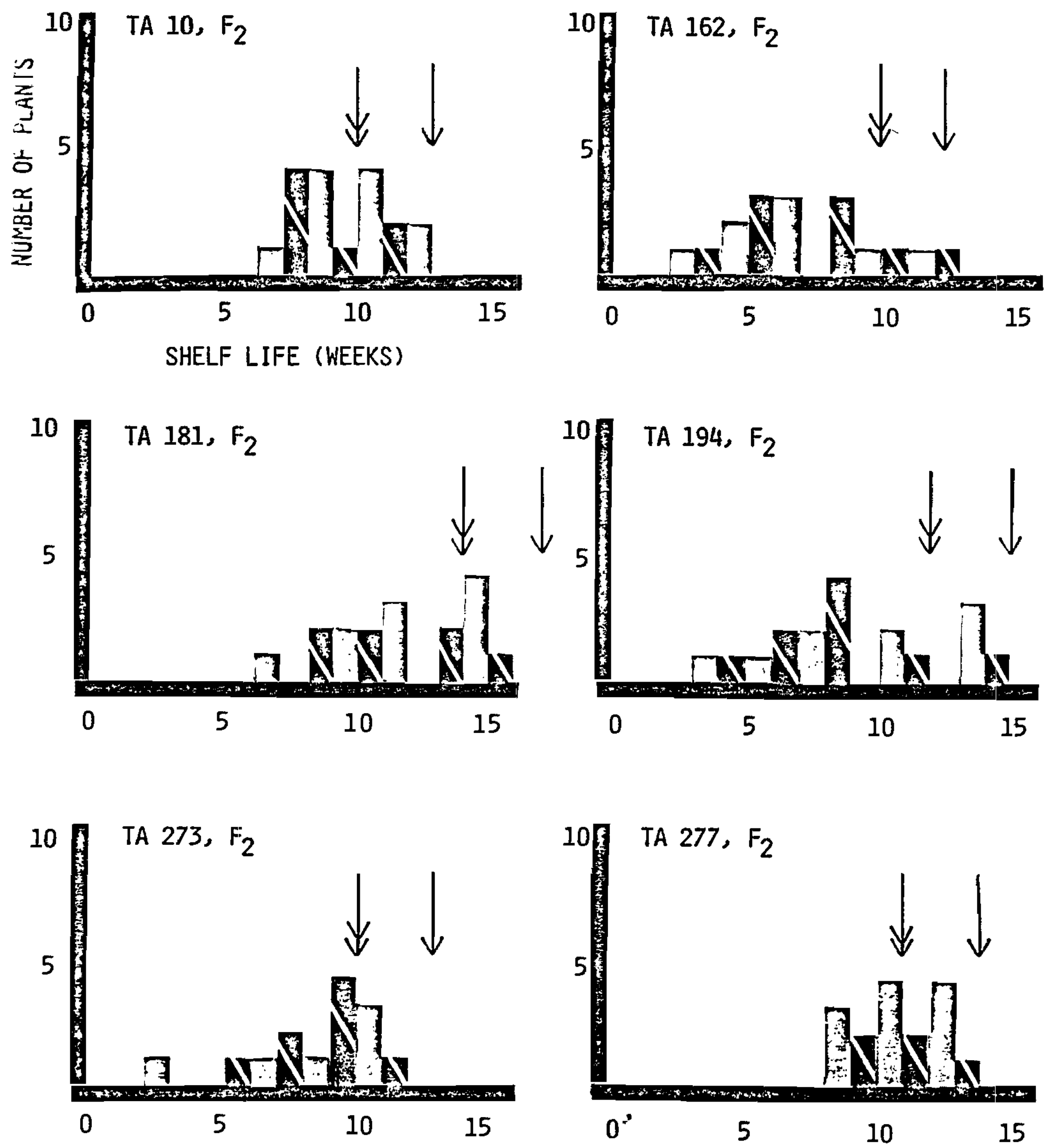

Fig. 2: Frequency distribution of tomato F_2's

Discussion

Current emphasis on major genes affecting fruit ripening has been useful in understanding the ripening process. Furthermore, some of 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 pure lines (homozygous for all genes).

As revealed by our 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 may be dominant in effect. In F_2, F_3, and BC generations considerable segregation occurred for shelf life suggesting that several genes control this characteristic. Although segregating populations were small, plants with outstanding shelf life were recovered from each population. Thus, the number of genes affecting shelf life appears to be small and manageable.

Therefore, it appears at the present time that the best strategy for the development of tomatoes with long shelf life is the use of the minor genes, transferred to suitable populations and combined with other characteristics of value. The varieties development in this fashion will have tomatoes that are normal in all respects but that have outstanding keeping quality.

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