CRC CRITICAL REVIEWS in FOOD SCIENCE AND NUTRITION

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It is proposed to describe briefly the rise in popularity of the tomato during the 20th century to become the world's fourth most significant fruit, making an important contribution to human nutrition. The grading standards for fruit used in various major tomato-producing countries will be outlined. A major part of the review will be devoted to describing changes in composition during the maturation, ripening, preservation, and storage of good quality tomatoes especially as regards carbohydrates, organic and amino acids, proteins, steroids, pigments, minerals, and the lipids, volatiles, and other minor constituents. A range within which composition should normally fall will be given. Additionally, the effects on composition of environment, cultivar, nutrition, and physiological disorders *inter alia* will be described. How new growing methods and genetic manipulation could influence the tomato of the future will also be considered.

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Wild rice (*Zizania aquatica*) is an annual aquatic grass which grows in shallow lakes, marshes and in sluggish streams in various parts of the world. The grain of wild rice has been harvested by the Indians of the United States and Canada for many centuries. Explorers entering the territories of the Northern Lake States of America a few centuries ago described wild rice as a spontaneous crop which does not require plowing or sowing, providing an abundant harvest of palatable and nourishing grain. Natural propagation assured the Indians of a yearly crop. As time passed, wild rice lost its importance as a staple for the Indian population, but it became a white man's delicacy because of its unique color and flavor characteristics. In the U.S. a commercial wild rice industry developed. The grain is now found on supermarket shelves, but at a rather high price compared to prices for other cereal grains. Today, most of the wild rice in the world is harvested as a cultivated crop from paddies in the state of Minnesota. Smaller amounts are produced in Wisconsin and in southern Canada. Wild rice has some desirable nutritional attributes. Its protein content is relatively high compared to other cereal grains. Wild rice is a good source of the B vitamins, thiamin, riboflavin and niacin and contains common mineral elements in amounts comparable to those in oats, wheat and corn. Wild rice is used as a main meal ingredient in regular or quick cooked form and has numerous possible secondary usages. Because of its good nutritional balance wild rice could help to provide another source of energy and quality protein for the diet of man.

THE CONSTITUENTS OF TOMATO FRUIT — THE INFLUENCE OF ENVIRONMENT, NUTRITION, AND GENOTYPE

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I. INTRODUCTION

The tomato is immensely popular both as a food and as a research tool. Information in the literature on the composition of the fruit is widely scattered, although mainly in journals devoted to food science, horticulture, or plant biochemistry. Our primary aims in this article have been not only to review recent work on the major components of tomato fruit, but also to complement and supplement previous accounts[1-3] where we felt gaps existed and the information was not easily accessible. In addition to providing data on what is "normal" in good quality tomato fruit, examples are given illustrating how, *inter alia*, environment, nutrition, and the introduction of mutant alleles can alter the balance between the constituents. Some information about tomatoes other than *Lycopersicon esculentum* has also been included.

II. HISTORY

The tomato is a member of the Solanaceae — the potato family — a collection of some 1500 tropical and subtropical species probably originating in Central and South America. It is an important family as a food source, although many of its members are characterized by the presence of relatively high concentrations of alkaloids, e.g., atropine, scopolamine, hyoscyamine, and nicotine.

Within the Solanaceae, the genus *Lycopersicon* (from the Greek for "wolf peach", as Anguillara writing in 1561 mistakenly thought Galen had so named the tomato in the second century A.D.) is a relatively small collection of species that are normally subdivided into two groups, the *Eulycopersicon* and the *Eriopersicon*. Fruit of the *Eulycopersicon* are usually red or yellow in color when ripe, and this group contains the cultivated tomato, *L. esculentum*. Fruit of the *Eriopersicon* remain green or purple-green throughout development. The outmoded spelling of the genus as *Lycopersicum* derives from the Latin form of the name seemingly first used by Hill in 1773 and perpetuated until 1914 when the error was pointed out by Druce.[4] It is recognized that the first adequate description of several species of tomato, including the common one, was made by Miller in 1768; hence texts refer to *L. esculentum* Mill., etc.

Various detailed descriptions of specialized aspects of the genus have been published over the last 40 years, notably by Muller (brief history, classification and description of species),[4] Luckwill (a more detailed history together with a taxonomic survey),[5] Jenkins (origin of the cultivated tomato),[6] McCue (historical bibliography),[7] and Rick and Butler (cytogenetics).[8] More modern, briefer accounts[1,9,10] may serve as an entrée to the subject.

Table 1
CHARACTERISTICS OF THE SUBGENERA OF *LYCOPERSICON*

Eulycopersicon

The fruit are glabrous at maturity, and when fully developed are attractive to man in both taste and color, which is normally yellow or red; the plants are usually grown in cultivation as annuals, although they can survive as perennials in frost-free conditions

Two species are included:
  L. pimpinellifolium (the currant tomato — Pls. 3 and 5[4]), fruit 1—1.5 cm in diam
  L. esculentum (the normal species cultivated — Pls. 2 and 3[4]); the wild form is *L. esculentum* var. *cerasiforme* (the cherry tomato — Pl. 4[4]), with fruit 1.5—2.5 cm in diam, from which the cultivated tomato probably originated, either directly or as hybrids with other species

Eriopersicon

The fruit are hairy and whitish-green in color, often with purplish striping; they are unattractive to man in appearance and flavor; the plants generally behave as perennials, dying down in adverse conditions to leave a woody stem-base from which new growth emerges with the return of more favorable weather

Includes:
  L. cheesmanii (Pl. 8[4]), found only in the Galapagos Islands, 6—9 mm in diameter; hybridizes easily with *L. esculentum*, hence an intermediate form (?)
  L. peruvianum (Pls. 6 and 10[4]), includes *L. glandulosum*, 1—2 cm in diameter with lavender stripes down the midlocular line; var. *typicum* has identical fruit to var. *humifusum* (Pl. 7e, f, and g[4]), but the latter has fewer leaflets and an absence of bracts on the inflorescence
  L. hirsutum (Pl. 9[4]), 1.5—2.5 cm in diam with purplish longitudinal stripes; forma *glabratum* is self-fertile, while forma *typicum* is more hairy and self-sterile
  L. chilense (Pl. 7a and c[4]), formerly called *L. peruvianum* var. *dentatum*), 1—2 cm in diam, leaves bipinnatifid, covered with short hairs; inflorescence with a long peduncle
  L. chmielewskii (Figure 2[11]), 1—1.4 cm in diam, yellow-green in color having a relatively large calyx at maturity
  L. parviflorum (Figure 1[11]), 1—1.4 cm in diam with two dark-green or purplish radial lines on the fruit; the last two species were formerly known as *L. minutum*[11]

III. CLASSIFICATION

As all species from the two subgenera of *Lycopersicon* can be hybridized with each other (admittedly sometimes only with difficulty),[11] classification is more a matter of convenience than absolute distinction (Table 1). The most prolific natural collection of *Eriopersicon* species is to be found on the coastal strip of western South America extending to about 80 km (50 miles) inland and growing to an altitude of 3000 m (9500 ft)[12] (Figure 1). Cooper[13] has explained that the coastal strip of Ecuador and Chile is much cooler than might be expected in these latitudes because of a very cold offshore current. This leads to persistent dense fog over the area, but there is little actual rainfall. Eventually in northern Ecuador the climate becomes too hot and wet for the tomato to grow. Tomatoes survive on this coastal belt for 3200 km (2000 miles) southwards from near the equator to well inside Chile, and the air temperature throughout this wide range of latitude remains remarkably constant during the natural growing season. Finally, excessive moisture and cold conditions prove too much for even the most adaptable races of the species. Cooper[13] argues that the eastern limit of the tomato line is probably not determined merely by the altitude at which frost occurs as the Andean mountains rise
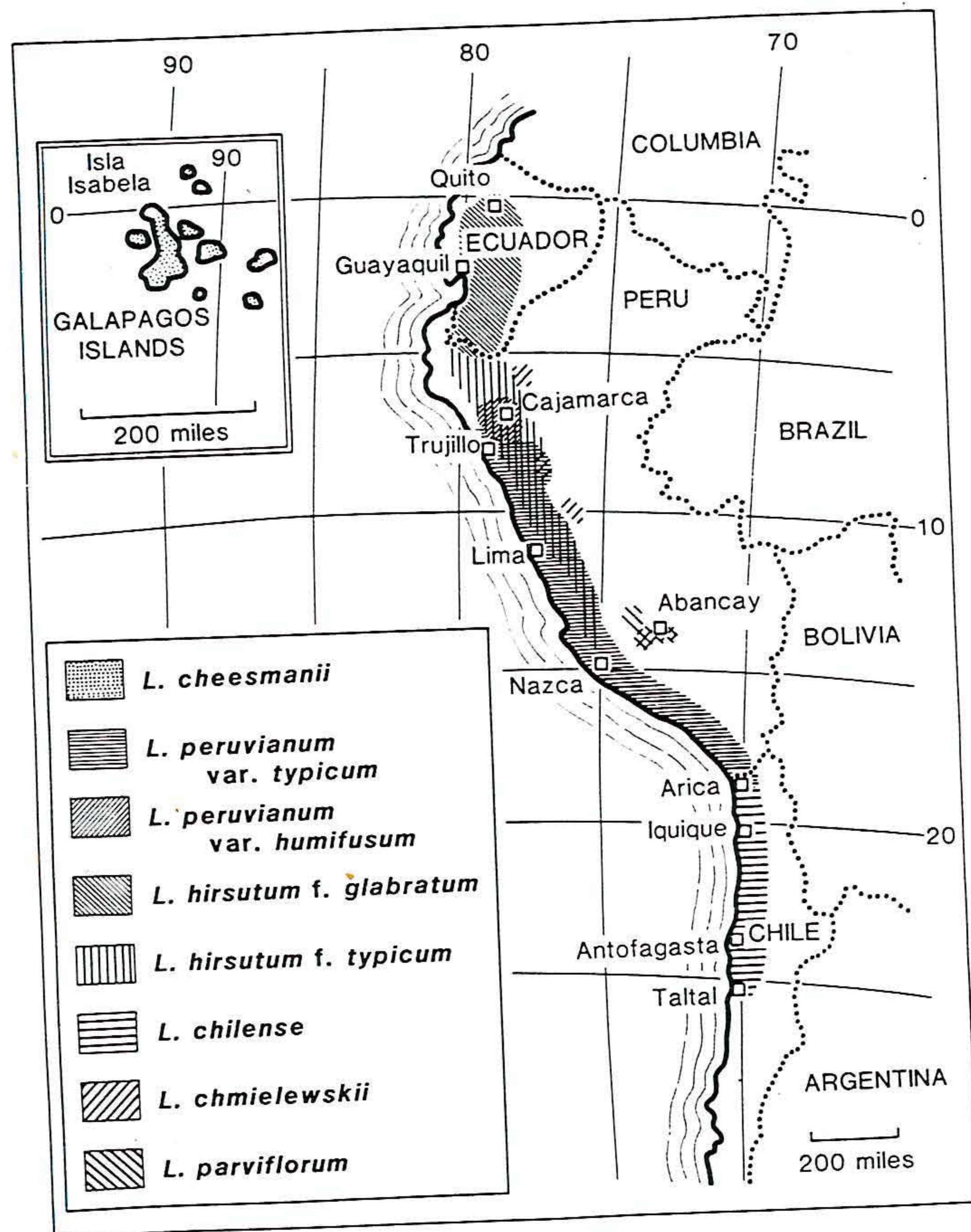
FIGURE 1.   Distribution of the various species of *Lycopersicon* in and around western South America. (After References 5 and 11. Copyright G.C.R.I.)

from the coast, but by a critical fall in a combination of night temperature and relative humidity. It is obvious that the Andes do not provide a complete barrier to the spread of the tomato, as a number of accessions have been found on their eastern slopes.[12] However, in Peru and Chile the species on both sides of the Continental Divide are confined to river valleys and regions that can provide appreciable moisture from the seasonal fog layers. From the ancestral forms, probably most prevalent in Peru,[5] plants bearing fruits that were palatable to man spread through his influence (e.g., down the main irrigation channels) to the warmer parts of North and South America.

Although the natural distribution of the economically important subgenus *Eulycopersicon* is difficult to follow, evidence from the diversity of cultivated types and culinary uses, and from the abundance of native names for the fruit all suggest that the original domestication took place in Mexico.[6] Selection over many generations, probably from the ancestral form now known as *L. esculentum* var. *cerasiforme,* has led to a gradual increase in the size of the fruit and in the ratio of fruit weight to seed content. Indeed, the introduction of improved varieties into the coastal strip of Peru and Chile has almost completely displaced the primitive native types[12] within the last two decades; thus a germ plasm bank containing potentially useful material is in danger of being lost.

The introduction of the tomato into southern Europe took place fairly soon after the

discovery of the New World. Mattiolus, whose writings were first published in Venice in 1544, described a golden-fruited *Pomi d'oro* ("golden apple") plant, which was almost certainly *L. esculentum.* The second edition, published 10 years later, mentions a red-fruited form, while Dodonaeus, writing in the same year, includes a list of synonyms largely based on the Italian name. A later woodcut clearly identifies the plant as the normal tomato we know today.

Although the names *Mala peruvianum* and *Pomi del Peru,* common in the 16th and 17th centuries, would seem to indicate Peru as the country of origin from whence the plant could have been brought back to Spain, Jenkins[6] argues that this is based on a misconception in Anguillara's *Semplici* published in 1561. Jenkins suggests, moreover, that it would be much more likely that the "tomatl", as the fruit was known in the Nahua language, came from Mexico which was conquered by the Spanish in the 1520s. Peru was not overrun until 1535, and Mattiolus was writing about the species from Venice in 1544. The tomato was only reluctantly accepted into Britain, going through the stages of being used for medical and decorative purposes before being adopted as an item of diet in the middle of the 18th century.

The cultivated tomato is a perennial plant normally grown as an annual, and the genus as a whole is tolerant of a wide range of climate and nutrition. For instance, *Solanum pennellii* (a species that readily hybridizes with the cultivated tomato) will survive in the very dry rolling, uneven ground of western Peru, while *L. cheesmanii* grows in the salt-laden atmosphere just a few meters above the high water mark along the northwestern shores of Isla Isabela in the Galapagos Islands,[12] 1120 km (700 miles) west of the Ecuador coast. The wide range of nutrient concentrations (e.g., 10 to 320 mg N/ℓ and 20 to 375 mg K/ℓ) in which commercial varieties may be grown in a flowing solution culture system known as the nutrient film technique (NFT)[14] illustrates the adaptability of *L. esculentum* as an efficient scavenger of both anions and cations, and it is likely that other tomato species share this attribute.

IV. ANATOMY OF THE FLOWER AND FRUIT

The following brief account is largely based on studies published in the 1930s and 1940s.[4,5,10,15-19] The corolla, which is normally lemon-yellow in *Eulycopersicon* and bright yellow in *Eriopersicon* spp., is composed of five segments except in cultivated forms of *L. esculentum* where the flowers are hexamerous or, as a result of fasciation, polyamerous.[5]

In the cultivated form, the stamens are attached by short filaments to the base of the corolla tube. The anthers which contain the pollen are partially fused to form a narrow-necked tube, as we have tried to indicate in Figure 2. Normally, the style and pollen-receptive stigma are within this tube,[10] and self-pollination is normally achieved. If, as happens in low light,[19] the style becomes longer than the anther tube, then the stigma will protrude, and the possibilities of cross-fertilization are enhanced.

The flower cluster is a short, forked racemose cyme, usually with several flowers open at the same time so that buds, open flowers, and young fruit all occur together on the same truss. The tomato flower is perfect, hypogynous, regular, and pendant. Anthers normally shed pollen from the second day of anthesis for 3 or 4 days, while stigmas are receptive from 1 to 2 days prior to anther dehiscence, remaining receptive from 4 to 8 days.[15] The time between pollination and fertilization appears to be more than 50 hr.

Botanically, the fruit of the tomato is regarded as a berry, since the seeds are formed within a fleshy mesocarp. The main divisions into which the fruit can be divided are skin, pericarp, and locular contents. The skin[18] consists of four or five layers of cells under a thin cuticle (Figure 3). Normally, the epidermal layer has a heavily cutinized outer
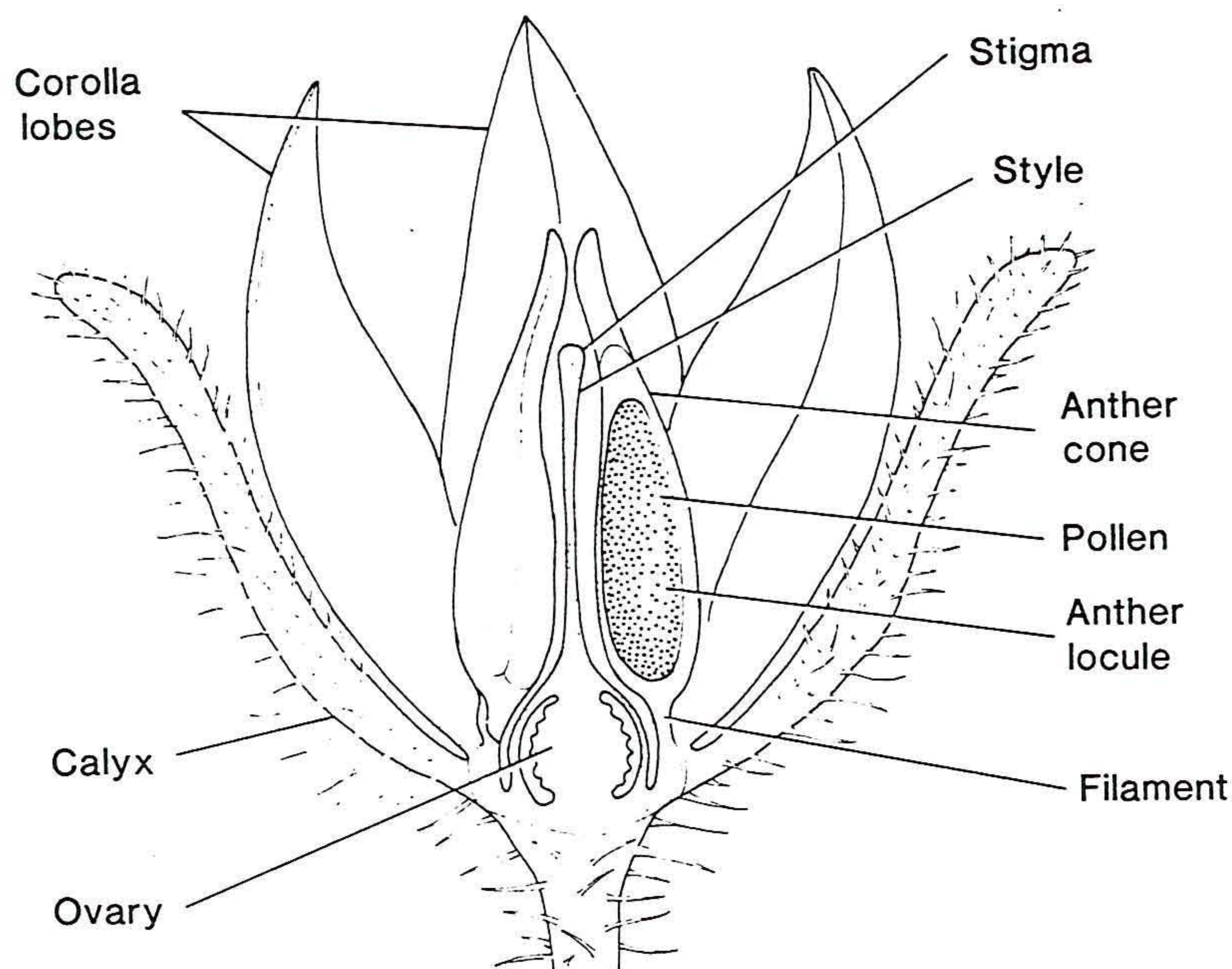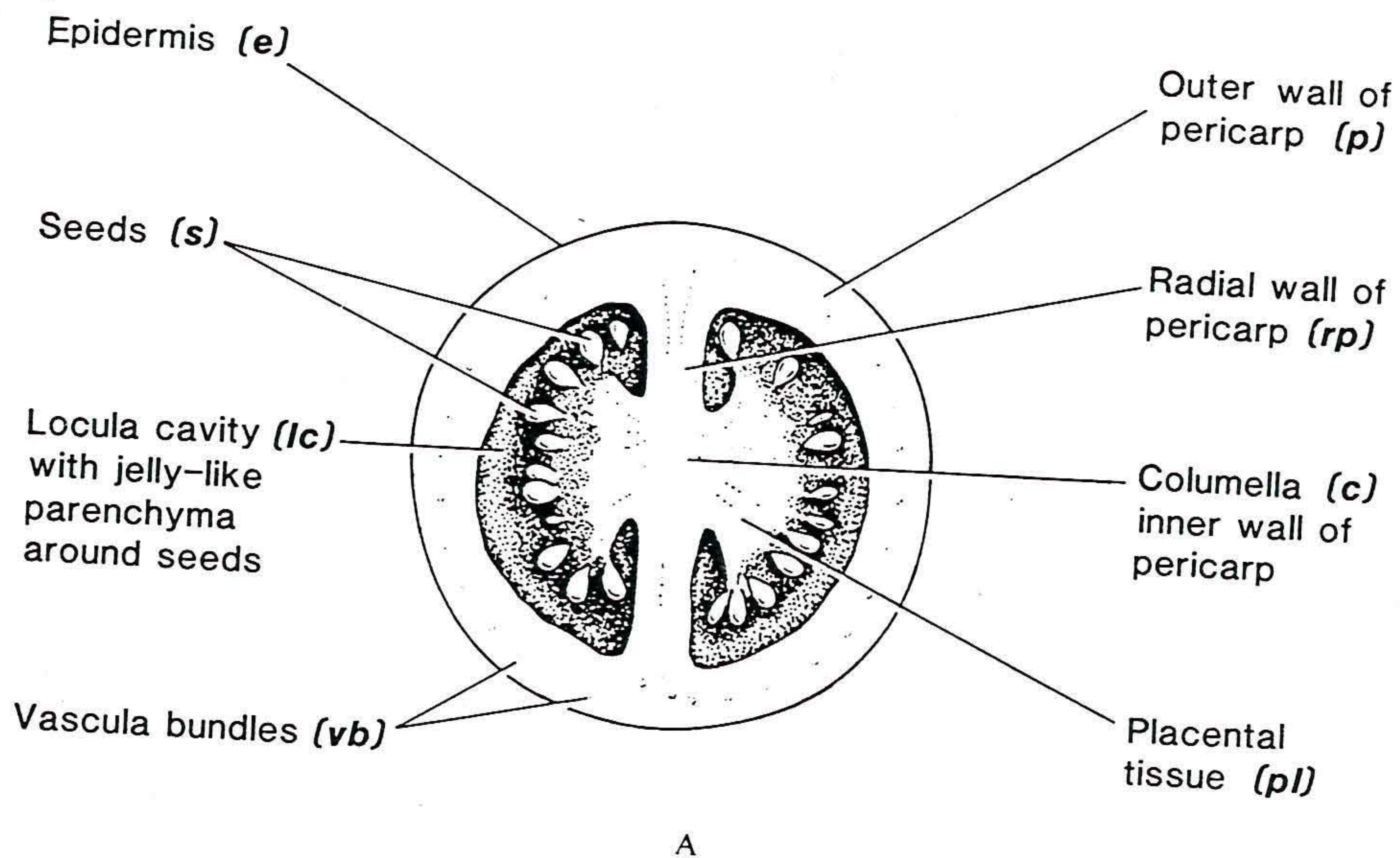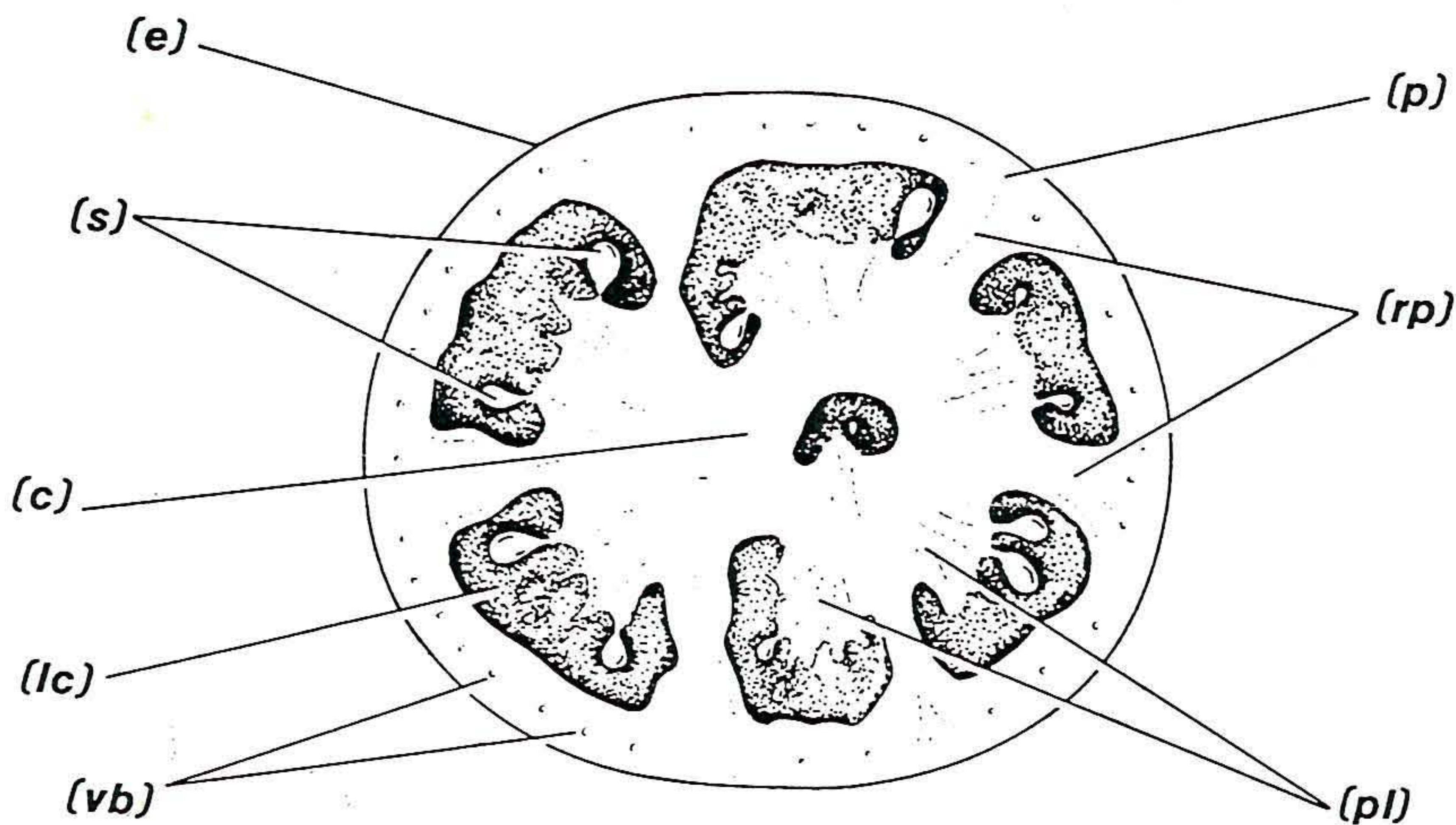
FIGURE 2.   Diagram of a section of a mature flower of *Lycopersicon esculentum* showing the main anatomical features. (Copyright G.C.R.I.)

surface, and both the epidermis and the underlying collenchyma are rather thick-walled. In some varieties, the cutin may surround the epidermal cells, even going between and below the first layer of collenchyma. This may explain part of the enhanced crack-resistance shown by the ripening fruit of such lines.[20] In immature tissue, the dense cytoplasm becomes peripherally orientated during the initial stages of cell enlargement to form a thin layer in which the nucleus, starch grains, chloroplasts, mitochondria, Golgi bodies, ribosomes, endoplasmic reticulum, small vacuoles and vesicles, microbodies, and lipid droplets can be identified.[16,17,412] The cells are traversed by plasmodesmata interconnecting the cytoplasm of adjacent cells.[16,17] Increase in the size of the fruit is by cell division for the first 7[21] to 14 days.[15] During the next few weeks, partial separation of cell walls at the middle lamella occurs, starting at the intercellular spaces. As the fruit matures, the pericarp cells become very large (100 to 500 μm) and thin-walled.[16] With ripeness, it has been found that the plasmalemma, tonoplast, and nuclei remain intact both physically[17] and physiologically;[22] indeed, all cytoplasmic structures detected in developing fruit persist into ripeness with no loss of density in the cytoplasm.[412] Although mitochondria appear to retain physical integrity in tissue that is fully ripe,[412] there is evidence of physiological impairment of these organelles when isolated from ripe and overripe fruit.[23]

Vascular strands radiate from the stem end of the fruit, both round the pericarp and down the columella to the blossom end. Cross connections in the pericarp are more common in the distal half of the fruit.[24] There is often a major vascular bundle in the center line of each carpel running from stem-scar to the blossom end of the fruit. From an early stage in development, the locules are filled by an outward growth of placental cells which enclose and engulf the seeds but do not unite with them or with the carpel walls.[15] As maturity approaches, the walls of these parenchymatous cells around the seeds become thin and wavy, and contain a large but diminishing number of starch grains.[25]

Epidermis *(e)*

Seeds *(s)*

Locula cavity *(lc)*
with jelly-like
parenchyma
around seeds

Vascula bundles *(vb)*

Outer wall of
pericarp *(p)*

Radial wall of
pericarp *(rp)*

Columella *(c)*
inner wall of
pericarp

Placental
tissue *(pl)*

A

(e)

(s)

(c)

(lc)

(vb)

(p)

(rp)

(pl)

B

FIGURE 3.   Transverse sections of mature tomato fruits showing the main anatomical features and the differences between (A) a bilocular structure favored in most modern varieties grown in northwestern Europe and in the more temperate parts of the world, and (B) a multilocular fruit, a feature of most varieties grown in warm climates enjoying good light conditions. (Copyright G.C.R.I.)

The appearance of the jelly-like material in the locular cavities provides an excellent criterion whereby fruit may be designated "mature" green,[26,27] and incipient ripening is often first seen as a pinkish tinge to this placental tissue.

The transformation of chloroplasts to chromoplasts has been studied during the development of normal and mutant tomatoes.[395,412] Initially, the chloroplasts lose starch and chlorophyll from the grana, followed by the production of osmiophilic globules and the formation of lycopene within a swollen granum compartment. Eventually lycopene

takes the form of elongated crystalloid structures. The rates of conversion of chloroplasts to chromoplasts in "nonripening" mutant material were much slower than normal, and minor differences in certain structural components were also detected.[412]

Fleshy fruits have been designated "climacteric" or "nonclimacteric" (see Reference 429 for a review). Climacteric fruit, including the tomato, show increased respiration when they ripen. In contrast to nonclimacteric fruit, they produce ethylene on exposure to low concentrations of this hydrocarbon, a phenomenon particularly marked in fruit at a stage of development immediately prior to the respiratory climacteric. A review of evidence relating the color of tomato fruit to changes in the respiration rate is available,[99] and the consensus of opinion is that respiration is at a maximum when the fruit are still somewhat underripe, most often coinciding with the assumption of yellow-orange color.

In most temperate countries, where the growing season is short and sunlight limits overall yield, the emphasis is towards the cultivation of varieties that are quick-maturing. These tend to be small-fruited types with few locules and uniform shape (Figure 3A). The anther cone fully encloses the stigma and style, thus enhancing the probability of self-pollination, especially in low light conditions. The bulk of the world's tomatoes are, however, grown in situations where for most of the year light is nonlimiting, and it is possible to grow the larger multilocular fruit (Figure 3B). The short trusses carry fewer but much larger fruit.

The backcross technique for introducing desirable characters into existing varieties has been widely used, and the tomato lends itself well to this method of breeding.[9,10,28] Pest and disease resistance, advantageous compositional characteristics, and resistance to physiological stress have all been transferred from primitive cultivars and related wild species.[10] The F_1 hybrid method for combining the attributes of two pure-breeding lines is now a well-tried technique in modern seed production. Most seed now used in protected cropping or intensive cultivation is of the hybrid type, largely produced by hand pollination at a cost of perhaps 20 times the parental material. The use of F_1 hybrid seed is increasing on a world scale.[10]

V. TOMATO PRODUCTION

In 1967, the tomato was the world's fourth most popular fruit, after grapes and citrus and pome fruits.[29] Since then,[30] its production has overtaken that of apples and pears, and even shaken off the challenge of the banana, whose total yield in the early 1970s surpassed that of the tomato, to take up third position. The most recent figures available are quoted in Table 2, and they emphasize the world-wide upsurge of interest in tomato growing that has occurred during the past decade.

The distribution of the tomato growing areas throughout the world is summarized in Table 3, and the trends in each continent are illustrated by examples of the situation in some of the major tomato-producing countries. The most rapid expansion is taking place in southern and eastern Europe, Russia (presumably southern!), Brazil, and a number of Asian countries. Some of the more traditional production areas in Europe and North America are obviously channeling their effort into yield improvements, as the area devoted to tomatoes is contracting. The proportion of total world production in 1979 contributed by each continent is shown in Table 4, together with the trends in yield since 1974. Not too much reliance should be placed on the percentage change, as the occasional bad harvest in an important area can alter the picture considerably.

Yield and total production figures for a number of European countries having a wide range of climates are quoted in Table 5, and are compared with typical values from North America. The data illustrate the broad spectrum of productivities, ranging from long-

Table 2
WORLD PRODUCTION OF TOMATOES IN 1974 AND 1979 COMPARED WITH OTHER WIDELY GROWN FRUITS

Commodity	Production in 1000s of tonnes in 1974	Production in 1000s of tonnes in 1979	Percentage change since 1974
Grapes[a]	61.553	67,597	+10
Citrus fruits	47.434	55,044	+16
Tomatoes	37.852	49,201	+30
Bananas	33.010	39,129	+19
Apples and pears	35,686	43,293	+21

[a] Estimates for some of the wine-growing countries are based on information available on the production of table grapes, raisins, and wines; see Yearbook 33, pages 6 and 7.

Data from F.A.O. Production Yearbook 29, Tables 58 and 79, and Yearbook 33, Tables 8, 43 and 61.[30]

Table 3
TOMATO PRODUCTION IN 1979 SHOWING TRENDS IN THE AREA GROWN AND IN YIELD FOR THE MAJOR PRODUCER COUNTRIES SINCE 1974

Region[a]	Area in 1000s of ha	Percentage change since 1974	Production in 1000s of tonnes	Percentage change since 1974
Europe	490	+4	13,871	+6
Greece	40[b]	+3	1,669[b]	+5
Italy	126	+8	4,294	+18
Romania	72[b]	+16	1,393[b]	+13
Spain	64	−22	2,050	−15
Asia	706	+73	11,251	+90
China	284[b]	+17[c]	3,930[b]	+44[c]
Japan	19[b]	+6	960[b]	+17
Turkey	108[d]	+35	3,136	+46
U.S.S.R.	395[b]	+75	6,400[b]	+68
North and Central America	314	−4	9,847	+7
U.S.	182[b]	−3	7,663	+5
Mexico	62	−20	1,082	−12
South America	135	+18	2,854	+29
Brazil	56	+22	1,500	+45
Africa	354	+27	4,769	+40
Egypt	139	+19	2,421	+40
Oceania	10	0	208	−15

[a] Constituent countries listed in F.A.O. Production Yearbook 33, Table 43.
[b] F.A.O. estimate.
[c] Increase since the 1969—1971 average, as given in F.A.O. Yearbook 33; the figures given in F.A.O. Yearbook 29, Table 58 for China during 1974 appear to be an underestimate.
[d] The F.A.O. regard this as an unofficial figure.

Data from F.A.O. Production Yearbook 29, Table 58 and Yearbook 33, Table 43.[30]

Table 5
YIELD AND TOTAL PRODUCTION OF TOMATOES IN EUROPE IN 1979 COMPARED WITH THAT IN NORTH AMERICA

Country	Yield		Production in 1000s of tonnes
	Tonnes per ha	Tons per acre	
Belgium-Luxembourg[a]	139.9	55.7	119[b]
Bulgaria	26.4	10.5	870[b]
France	27.5	10.9	825
Greece	41.8	16.6	1,669[b]
Hungary	27.8	11.1	500[b]
Italy	34.1	13.6	4,294
Netherlands[a]	146.3	58.2	395
Poland	5.2	2.1	164[b]
Portugal	28.4	11.3	685[c]
Romania	19.3	7.7	1,393[b]
Spain	32.0	12.7	2,050
United Kingdom[a]	139.0	55.3	139
Yugoslavia	11.8	4.7	455[b]
Europe as a whole	28.3	11.3	13,871
U.S.	42.1	16.8	7,663
North America as a whole	41.9	16.7	8,149

[a] Major part of the crop grown under glass or plastic, mostly heated.
[b] F.A.O. estimated figure.
[c] Unofficial figure quoted by the F.A.O.

Data from F.A.O. Production Yearbook 33, Table 43.[30]

VI. QUALITY AND INTERNATIONAL GRADING STANDARDS

The efficient grading of tomatoes for either the fresh market or for processing is an important aspect of fruit quality. Most schemes lay down limits governing size and shape — also freedom from damage, disorder, and disease — without any criteria for composition being involved. This has favored the selection of varieties that grade and travel well, but which are often poor in both major and minor flavor components. Avocados and dessert grapes have both been subject to minimum compositional requirements for many years, and it is high time similar obligations were implicit for tomato fruit offered for sale.

The U.S. Department of Agriculture publishes suggested standards for grades of fresh tomatoes[34] and statutory standards for processing tomatoes.[35,36] American guidelines for fresh fruit include size categories and color classifications for fruit of various stages of development.[37] California, however, has its own mandatory standards for fresh fruit,[38] and their provisions amplify some aspects of the general standards. The Organisation for Economic Co-operation and Development (OECD) also produces a standard concerning the marketing and quality control of tomatoes;[39] the original 1963 version was amended a few years ago,[40] and copious (sometimes poor) color illustrations added. The United Nations Economic Commission for Europe has its own slightly different

guidelines,[41] upon which are based the standards in force within the European Economic Community (EEC), such as those published by the Ministry of Agriculture, Fisheries, and Food in the U.K.[42]

In a number of countries, OECD standards have been adopted for export tomatoes, especially those destined for northwestern Europe. Most of the defects obvious in fruit beginning to ripen usually disappear by the time they are nearly fully ripe. Such fruit, rejected for export during grading, are marketed locally as they have a limited shelf life. Most countries insist on imported tomatoes being graded, which at worst provides a basis for trading and at best helps to ensure that imports are not inferior to home-grown produce. In Australia, legislation concerning tomato grading exists in New South Wales (NSW), Queensland, and Victoria; in NSW, tomatoes are sized into categories of less than 45 mm, 45 to 50 mm, and then in 10 mm steps to 90 mm, with a final size of more than 90 mm.

The OECD requirements demand that fruit be intact, sound, clean, and taint-free. In the "Extra" Class, the quality must be superior, with an appearance characteristic of the variety, the shape round or discoid, at worst only slightly ribbed, firm, and free from obvious defects. For Classes "I" and "II", relaxation of the guidelines for shape, firmness, and ripening defects are progressively allowed.[40] However, nowhere are warnings given pointing out that tomatoes picked prematurely will, when ripened, be lacking in quality compared with fruit left on the plant to ripen either partially or completely.[43]

An illustrated comparison between sizes of tomatoes, as defined by the U.S. and the EEC grading standards, has already been made.[44] Irregularity of shape is often associated with a multilocular structure of the fruit (see Figure 3B), which alters the ratio of pericarp to locular material and thus the relative proportions of the major taste constituents (see later). Small-fruited varieties have a higher acidity and a more regular shape than larger-fruited ones.[45] However, examination of partial correlations shows that if the fruit size is kept constant, the relation between fruit shape and acidity becomes nonsignificant. Nevertheless, a positive correlation between fruit size and incidence of ripening disorders has been found within a single variety.[46]

Perhaps second only to visual appearance in importance to both producers and consumers is the attribute of firmness. Soft fruit do not travel well and are often associated in the consumer's mind either with overripeness or with hollowness (also called "puffiness' or "boxiness"), which results from poor expansion of the locular contents leaving a gap between them and the pericarp. Such hollow fruit could, and from the consumer's viewpoint should, be removed during grading by making use of their tendency to float in water, in contrast to normal fruit which sink.[47,48]

Two reports[44,49] categorize some of the causes for which fruit are downgraded or rejected at the packing shed. The batches of fruit upon which the figures were based are in many ways not comparable; the U.K. sample would have had the very small and overripe fruit already removed before grading. However, Table 6 does illustrate the high proportion of fruit that are mechanically damaged in California, also the importance of "blotchy ripening" and "hard top" in tomatoes grown in the U.K. 20 years ago. Nowadays, most modern varieties being grown here produce a much more uniformly colored crop,[50] in part because they almost all contain an "even ripening" gene, which provides a measure of resistance to "hard top". We have been unable to find up-to-date information on the causes for rejecting fruit during grading in this country, but among the most common ripening disorders are severe forms of chimera and hollowness, blossom-end rot, ghost spotting (from *Botrytis*), and splitting. "Hard top" still remains a problem in nonresistant varieties. Specialized publications are available describing the major pathological[51] and physiological disorders.[52]

Table 6
MAJOR REASONS FOR DISCARDING TOMATOES DURING GRADING (PERCENT NUMBER OF FRUIT IN THE TOTAL PICK)

	Stage of development	
Defect[a]	Mature green	Partly ripe
U.S., 1972—1973[44]		
Undersized	25	8
Physical damage	21	25
Catfacing	10	14
Solar injury	10	16
Insect damage	7	5
Overripe	5	20
Blossom-end rot	5	1
Puffiness	4	1
Cracking	3	4
Other factors	10	6
U.K., 1959[49]		
Blotchy		38
Severe blotch ("waxy")		5
Hard top (perhaps equivalent to "solar injury")		33
Blotch and hard top together		4
Chimera or silvering		2
General pale top		10
Deep green shading around the calyx		2

a Descriptions of the ripening disorders are given in the publications by Barksdale et al.[51] and Hobson et al.[52]

VII. BASIC COMPOSITION AND DRY MATTER ANALYSIS

Numerous studies on the constituents normally found in tomato fruit have been made, and many nutritional tables comparing the composition of tomatoes with other fruits and vegetables are available.[53-55,57-61] One of the best ways of depicting the relative amounts of the various components is that devised by Stevens and published in 1974,[62] which we have modified and brought up to date in the light of recent work (Figure 4).

Although the dry matter of tomatoes can vary from below 5% to nearly double that figure,[63] for most modern varieties it lies between 5 and 7.5%. Of this dry matter, about half is in the form of reducing sugars, with slightly more fructose than glucose. Sucrose concentration rarely exceeds 0.1% on a fresh weight basis except in species of tomato other than *L. esculentum*.[64] A further quarter of the dry matter consists mainly of citric, malic and dicarboxylic amino acids, lipids, and most of the minerals. The composition of the remaining quarter, separable as alcohol-insoluble solids, we are less certain about. We have decided that the evidence favors protein as the most prevalent constituent, followed by pectic substances, cellulose, and hemicellulose in that order. The last three very probably have an intrinsic mineral content as well. The values we have selected are compromises, but ones we feel justified in putting forward as representative of a typical tomato.

Fresh tissue

5.0 – 7.5% Dry matter

Subsequent analysis of the dry matter

25% Fructose

22% Glucose

Ascorbic acid 0.5%

Pigments 0.4%

Volatiles 0.1%

Other amino acids, vitamins and polyphenols 1.0%

48% SUGARS

2%

1% Sucrose

27% A.I.S.

9% Citric acid

8% Protein

4% Malic acid

7% Pectic substances

2% Lipids

4% Hemicellulose

2% Dicarboxylic amino acids

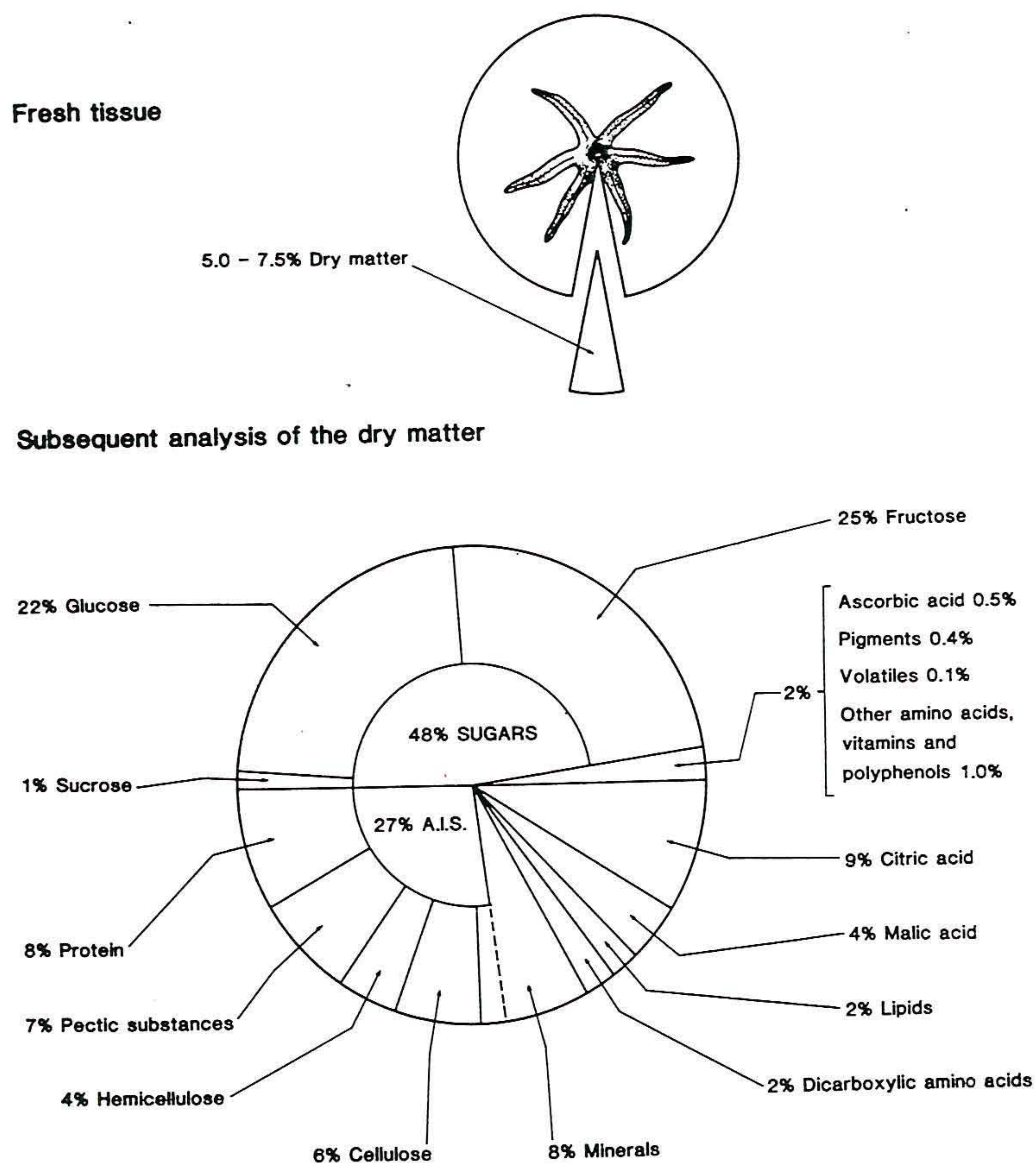6% Cellulose   8% Minerals

FIGURE 4.   Composition of tomato fruit in terms of dry matter in the fresh tissue, and the subsequent balance of constituents in the dry matter fraction. (Copyright G.C.R.I.)

Analytical data drawn from both general and specialized reference works are compared in Table 7. Apart from a few aberrant values, most figures are remarkably consistent, perhaps suggesting plagiarism! Much of the data has been verified many times, but it seems to us that a protein figure of between 0.95 and 1.1 g/100 g fresh tissue is based on the total N content of the alcohol-insoluble solids.[65] Rowan et al.,[66] however, showed that protein-N is only 35 to 50% of the total N; hence the protein figures generally quoted are almost certainly too high. We would also suggest that the 0.2 to 0.3% often given for the fat content is too high, and that 0.15% is a more realistic upper limit.

The range of values for some of the constituents listed in Table 7 are quoted in Table 8, and a few of the reasons for divergent values are indicated. For instance, the level of the dry matter depends to a considerable extent on season,[88] nutrition,[89] and environment,[68] while the concentration of a number of vitamins depends upon light levels. The uptake of many elements is a result of a complex series of interactions with environment, pH of the growing medium, and with the other elements present. While it is noticeable that the tomato has a fairly high content of fiber, vitamins A and C, and folic acid, with potassium and phosphate as the predominant cation and anion, respectively, Table 8 emphasizes that some of the constituents can vary enormously in their concentrations. Until there is legislation concerning the minimum compositional standards for tomatoes offered for sale, their contribution to human diet[10] will inevitably be less than it should be.

Table 7
BASIC ANALYTICAL DATA FOR RIPE TOMATO FRUIT (VALUES PER 100 g RAW EDIBLE PART)

Constituent	Year of publication and source of data							
	1963[53] and 1974[54]	1970[55]	1976[56]	1977[57]	1977[58]	1978[59]	1978[60]	1978[61]
Dry matter (g)	6.5	6.5		5.9	2.75		6	6.6
Total carbohydrates (g)	4.7	4.7		4	1.0	4.7	3	2.8
Protein (g)	1.1	1.1	0.96[a]	1		1.1	1	0.9
Fat (g)	0.2	0.2		0.3	0	0.2	—	Trace
Fiber (g)	0.5	0.5		0.6		0.5		1.5
Vitamin A, IUs (= 0.6 μg β-carotene)	900	900	1271[b]	1100	192	1.5×10^6 (sic)	1083	1000
β-carotene								(333—1667)
Vitamin B$_1$, thiamine (μg)	60	60	55[c]	60	40	60	50	60
Vitamin B$_2$, riboflavin (μg)	40	40	50[d]	40	40	40	20	40
Vitamin B$_3$, pantothenic acid (μg)		310			50	700		330
Vitamin B$_6$ complex (mg)	0.7	0.1		0.5		0.1	0.08	0.11
Nicotinic acid (niacin) (mg)		0.6	0.5		0.7	6.4		0.7
Folic acid (μg)		8			20			15 free, 28 total
Biotin (μg)		4			1.2			1.5
Vitamin C (mg)	23	23	16[e]	23	20	23	15	20 (10—30)
Vitamin E, α-tocopherol (mg)		0.27			0.3	0.04		1.2
Potassium (mg)	244	268	202[f]	230	290	244	300	290
Phosphorus (mg)	27	27	25	27	20	27	20	21
Calcium (mg)	13	13	9.7	11	15	13	10	13
Magnesium (mg)		11	11		10		10	11
Sodium (mg)	3	3	11	3	5	3		3
Iron (mg)	0.5	0.6	0.6	0.6	0.4	0.5	0.2	0.4
Aluminum (mg)			1.17					0.10
Boron (mg)		0.10	0.08					
Copper (mg)			0.09					
Lead (mg)			0.032					

Manganese (mg)	0.19	0.15	0.6	0.2
Zinc (mg)	51	0.09	20	51
Chlorine (mg)	11			11
Sulfur (mg)	0.5		16	14
Ash (g)	22		22	
Calories	22		15	

a Combination of Tables 10, 11, and 12.
b Tables 4, 5, and 6.
c Table 7.
d Table 8.
e Tables 1, 2, and 3.
f Potassium to zinc taken from Table 9 of Reference 56.

Table 8
CONCENTRATION RANGE OF CONSTITUENTS FOUND IN NORMAL RIPE TOMATO FRUIT PER 100 g FRESH TISSUE

Constituent	Normal range	Other examples
Dry matter (g)	4.71^{67}—8.30^{68}	Species other than *L. esculentum*, 8.99—11.86[69] and 3.4—16.8[70]; tomatoes with "waxy patch", 4.67^{71}
Vitamin A (IUs)	833—1667^{72}	"Yellow apricot", 67^{73}; *L. esculentum* × *L. hirsutum* backcross, 11250^{70}
Vitamin B$_1$ (μg)	16—80^{74}	
Vitamin B$_2$ (μg)	20^{74}—78^{56}	
Vitamin B$_3$ (μg)	280—340^{74}	James' results,[75] although low by modern standards, suggest that indoor tomatoes have a lower content than outdoor-grown
Vitamin B$_6$ (mg)	0.074—0.15^{74}	
Nicotinic acid (mg)	3.0—8.5^{74}	
Folic acid (μg)	7.4—8.6^{74}	
Vitamin C (mg)	8.4^{76}—59^{77}	*L. peruvianum*, 119^{70}
Potassium (mg)	92^{78}—376^{67}	Highly dependent on the level of K nutrition,[78,79] also on the truss position[79]
Phosphorus (mg)	7.7^{56}—53^{80}	
Calcium (mg)	4.0^{56}—21^{74}	Less than a value of 5 often leads to the appearance of blossom-end rot[81,82]
Magnesium (mg)	5.2^{83}—20.4^{56}	
Sodium (mg)	1.2^{84}—32.7^{56}	Highly dependent on the level of K nutrition[85]
Iron (mg)	0.35—0.95^{56}	
Aluminum (mg)	0.5—2.95^{56}	
Boron (mg)	0.04—0.13^{56}	
Copper (mg)	0.05—0.2^{56}	
Lead (mg)	0.02—0.05^{56}	
Manganese (mg)	0.04—0.3^{56}	
Zinc (mg)	0—0.25^{56}	
Chlorine (mg)	24—69^{74}	
Nitrate (mg)	1.3^{86}—30^{87}	Influenced by levels of P and N,[86] temperature and light levels[87]
Ash (g)	0.51—0.70^{84}	

VIII. SUGARS

After water, sugars form the next most important constituent of the tomato. They account for some 50% of the total dry matter of the whole fruit of commercially grown varieties, and form about 65% of the soluble solids in the expressed fruit juices of English varieties,[90] or 53% of the total solids content of American lines.[84] The free sugars are almost entirely reducing sugars, ripe fruit consisting of glucose and fructose in approximately equal amounts but usually with a preponderance of fructose.[91-96] Although traces of raffinose have been reported in an Indian variety[97] and of a ketoheptose in an American variety,[98] recent work has failed to detect these sugars in English cultivars.[95] The presence of sucrose has been reported in tomato varieties from various parts of the world, but seldom in amounts exceeding 0.1% of the fresh weight.[91-93,95] However, in the fruit of some species of *Lycopersicon* belonging to the subgenus *Eriopersicon,* sucrose is the dominant sugar and only small amounts of reducing sugars are present.[64] Myoinositol has also been detected in tomatoes at all stages of development, but amounts are very small (<0.02% fresh weight).[95] Such a finding is,

Table 9
CHANGES IN THE SUGAR CONTENT OF VARIOUS PARTS OF TOMATO FRUIT HARVESTED AT FIVE STAGES OF RIPENESS, EXPRESSED AS PERCENT FRESH WEIGHT

	Stage of ripeness					Significance P	Least significant difference P = 0.05
	Green	Green-yellow	Yellow-orange	Orange	Red		
Whole fruit[a]	2.69	3.07	3.16	3.23	3.27	<0.001	0.27
Locular contents[a]	2.15	2.58	2.74	2.72	2.79	<0.001	0.14
Walls[b]	2.87	3.13	3.28	3.22	3.55	<0.001	0.12

[a] Data from Reference 99.
[b] Data from Reference 102.

perhaps, not surprising in view of the probable ubiquity of this carbohydrate in living tissues.

Many investigators have studied the changes in sugar content that occur during ripening (see References 99 to 101 for early reviews). Several have concluded that the total sugar content increases progressively from the mature green to the red stage of ripeness (see Table 9). Exceptions to this generalization have been found, however, the most frequent finding being a decrease in sugar content as the fruit approaches full ripeness (see Reference 99). Nevertheless, it is generally agreed that the first appearance of yellow pigment in the walls is accompanied by a pronounced rise in sugar concentration. Similar changes can be found on analyzing whole fruit, locular juices, or outer locular (pericarp) walls, as is shown in Table 9. These are largely due to alterations in fructose content, as glucose concentrations do not vary significantly during this time, as is illustrated in Table 10.[95] Neither fructose nor glucose change significantly in concentration in either the locular contents or whole fruit during the color change from green-yellow to red, irrespective of whether the results are expressed on a percentage or on a "per fruit" basis.[95]

Davies and Kempton found that concentrations of both fructose and glucose were higher in the walls of tomatoes than in the locular juices.[95] Similarly, the pericarp tissue of seven American cultivars used in a study of genotypic variation in flavor always contained more glucose than did the locular tissue; fructose concentrations were similar in both parts of the fruit in all but one of the cultivars.[96]

Little attention has been paid to the changes that occur in immature fruit. The reducing sugar content of two tomato varieties grown either outdoors or in a glasshouse in Utah increased progressively throughout nine stages of development, ranging from young green fruit 12.5 mm in diameter to red ripe.[103,104] Davies and Kempton[95] noted that as immature fruit developed, there was a progressive increase in both glucose and fructose concentrations, with a particularly dramatic increase during the initial stages of cell enlargement (Table 11). The glucose/fructose ratio decreased rapidly as the fruit increased in size. A previous investigation[21] had indicated that the reducing sugars per cell of tomato fruit from fertilization to ripeness increased rapidly during this period, generally in line with the changes in cell volume. It is of interest in this connection that McCollum and Skok[105] found that when ^{14}C-glucose was applied to tomato leaves, the sugar moved most rapidly into developing green fruit. Translocation was more limited into mature green fruit, only to increase again with fruit at the turning stage. The labeled sugar was not, however, incorporated into ripe fruit.

Table 10
GLUCOSE AND FRUCTOSE IN THE OUTER LOCULAR WALLS AND LOCULAR JUICES OF TOMATO FRUIT AT FIVE STAGES OF RIPENESS, EXPRESSED AS PERCENT FRESH WEIGHT

	Stage of ripeness					Significance P	Least significant difference P = 0.05
	Green	Green-yellow	Yellow-orange	Orange	Red		
Glucose							
Walls	1.61	1.71	1.74	1.69	1.62	—	0.17
Locular contents	1.05	1.25	1.21	1.23	1.22	—	0.15
Fructose							
Walls	1.68	1.87	1.87	1.68	1.70	<0.01	0.12
Locular contents	1.26	1.55	1.56	1.59	1.60	<0.01	0.19

Data from Reference 95.

Table 11
GLUCOSE AND FRUCTOSE IN IMMATURE GREEN TOMATO FRUIT OF VARIOUS SIZES, EXPRESSED AS PERCENT FRESH WEIGHT

	Fruit diameter (mm)				Significance P	Least significant difference P = 0.05
	<12.5	12.5—18.5	18.5—25	25—31		
Glucose (G)	0.48	0.97	0.94	1.08	<0.001	0.24
Fructose (F)	0.23	0.59	0.68	0.81	<0.01	0.16
G/F ratio	1.83	1.65	1.38	1.33	<0.05	0.27

Data drawn from Reference 95 using G.C.R.I. variety J168.

It is probable that light has a more profound effect on sugar concentrations in the tomato than any other environmental factor. Winsor and Adams[106] showed that seasonal trends in the sugar content of glasshouse-grown tomatoes at the green-orange stage of ripeness were broadly similar to the pattern of solar radiation (Figure 5). Similar work with glasshouse fruit in Ohio[107] demonstrated a fall in sugar content from 3.5 to 2.8% with successive crops in November and December, and a rise from 2.9 to 3.5% (all fresh weight figures) with crops between late April and early June. A close correlation between sugar content and the hours of sunlight per day during the 6 weeks prior to harvest was also established. Further evidence for the influence of solar radiation on sugar content is provided by analyses of fruit imported into the U.K. from Spain (about 38° N) and the Canary Islands (about 28° N).[106] During April, such fruit contained 3.95 to 4.8 g/100 mℓ expressed sap and this is well beyond the range of values normally encountered in tomatoes grown in more northerly situations (cf. Figure 5 which gives the range of sugars for fruit grown at about 51° N). In work some years ago, Yamaguchi et al.[108] detected a steady decline in the sugar content of field-grown tomatoes during September and October which they attributed to a lack of foliage.
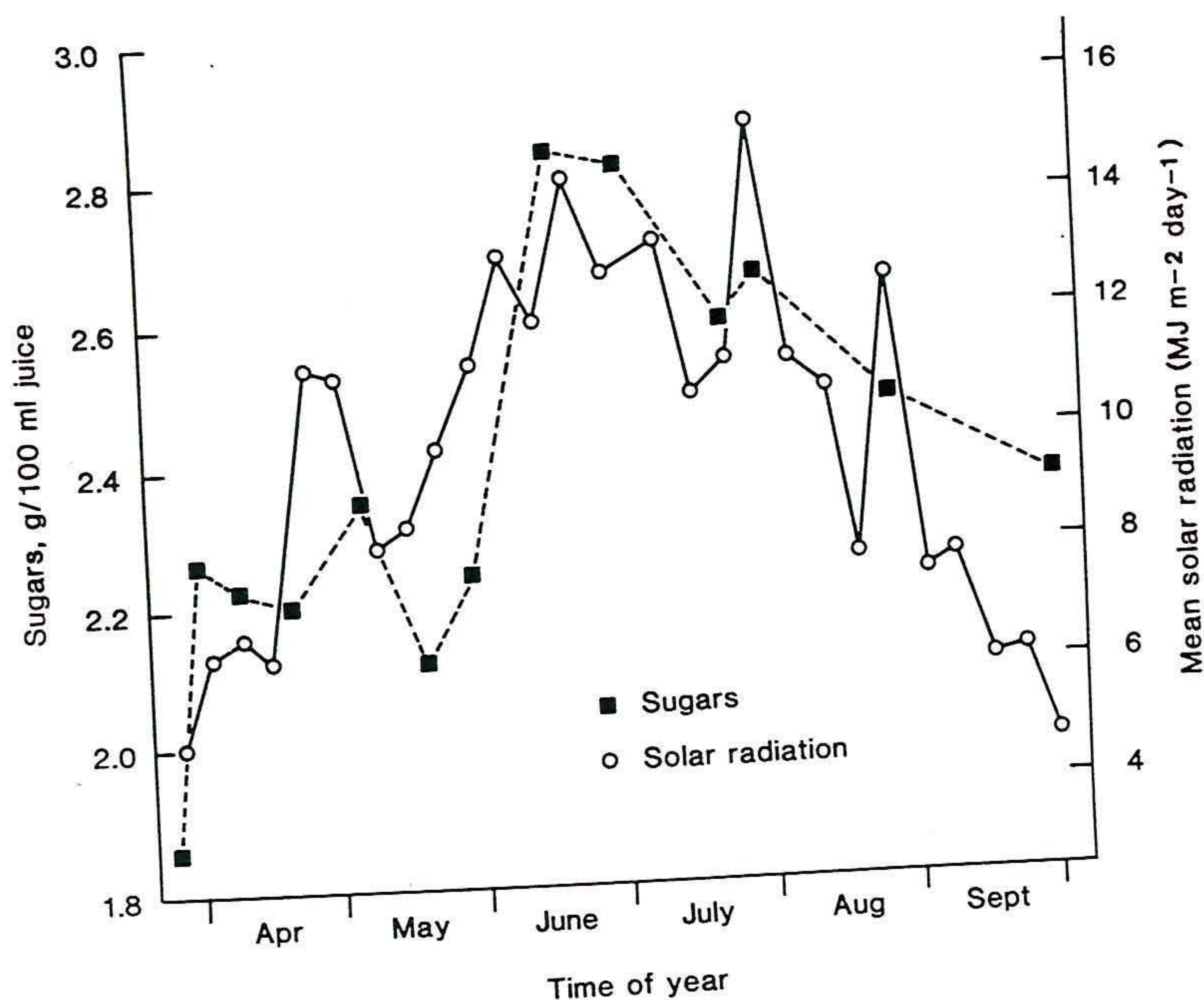
FIGURE 5.   Seasonal trends in the sugar content of the expressed sap of tomato fruit (cv. Grenadier), together with integrated data for solar radiation. (After Reference 106.)

Shading the plants has an adverse effect on sugar content. In one series of experiments with glasshouse tomatoes, heavy shading reduced the radiation level to about 20% of that reaching unshaded plants and led to a decrease of some 27% in the sugar in the fruit (Davies and Winsor[534]). Even the relatively light shading provided by the foliage has been reported to reduce the total sugar content by up to 13%,[109] and there were also marked differences in this constituent between the upper (exposed to sunlight) and lower (away from direct light) sectors of unshaded fruit but not when shaded. Details are given in Table 12, but whether differences in temperature or photosynthetic activity of the fruit affected the sugar levels is unknown.

As might be expected from a knowledge of source/sink relationships, the ratio of leaves to fruit on the plant affects the sugar content of the fruit. Thus a restriction of the number of leaves per truss decreases the sugar, while the retention of a side-shoot below a truss and allowing two leaves to expand fully has the opposite effect.[110] Similarly, limiting the number of fruit that are allowed to develop leads to increased sugar in those that remain. The phenomenon is particularly striking when expressed on a "per fruit" basis, as is demonstrated in Table 13. Such data suggest that excessive removal of healthy foliage as practiced by some growers can have a detrimental effect on fruit quality.

Significant differences in the sugar content of the fruit from different varieties grown under the same conditions have been reported from various parts of the world.[45,84,111] In a particularly extensive field trial carried out in the U.S. with 55 lines of diverse genetic backgrounds, the sugar content ranged from 1.66 to 3.99%.[84] In studies of glasshouse-grown fruit in the U.K., however, varietal differences in sugar levels were often small and within 0.5 g/100 mℓ expressed juice.[45] The results were not always consistent, and changes during the harvest period generally exceeded differences between varieties at any one time. Fruit of various species of *Lycopersicon* contain much higher concentrations of sugars than the average commercial variety.[112] Thus, some strains of *L. pimpinellifolium*

Table 12
SUGAR CONTENT OF THE UPPER AND LOWER QUARTER SECTORS OF SHADED AND UNSHADED TOMATOES, EXPRESSED IN g/100 g FRESH WEIGHT OF TISSUE

	Unshaded		Shaded	
Fruit sector	Reducing sugars	Total sugars	Reducing sugars	Total sugars
Upper	2.93	3.10	2.10	2.20
Lower	2.72	2.80	2.05	2.17

Data from Reference 109 using the variety Garden State.

Table 13
EFFECT OF LEAF AND FRUIT RESTRICTION ON THE REDUCING SUGAR CONTENT OF TOMATO FRUIT OF THE VARIETY POTENTATE HARVESTED IN MIDSUMMER IN THE U.K., EXPRESSED IN g/FRUIT

	Number of leaves retained per truss			
	All	Two	One	Means
Fruit restricted to eight in number	2.45	2.11	1.78	2.11
Fruit restricted to two in number	3.94	3.67	2.88	3.49 (L.S.D. at $P = 0.05$ is 0.17)
Means (L.S.D. at $P = 0.05$ is 0.14)	3.19	2.89	2.32	

have more than 6% sugars, while fruit of *L. chmielewskii* have a very high soluble solids content of about 10%,[113] which would imply a very high level of sugars. Detailed analyses do not appear to be available. In the U.S., much attention is now being paid to exploiting such characteristics by the development of tomatoes suitable for machine harvest while maintaining both a high sugar content and a high yield.[114] Unfortunately, there is often an inverse relation between yield and total solids content, due primarily to physiological limitations such as photosynthetic efficiency, sink-source relationships, and respiratory losses. Tomato genotypes differ considerably in their photosynthetic capabilities which are related to chlorophyll content. This, in turn, is related to ribulose 1,5-biphosphate carboxylase activity. High chlorophyll content can be readily selected for, but breeding for translocation efficiency is not so easy as this is relatively low in most cultivars whether of determinate or indeterminate habit. Furthermore, attempts to increase one component usually result in a decrease in some other constituent. Thus, a cross between

L. esculentum ("VF145") and *L. chmielewskii* produced a breeding line with fruit having a total solids content some 40% greater than that of the recurrent parent without loss of yield, size, or color, but the fruit were soft and tended to deteriorate rapidly.[113] More recently, a high-sugar breeding line has been developed from this high-solids line, and this has been crossed with three high-acid lines. Fruit of the resulting F_1 hybrids have been examined for flavor and various taste attributes, and compared with a standard cultivar "Cal Ace".[115] The hybrids were all rated superior in flavor to the standard cultivar, and all had sugar contents in excess of 5%. Despite their excellent flavor qualities, however, many of their other characteristics (unspecified) were unsuitable. Nonetheless, there do appear to be possibilities for the development of a tomato combining high sugar levels in the fruit with acceptable yield, harvesting, and marketing characteristics. Breeding programs to such an end are time-consuming, but we hope they will eventually be successful.

In general, nutrition has relatively little effect on the sugar content of tomato fruit from plants grown in soil or peat, but high nitrogen fertilization has an adverse effect.[85,116-118] This is probably only a reflection of the well-known tendency of nitrogen-deficient plants to accumulate carbohydrates.[119] Subsequent work has shown that tomatoes grown with nitrogen in the ammonium form have a higher sugar level than those fed exclusively on nitrate-nitrogen. Ammonium-nitrogen had an adverse effect on fruit yield.[120] The effects of minor element deficiencies or toxicities on the sugar content has been relatively neglected. Some micronutrients have been reported to decrease the sugars in fruit, notably boron deficiency[121] and toxicity,[122] and manganese deficiency.[121,123] On the other hand, zinc deficiency has been reported to have the opposite effect.[124]

The refractive index of tomato fruit sap is closely correlated with the total solids content ($r = >0.95$), and both these characteristics reflect the sugar status of the fruit.[125,126] The amount of variation commonly encountered, however, precludes the use of either refractive index or solids content for anything but a rough guide to the sugar level. No more than some 60 to 80% of the variation in the total solids figure of expressed tomato sap can be accounted for by the sugars. To some extent, the variability is due to the differing ratios of sugars to total solids which occur in different cultivars. Attempts have been made to improve the relation by including titratable acidity as meq/100 mℓ sap in a multiple regression equation.[127] Using data for some 600 samples covering a wide range of analytical values (1.2 to 4.3 g sugar/100 mℓ; 2.9 to 6.3 g/100mℓ total solids; acidity 5.8 to 13.6 meq/100 mℓ), the following equation was obtained:

$$\text{Sugars} = -0.26 + 0.91 \text{ (total solids)} - 0.124 \text{ (acidity)}$$

While such an equation is more precise than a simple linear regression relating total solids and sugar levels, it still accounted for only 86% of the variation. Other aspects of fruit composition that should be taken into account in order to improve the accuracy of the prediction still further are, at present, obscure. Possible candidates include the pectic substances, but their determination is relatively complex and time-consuming. The advent of high pressure liquid chromatography (HPLC) now makes the analysis of sugars a much more rapid procedure, but it is, nonetheless, expensive. The concept of the indirect determination of sugars by the use of refractive index and titratable acidity is thus still attractive for field use or for quality control in underdeveloped countries without elaborate laboratory facilities.

From the foregoing, it is apparent that some aspects of the sugar content of tomatoes have been extensively investigated (the effects of storage and of introducing mutant genes are described in other sections), but other areas are relatively little explored. Thus, apart

Table 14
SUGARS IN EXPRESSED SAP FROM TOMATO FRUIT OF THE VARIETY POTENTATE OF VARYING VISUAL QUALITY (g/100 mℓ)

Appearance	Reducing sugar content
Evenly ripened, regularly shaped	3.15
Evenly ripened, slightly irregular in shape	3.07
Evenly ripened, highly irregular in shape	3.08
Upper half of fruit relatively pale in color	2.66
Mild blotchy ripening	2.68
Severe blotchy ripening (known as "waxy")	2.09
Deep green shading around the calyx (not to be confused with "hard top" where the inner tissue is hard or immature)	3.36

Data adapted from Reference 125.

from blotchy ripened fruit, the walls of which are characterized by a particularly low sugar content (for a review, see Reference 128), practically no such data is available for tomatoes affected by any of the other commoner ripening disorders. What little information is available is summarized in Table 14. Although not usually regarded as top-grade fruit, tomatoes with deep-green shading around the calyx appear to be of better quality than evenly-ripened fruit. Data for "hollow" (also known as "boxy" or "puffy") fruit shows that their outer locular walls contained less sugar than those of normal fruit, but the difference was not significant.[129]

Other factors whose effect on the sugar content of tomatoes are inadequately documented include watering[130,131] and temperature levels,[131] while the effects of parthenocarpy and growth regulators have received little attention.

For the most part, carbohydrate metabolism in the tomato has been studied in detached fruit, and brief reviews may be found elsewhere.[1,132] The distribution of acid invertase in the fruit and leaves of both cultivated and wild species of *Lycopersicon* and its relation to sucrose content has been investigated by Manning and Maw.[133]

IX. ASCORBIC ACID (VITAMIN C)

In an extensive review of vitamin C in tomatoes published during World War II, Hamner and Maynard[76] remarked on the many contradictions in the literature. Similar comments are still appearing in more recent papers,[134-136] and of all the aspects of tomato composition, none has been more popular or controversial than the ascorbic acid content. Much work was carried out between 1930 and 1955, but recent investigators[134,136] have set out to clarify the previous confusion. However, perhaps more questions are raised by their work than are answered.

The extensive literature on vitamin C is, no doubt, a reflection of its importance in human nutrition and the contribution that the tomato can make to it.[137] It has been estimated that tomato production in the U.S. could provide about one third of the recommended daily dietary allowance (RDA) for Americans.[138] The actual contribution to the vitamin C supply is considerably lower than this (12.2% in 1972), but, nevertheless,

only oranges (20.4%) and potatoes (19.7%) contribute more to the American diet.[139] A very similar situation obtains in the U.K., where in 1977 fresh tomatoes contributed 5.9% of the vitamin C content of household food consumption, a value only exceeded by potatoes (25.5%), oranges (9.3%), Brussels sprouts, cabbage and cauliflower combined (7.9%), and liquid milk (7.6%).[140]

In plant tissues, ascorbic acid is present principally in the reduced form (RAA).

L-ascorbic acid
(RAA)   L-dehydroascorbic acid   2,3-dioxo-L-gulonic acid
               (DHA)   (DGA)
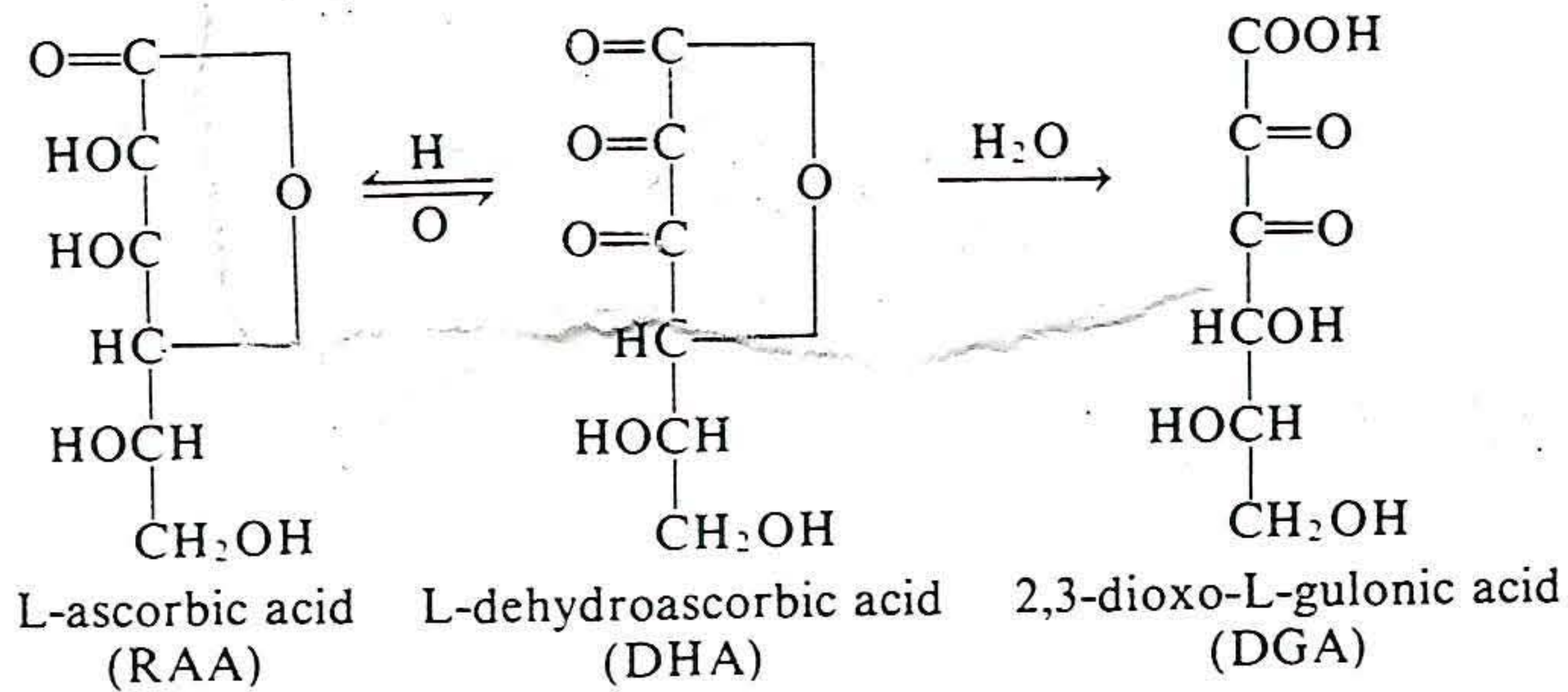
Its primary oxidation product, dehydroascorbic acid (DHA), is relatively unstable, and there is considerable evidence that in plant tissues it is readily interconvertible with the reduced form.[141] In some circumstances, DHA can be irreversibly converted to 2,3-dioxo-L-gulonic acid (DGA) by the opening of the lactone ring. Both RAA and DHA possess antiscorbutic properties since the latter is readily reduced to the former in the animal body; DGA has no such activity.[142]

Most vitamin C assays employ redox indicators such as 2,6-dichlorophenol-indophenol (see, e.g., Reference 143). Such methods are reliable only if the antiscorbutic substances present are exclusively ascorbic acid and other reducing substances do not interfere, conditions that are difficult to ensure. An alternative analytical method using 2,4-dinitrophenylhydrazine (DNPH)[144] does not differentiate between DHA and DGA, both of which react with DNPH to give the same derivative. A refinement of this procedure,[145] however, allows RAA, DHA, and DGA to be determined in the same tissue extract, but this method, as will be discussed below, has seldom been applied to tomato fruit. Hughes[146] has shown that DHA is rapidly reduced by homocysteine above pH 6.8, and the RAA so formed can be estimated by indophenol dye in the usual way. Despite the comparative simplicity of this procedure, it has been little used in studies on fruits.

The range of values for the reduced ascorbic acid content of tomatoes of from 10 to 30 mg/100 g fresh tissue already quoted (see Table 7) compares well with those from other parts of the world given in Table 15. Figures for vitamin C in fruit of the cultivated tomato are remarkably uniform considering the differing environments and cultivars, and the long period of over 40 years covered by the data. There is some indication that the ascorbic acid content of tomatoes has increased slightly since the 1950s,[155] but the hopes of the previous decade for breeding varieties with high vitamin C contents do not appear, with one or two exceptions, to have been fulfilled. Nowadays, vitamin C content is considered among many other factors when new cultivars are being developed. There is still no guarantee that people deficient in vitamin C would ever consume such cultivars high in vitamin C even after they had been bred and grown, and the fruit marketed.

Because of the many conflicting results that have been obtained, it is difficult to draw general conclusions concerning the effects of various inherent and environmental factors on the reduced ascorbic acid content of tomatoes. We have accordingly listed the principal sources of information in Table 16. The general reviews cited in this table discuss to a greater or lesser extent the merits of the various contradictory results that have been obtained.

Table 15
REDUCED ASCORBIC ACID CONTENT, AS mg/100 g
FRESH WEIGHT, OF RIPE TOMATO FRUIT GROWN IN
VARIOUS PARTS OF THE WORLD.

Country	Species	Field (F) or glasshouse (G) grown	Number of samples	Range	Ref.
		Subgenus *Eriopersicon*			
Poland	*L. minutum*	G	—	31—47	147
U.S.	*L. peruvianum*	F	21	48—78	148
U.S.	*L. peruvianum*	F	18	39—119	70
Hawaii	*L. peruvianum*	—	—	56—110	149
		Subgenus *Eulycopersicon*			
Czechoslovakia	*L. pimpinellifolium*	G	1	70	150
U.S.	*L. pimpinellifolium*	F	15	35—73	148
U.S.	*L. pimpinellifolium* *L. esculentum*	F	30	40—87	70
Australia	Commercial varieties	F	18	23—43	151
Canary Islands	Retail produce in U.K.	F(?)	—	7—31	152
Germany	Commercial varieties	G	20	15—45	153
Germany	Commercial varieties	G		20—30	194
Germany	Commercial varieties	F		30—40	194
Israel	Commercial varieties	F	1	27—32	154
Japan	Commercial varieties	—	—	10—12	202
U.S. (Mass.)	Commercial varieties	F	98	13—44	77
U.S. (Fla.)	Commercial varieties	F	41	11—21	155
U.S. (Mich.)	Commercial varieties	F	55	11—24	56
U.K.	Commercial varieties	G	8	11—15	156
U.K.	Commercial varieties	F	8	20—27	156
U.K.	Commercial varieties	G	8	21—26	157
U.K.	Commercial varieties	F	6	11—42	158
U.K.	Retail produce	G(?)	—	12—22	159

A great deal of information on the reduced ascorbic acid content of tomatoes has been based on the tacit assumption that this is a complete measure of the vitamin C content. Mapson[141] considered that the cell normally maintains most of its ascorbic acid in the reduced state, and DHA seldom exceeds 5% of the total ascorbic acid in fresh tissue. These conclusions have been assumed to hold for the tomato until recently, and even now only limited data is available concerning DHA concentrations in the fruit (see Table 17). An analytical method used some years ago by Baker and Parkinson[158] measured DHA as ascorbic acid after its reduction with hydrogen sulfide. The excess reductant was removed with carbon dioxide, a procedure that may not go to completion. In more recent methods involving the use of DNPH, any DGA present would have been estimated together with the DHA.[144,145] We have only come across one report on the DGA content in fresh tomato fruit,[203] and the sample chosen was of particularly poor quality, as the reduced ascorbic acid level was only 5.75 mg/100 g fresh weight! The DGA concentration was 0.6 mg/100 g fresh weight, which was dismissed as negligible by the authors. Nevertheless, it accounted for some 7% of the total, while DHA accounted for a further 23% (see Table 17).

Table 16
SOME SOURCES OF INFORMATION CONCERNING THE REDUCED ASCORBIC ACID CONTENT OF TOMATO FRUIT IN RELATION TO VARIOUS INHERENT AND ENVIRONMENTAL FACTORS

	Ref.
General reviews	1, 3, 76, 160, 161
Cultivar	56, 134, 151, 155—158, 160, 162, 165, 176, 179, 180, 195, 201
Stage of ripeness	77, 103, 104, 108, 134, 135, 158, 160, 161, 166—171, 180, 191, 193, 195, 207
Fruit size	77, 151, 163, 172, 173, 185, 187, 192, 193
Truss position	169, 173, 176, 179, 192—194
Mineral nutrition	161, 164, 174, 178, 195—199
Light	109, 156, 161, 172, 173, 175, 200
Season	157, 161, 164, 173, 179, 181, 192
Indoor vs. outdoor culture	103, 104, 158, 190, 192, 194, 195
Distribution within fruit	109, 176, 179, 185
Storage	77, 135, 136, 138, 177, 182—184, 188, 207
Ethylene effects	135, 180, 189
Growth regulators	186

From the available data, it would seem that of the total ascorbic acid in ripe tomatoes, as much as 20% can be present as DHA and/or DGA, while in mature green fruit the proportion can be as high as 80%. Differences in the total ascorbic acid content between mature green and ripe fruit are, however, relatively small and probably within the limits of experimental error. In other studies[535] using Hughes's method,[146] DHA was detected in "quarter ripe" tomatoes, but not in either mature green or red-ripe fruit.

The whole question of ascorbic acid in tomato fruit merits further research, with particular attention being paid both to the specificity and precision of the analytical methods and to the possibility of oxidative destruction, both chemical and enzymic, of ascorbic acid during its extraction from the tissue. The recent development of highly specific fluorometric procedures[204,205] for vitamin C assay, one of which is now an official AOAC method,[206] holds considerable promise. It is only by adopting sound analytical methods, coupled with an awareness of the ephemeral nature of vitamin C, that some of the anomalies concerning various genetic, physiological, and cultural effects on its concentration in tomatoes will be cleared up.

X. ORGANIC ACIDS

As one of the major taste components, the acids of the tomato have attracted considerable attention for many years, and the presence of citric and malic acids was in fact, first reported soon after the turn of the century.[208] However, detailed research into

Table 17
TOTAL ASCORBIC ACID, DEHYDROASCORBIC AND (DHA), AND 2,3-DIOXO-L-GULONIC ACID (DGA) IN TOMATO FRUIT AS mg/100 g FRESH WEIGHT

	Total ascorbic acid[a]	DHA	DHA plus DGA	DGA	Percentage of total		Ref.
					DHA	DGA	
Red-ripe	8.25	1.9		0.6	23	7	203
Range for six varieties at the red stage	24—27[b]	2—5			8—20		158
Range for eight varieties at the							
Mature green stage	13—24		4—13		27—79		134
Red stage	14—23	0—3			0—17		
"Fireball" X Cornell 54-149 at the							
Mature green stage	17.2		13.1		76		135
Red stage	18.6		2.4		13		
"Fireball" X Cornell 54-149 containing the *rin rin* gene at the							
Mature green stage	16.2		11.2		69		
Yellow stage	18.0		7.9		44		

[a] The values in this column may or may not include DGA since the analytical methods employed did not distinguish between DHA and DGA.
[b] Sum of RAA and DHA only.

the individual acids of the fruit only occurred after World War II. Previously we have surveyed the literature up to 1970 in some depth,[1] and more recent supplementary information may be found in the review by Herrmann.[3] A summary of the available data on the concentration ranges of the individual acids is given in Table 18. Values are most commonly expressed as milliequivalents per unit fresh weight or per unit of juice volume, but results on a percentage basis or as molarities are not infrequently found. To facilitate comparison, we have recalculated published values in terms of milligrams acid per 100 g fresh weight or, where appropriate, milligrams per liter of juice. A factor to convert milligrams to milliequivalents for each acid is also included in the table.

There is evidence for the operation of the Krebs (tricarboxylic acid) cycle in tomato fruit,[231,232] and the majority of the acids in the cycle have been reported to be present, but the observations of different workers do not always agree. Although, in certain instances, the masking effects of the major acids, malic and citric, make positive identification of the minor constituents difficult, some of the claims are still open to question. Lactic acid may well be an artifact, resulting either from the action of microorganisms or, perhaps, from reaction with the ion exchange resins, as under certain conditions sugars may be transformed into organic acids. It has also been suggested that succinic acid could have arisen from the action of molds.[233] A detailed study of the acids from English glasshouse-grown tomatoes using a gradient-elution technique failed to show any trace of acids such as aconitic, fumaric, or succinic,[224] even though the threshold of detection (about 2.5 mg per 100 g tissue) is well below the values quoted in Table 18. Similarly, later work by Stevens and Long[234] on American field-grown tomatoes using a combination of ion exchange and gas-liquid chromatographic procedures also failed to detect any

Table 18
ORGANIC ACIDS REPORTED AS PRESENT IN TOMATO FRUIT

Compound	Concentration		Factor to convert mg to meq	Ref.
	mg/100g fresh weight[a]	mg/ℓ juice		
Aliphatic Monocarboxylic Acids				
Acetic	9—17 (locular contents); 11—26 (walls)	30—100	0.0167	212, 214, 215, 219
Formic	(+)—18 (locular contents); (+)—16 (walls)		0.0217	209—213
Lactic	(+)—32 (locular contents); (+)—12 (walls)	123	0.0111	209, 210, 213—215
Mevalonic	0.3—0.4 (whole fruit)		0.0083	216
Pyruvic	0.12—0.26 (whole fruit)		0.0114	217, 218
Aliphatic Di- and Tricarboxylic Acids				
trans-Aconitic	(+)—16 (locular contents); (+)—48 (walls)		0.0115	92, 209
Citric	135—675 (whole fruit); 634—1560 (locular contents); 218—770 (walls)	1920—4736	0.0156	78, 84, 96, 210, 217, 224—226
Dihydroxy-tartaric		5—7	0.0110	218
Fumaric	23—46 (whole fruit)		0.0172	217
Malic	21—225 (whole fruit); 30—412 (locular contents); 40—220 (walls)	399—2061	0.0149	78, 84, 96, 210, 217, 224—226
Malonic	(+)—112 (whole fruit)		0.0192	222, 223
Oxalacetic	18—29 (whole fruit)		0.0151	217
Oxalic	(+)—90 (whole fruit)		0.0222	212, 219, 220
2-Oxoglutaric		13—15	0.0137	218
Succinic	(+)—35 (whole fruit)	35	0.0169	213, 215, 219, 221, 222
Tartaric	(+)—110 (whole fruit)		0.0133	219
Sugar Acids				
Galacturonic	(+)—42 (whole fruit)		0.0050	92, 210, 227—230
Alicyclic Monocarboxylic Acids				
Quinic	8 (whole fruit)		0.0052	221, 222

[a] (+) Represents trace amounts.

nonvolatile organic acids other than citric, malic, galacturonic, and pyrrolidonecarboxylic (PCA). This last acid, not included in Table 18, has often been reported to be present in tomato fruit, but it is an artifact and does not occur naturally.[78,210,211,214,235] PCA can be produced from either glutamine or glutamic acid, but under normal

Table 19
MALIC AND CITRIC ACID CONCENTRATIONS, AS mg/100 g FRESH TISSUE, IN WHOLE TOMATO FRUIT, OUTER WALLS OF THE LOCULES, AND IN THE LOCULAR JUICES SURROUNDING THE SEEDS HARVESTED AT EACH OF AT FIVE STAGES OF RIPENESS (cv. MONEYMAKER)

Tissue	Stage of ripeness					Significance P	L.S.D. between means $P = 0.05$
	Mature green	Green-yellow	Yellow-orange	Orange	Red		
Whole fruit						<0.01	54
Malic acid (M)	246	212	168	141	111	—	57
Citric acid (C)	187	231	215	195	197	<0.05	0.32
M/C ratio	1.29	0.90	0.78	0.69	0.56		
Outer locular walls						<0.05	48
Malic acid	222	175	167	143	163	—	58
Citric acid	220	255	251	205	252	<0.05	0.14
M/C ratio	1.01	0.69	0.67	0.70	0.65		
Locular juices						<0.01	54
Malic acid	415	359	298	247	239	—	131
Citric acid	678	684	652	573	680	<0.05	0.13
M/C ratio	0.61	0.52	0.46	0.43	0.35		

Note: Each value in the body of the table is the mean of three determinations except in the case of the locular juices where only two samples were analyzed.

conditions of either processing or alcohol extraction of the tissue, it is formed exclusively from glutamine.[78,235]

In common with the majority of fruits, the most abundant acids in ripe tomatoes are citric and malic,[78,209,212,226,236,237] and of recent years interest has tended to center almost exclusively on these components. In immature green fruit, the predominant acid is malic,[238,239] while citric forms only about 25% of the total acidity.[238] With increasing maturity, citric acid concentrations rise to a peak as the fruit just begins to ripen (Table 19) or slightly later in development.[224] In ripe fruit, citric acid accounts for between 45 and 66% of the total acidity of English cultivars,[240] while a range of between 40 and 90% has been quoted for American cultivars.[84] During ripening, malic acid concentrations decline rapidly in whole fruit and in outer fruit walls, and even more rapidly in the locular juices (see Table 19 and Reference 224). As a result of their different rates of change during ripening, the malic to citric acid ratio decreases rapidly.[78,212,224] Tracer studies with ^{14}C-labeled citric and malic acids have shown that in the ripe fruit there appears to be a more active turnover of malic than of citric acid.[241] Changes in the titratable acidity of the tomato have been attributed to changes in citric acid alone,[242] or to changes in both citric and malic acids.[78]

It is well established that tomato varieties can vary markedly in acidity,[45,92,101] and much of this intercultivar variation is accounted for by differences in the citric and malic acid contents. The malic to citric acid ratio is, in fact, considered to be a varietal attribute.[240] An examination of the acids of five distinct morphological types of tomato fruit has revealed significant differences in their content of malic acid, but not citric acid.[226] Further information has become available in the last decade regarding the heritable basis for variation in acidity. In earlier inheritance studies where titratable acidity or pH was used as a criterion, it was concluded that acidity was under monofactorial control,[243] but breeding studies have indicated polygenic control of

acidity.[244,245] Subsequent examination of the inheritance of malate and citrate suggested that they were independently inherited,[234,237] and there may be genes controlling the relative distribution of these acids in the fruit.[96] Malate appears to be simply inherited, with dominance for low concentrations and with more than two alleles involved,[234] and high concentrations of the acid also seem to be controlled by more than one factor.[237]

Several investigators have made extensive studies of the relation between the acidity of tomato fruit and other quality attributes.[78,84,115,226,249,250] Titratable acidity has invariably been found to be significantly correlated with the potassium or total anion contents,[78,84,85,226] but not so closely as the combined acidity.[78,85] Citric, but not malic, acid and the titratable acidity are also closely correlated. Titratable acidity and pH might be expected to be closely associated, but poor correlations have been reported by several workers.[245,251,252] Stevens[84] has pointed out that when the malic to citric acid ratio of a population varies widely, the differing dissociation constants could explain such a poor relationship.

Acid concentrations and pH in the tomato are also important in processing, and recently there has been considerable public anxiety in the U.S. concerning the potential health hazard to consumers of home-canned tomatoes. This topic has been discussed and reviewed in some detail elsewhere,[252-255] and will not be reiterated here.

Many factors have been reported to affect the pH of tomatoes, including *inter alia* variety[134,211,245,254,255] (but not all authors agree[92]), stage of ripeness with the pH increasing with maturity[108,211,251,254,255] (but the reverse has been reported in both whole fruit[134,167] and walls[102]), location,[229,252] time of year,[101,251] incidence of decay and bruising,[254] and ripening disorders.[67,71] The pH of the locular contents is invariably lower than that of the pericarp.[134]

A few years ago, Sapers et al.[252] sorted and collated a vast amount of pH data for American cultivars. The overall range of pH encountered for different tomato types was wide (3.9 to 4.9), with light-colored and small cultivars tending to have the lower values, while those for "square", pear-shaped, and elongated cultivars developed for processing were somewhat higher. The pH of "standard" cultivars, however, was confined to between 4.0 and 4.7.

Much of the work on the pH of the tomato serves to emphasize the extreme variability of this property, a conclusion typified by one investigation[251] in which differences in pH between two fruits on the same plant were often as great or greater than between fruits of different plants.

In contrast to pH, results concerning the effects of various factors on the titratable acidity of the tomato are generally consistent. Much of the data was summarized in 1970.[1] Since then, relatively little fresh information has come to light. However, there has been an increasing recognition of the importance of acidity in tomato fruit flavor, and several contributions (see, e.g., References 96, 115, and 256) have explored this aspect.

As with the sugars (*vide supra*), there is comparatively little data available on the effect on the acidity of tomato fruit of the commoner ripening disorders, apart from "blotchy" ripening.[128,257] Results obtained over 20 years ago with the cv. Potentate suggest[125] that low acidity is a characteristic of most fruit of poor visual quality.

XI. PHENOLIC COMPOUNDS

Until 1970, few analyses of the phenolic constituents of the tomato had been reported,[1] but much information has accumulated since then, mainly as a result of the efforts of Herrmann and co-workers[3,258-260] in Germany, and Fleuriet and Macheix[261-263] in France. The available quantitative data are summarized in Table 20.

Although flavanols are relatively abundant in tomato foliage (for a review, see

Table 20
PHENOLIC COMPOUNDS IN TOMATO FRUIT AS μg/g FRESH WEIGHT

Compounds	Concentration	Part of fruit	Stage of development	Ref.
Quercetin glycosides[a]	12—24	Whole	Immature green	258
	3—7	Whole	Red	
Kaempferol glycosides[a]	0.8—1.9	Whole	Immature green	258
	0.2—0.8	Whole	Red	
Naringenin	8—42	Whole	Red	259,265
	1.3	Flesh	Breaker	265
	0.8	Flesh	Red	
	1.1	Skin	Mature green	265
	64	Skin	Red	
Rutin	<10—15	Whole	Red	3
Chlorogenic acid	14—41	Whole	Green	265
	13—38	Whole	Red	
	300—900[b]	Whole	Immature green	262
	<200[b]	Whole	Red	
	221	"Pulp"	Green	267
	56	Flesh	Green	
	13	Whole	Unripe	260
	97	Whole	Red	
Caffeic acid[a]	76	"Pulp"	Green	267
	38	Flesh	Green	
	42	Flesh	Half-ripe	265
	29	Flesh	Ripe	
	65	Skin	Breaker	265
	56	Skin	Ripe	
p-Coumaric acid[a]	2	Whole	Green	260
	16	Whole	Red	
Ferulic acid[a]	1	Whole	Green	260
	7	Whole	Red	
Sinapic acid[a]	<0.5	Whole	Green	260
	2	Whole	Red	
Vanillic acid[a]	Trace	Whole	Green	260
	1	Whole	Red	
Salicylic acid[a]	Trace	Whole	Green	260
	1	Whole	Red	

[a] Calculated as the aglycone.

[b] *Lycopersicon esculentum* var. *cerasiforme*.

Reference 258), the fruit contain only very small amounts confined almost entirely to the skin. Rutin (quercetin-3-rutinoside) is present in trace amounts (15 μg/g fresh weight[3]), and the presence of kaempferol-3-rutinoside, quercetin-3-glucoside, and some tri-glycerides have been reported.[3] In general, flavanol concentrations appear to decline as the tomato ripens, while field-grown fruit contain more quercetin and kaempferol glyco-sides than do those grown under glass.[3] Although some investigators have only detected the flavanone naringenin (4',5,7-trihydroxyflavanone) in the skin,[259,264] low concentra-tions (<1.5 μg/g fresh weight) have been reported to occur in the flesh.[265] On the other hand, Fleuriet[262] could not detect naringenin in the fruit of *L. esculentum* var. *cerasiforme*. Wardale[265] observed that during ripening, naringenin increased rapidly in the skin, but little or no changes were noted in the flesh. In addition, it was shown that during the climacteric respiration rise, ethylene production was mainly confined to the skin. It was

also shown that in the in vitro synthesis of ethylene from 4-methylmercapto-2-oxobutyric acid in the presence of peroxidase, naringenin and p-coumaric acid were the only two phenolic compounds present in extracts of tomato fruit that were capable of stimulating the reaction.[265] This system of ethylene production is not thought to be important in vivo[448,449] where the main mechanism involves S-adenosylmethionine. Other work has shown that mechanical injury of preclimacteric "cherry" tomatoes hastened ripening, and was accompanied by the production of derivatives of p-coumaric acid, resulting in a change in the balance of mono- and o-di-hydric phenols.[261] It would appear possible that the balance of naringenin and caffeic or chlorogenic acids could regulate ethylene synthesis in the tomato.

Of the other phenolic compounds in the tomato, hydroxycinnamic acids, particularly caffeic acid and its derivatives, occupy an important position. Thus, chlorogenic acid is present in amounts approaching 1000 μg/g fresh weight in young fruit of L. esculentum var. cerasiforme,[262] but as the fruit develops and ripens, concentrations fall rapidly. In ripe fruit of commercial varieties, only small amounts ($>$40 μg/g fresh weight) of chlorogenic acid are found.[260,265] Nevertheless, between 50 and 75% of the total phenols found in mature green fruit (cv. Eurocross BB) were shown to be accounted for by chlorogenic acid, but the proportion fell with ripening because of a sharp increase in other phenolic compounds.[265]

Although caffeic, ferulic, and p-coumaric acids were reported to be present as free acids in the outer walls of tomato fruit,[266] other investigators have detected them in combined form only.[260,265] Small amounts of sinapic acid have also been found, together with traces of two hydroxybenzoic acids, vanillic and salicylic,[260] while Fleuriet[262] identified 1-p-coumarylglucose and 1-ferulylglucose in fruit of L. esculentum var. cerasiforme.

Some ripening disorders of tomato fruit have been associated with abnormal phenolic content. Whereas "blotchy" fruit, in general, contained lower levels of the main phenolic acids than evenly ripened fruit,[266] tomato tissue affected by blossom-end rot contained significantly more chlorogenic and caffeic acids than normal healthy tissue.[267]

XII. AMINO ACIDS

Early studies of the amino acid composition of tomatoes were handicapped by the relatively high concentrations of some components which masked the detection of less abundant constituents. Thus, in some pioneering work using paper chromatography or simple ion exchange techniques, less than 10 amino acids were identified,[268-270] whereas other investigators detected 15 or 16, most of which were roughly quantified.[209,218,271] Subsequently, 18 amino acids plus asparagine, glutamine, and ammonia were detected by thin-layer chromatography in glasshouse tomatoes,[272] and similar identifications were made in tomato juice[215] and paste.[273,274] The introduction of increasingly sophisticated ion exchange techniques has facilitated assays of both the minor and major amino acids; 31 and 27 ninhydrin-positive compounds have been reported in processed tomato juice[275] and paste,[276] respectively, together with quantitative data for some 20 of them in each case. The predominant amino acids of the tomato are glutamic, γ-aminobutyric, and aspartic acids, while amides such as glutamine and asparagine are also abundant.[271,275-280]

Data on the amino acid content of tomato fruit are remarkably variable, and those expressed on a fresh weight basis are comparatively rare. The various results have been expressed in so many different ways that it is not easy to find a common basis. A selective summary of data for fresh fruit is given in Table 21. In recent years, more results have appeared on the amino acid content of tomato products, particularly juices and pastes, than on that in fresh tissue, but in view of the effects that processing has on the

Table 21
FREE AMINO ACIDS IN RIPE TOMATO FRUIT
EXPRESSED AS mg/100 g FRESH TISSUE OR
mg/100 mℓ JUICE

	Method of analysis				
	Semiquantitative paper chromatography[282]	Amino acid analyzer[283]	Amino acid analyzer[278]	G.L.C.[279]	Amino acid analyzer[280]
	Source of material				
Amino acids	Fresh tissue	Fresh tissue	Fresh tissue	Fresh tissue[a]	Juice
α-Alanine	3.7	3.3	2.8	3.4	6.9
β-Alanine	0.6	—	—	—	—
γ-Aminobutyric acid	21.9	—	55.7	158	71.0
Arginine	58.2	3.9	6.6	2.3	3.8
Asparagine	30.0	—	—	—	10.1
Aspartic acid	25.9	50	52.5	29	43.4
Cysteine	—	—	—	—	—
Glutamine	—	—	—	—	62.9
Glutamic acid	76.8	240	252	69	112.8
Glycine	—	2.3	1.1	1.1	1.1
Histidine	—	3.3	5.7	—	5.0
Isoleucine }	7.5[c]	3.3	3.0	4.6	2.9
Leucine }		3.0	2.3	9.7	3.0
Lysine	—	4.2	10.9	4.0	3.6
Methionine	—	0.5	0.5	1.7	1.5
Phenylalanine	—	7.2	7.3	11.4	6.7
Proline	—	—	1.6	0.6	—
Serine	12.7	5.7	49.8[b]	7.4	11.8
Threonine	6.6	6.5	—	—	6.8
Tryptophan	—	—	—	—	1.3
Tyrosine	—	3.8	1.5	6.3	1.7
Valine	2.1	1.9	0.8	7.4	1.6

[a] Mean of three contrasting nitrogen treatments; data originally given as % dry matter which has been converted to mg/100 g fresh tissue using an arbitrary factor of 17.5 in the absence of dry matter data.

[b] Includes threonine, glutamine, and asparagine.

[c] Combined isoleucine and leucine.

amino acid profile,[215,218,274,275] most of these results are not included in this account. The amino acids in processed products have been reviewed by Stadtman[275] and, more recently, by Liu and Luh.[276]

The concentrations of the free amino acids from various investigations given in Table 21 are fairly consistent, with the exception of those (i.e., glutamic, aspartic, and γ-aminobutyric acids) that are both abundant and change rapidly during ripening. In fact, glutamic, aspartic, and γ-aminobutyric acids, together with glutamine, comprise some 80% of the total free α-amino nitrogen-containing compounds in fruit ripened on or off the plant,[280] with glutamic acid making the greatest contribution.

Glutamic acid concentrations are particularly variable, and values can range between 50 and 300 mg/100 g fresh tissue (see Table 21 and References 78, 282, 283). As the concentration of this amino acid rises dramatically during the period of color change in the fruit,[224,278,283] this may account for the wide discrepancy in the results obtained. Aspartic acid increases similarly during ripening, but to a more limited extent.

Table 22
EFFECT OF NITROGEN AND PHOSPHATE FERTILIZERS ON THE GLUTAMIC ACID CONTENT OF RIPE TOMATO FRUIT, EXPRESSED AS mg/100 g FRESH TISSUE

Nitrogen level	Phosphate level		Nitrogen level means
	Incipient deficiency	Adequate	
Incipient deficiency	73	51	62
Adequate	147	96	121
Phosphate level means	110	74	

Note: L.S.D. at $P = 0.05$ in the body of the table (significantly different at $P < 0.05$) = 18; L.S.D. at $P = 0.05$ between the mean values for N ($P < 0.001$) and P ($P < 0.001$) = 13.

Adapted and recalculated from Reference 78.

Nutrition can also influence the amino acid concentration. For example, significantly greater levels of glutamic acid resulted from high nitrogen being combined with low phosphate fertilization (Table 22).[78] Similar interactions with respect to nitrogen and phosphorus nutrition were observed for aspartic acid and PCA (i.e., glutamine). Potassium fertilization, on the other hand, had no significant effect on the total dicarboxylic amino acids in the fruit. Furthermore, the actual form of nitrogen in the fertilizer has a pronounced effect; applications of ammonium-nitrogen resulted in higher glutamic acid levels in the fruit than nitrate-nitrogen.[279]

As well as stage of ripeness and mineral nutrition altering the glutamic acid content of tomatoes, there is some evidence that cultivar also has an effect;[274,276,281] fruit of *Lycopersicon pimpinellifolium* and other wild species (de Bruyn et al.[284] and Davies[536]) contain particularly high concentrations. While Yamanaka et al.[278] indicated that field-grown tomatoes contained very much more glutamic acid than glasshouse-grown fruit, this result may have been due either to season or varietal effects. The influence of other environmental factors on the glutamic acid content of tomatoes, or on any other amino acid for that matter, remains obscure.

The aspartic acid content of tomato fruit is, in general, affected by nutritional and environmental factors in a similar manner to glutamic acid (see References 78, 224, 278—280, 282, 283). The data for γ-aminobutyric acid are not, however, so well defined. Some investigators have found little change during ripening,[279,280] while others showed either an increase[276] or a decrease.[282] Of the other amino acids, the majority tend to decrease during ripening. Yu et al.[283] demonstrated that alanine, arginine, cysteine, leucine(s), methionine, phenylalanine, tyrosine, and valine all tended to decrease up to the time of the climacteric respiration rise, and then either continued to fall or underwent little change as ripening continued. Serine and threonine, however, both reached maxima at partial ripeness and then declined.[280,282,283] It has been suggested that these changes could be accounted for by continuing protein synthesis.[282,283]

Waste products from the processing of tomato fruit mainly consist of skin and seeds, and as these have been used for animal feedstuffs, their amino acid composition has been studied.[285-287] In the seed protein, glutamic acid predominates, with aspartic acid and arginine as the next most abundant amino acids. Whereas Lech et al.[285] concluded that

Table 23
THE CONTENT OF SOME AMINES IN TOMATO FRUIT, AS mg/100 g FRESH TISSUE

Amine	Concentration and range according to color stage	Ref.
Serotonin (3-(2-aminoethyl)-1 *H*-indol-5-ol)	1.2	288
	0.02 (green)—0.34 (red)	289
Tryptamine (1 *H*-indole-3-ethanamine)	0.4	288
	0.1 (green)—0.4 (red)	289
Tyramine (4-(2-aminoethyl)-phenol)	0.4	288

the nutritive value and the amino acid profile of tomato seed protein was similar to that of sunflower and soybean, Rymal et al.[286] indicated that it contained less protein than soybean, but the lysine content was higher.

XIII. OTHER NITROGENOUS COMPOUNDS, NITRATE, AND AMMONIA

A. Nitrogenous Compounds

Several reports of the presence of indole derivatives in tomato fruit appeared some years ago,[288,289] and these are summarized in Table 23. More recent work concerning these compounds does not appear to have been carried out. However, nine aliphatic amines have been detected in both raw and processed tomatoes,[290] but quantitative data is not available. Of the other nitrogen-containing volatile constituents, 2-isobutylthiazole is perhaps, the most noteworthy.[291] The concentration of this compound is believed to play an important role in the flavor of various tomato cultivars.[84,292]

B. The Content of Nitrate and Nitrite

The levels of inorganic nitrate in vegetables is a subject of long-standing interest both to toxicologists[293-295] and to the canning and food processing industries, particularly in the U.S.[293,296-298] and in Japan.[299] In the latter country, the maximum permitted tin concentration in canned foods is 150 ppm, and higher concentrations may build up when tomato products contain more than 3 ppm nitrate-nitrogen. A detailed study of nitrate accumulation in tomato fruit grown either outdoors or in sand culture has been made by Miyazaki and his collaborators,[299] who also looked at the effects of variety, nutrition, and management practices.[300-302]

Limited data for nitrate in tomato fruit are available, but mean values of more than 2 mg/100 g fresh weight nitrate-nitrogen (88 ppm nitrate) are seldom encountered.[86,296-299,303,304] However, the range from a factorial nutritional trial was between 0.29 and 5.03 mg NO_3-N/100 mℓ expressed juice (13 to 221 ppm nitrate), the highest values being found in fruit from plants receiving high nitrogen, high phosphate, and lime in combination with low or intermediate potassium levels (see Table 24).[86] Low light also favors nitrate accumulation, but the effect is an indirect one as light induction is necessary for significant nitrate reductase activity. A temperature of 26.7° C was found by Hoff and Wilcox[296] to increase the nitrate content compared with 21.1° C, but Luh et al.[298] reported that the nitrate content decreased from 73 to 0.4 ppm as the day temperature increased from 20 to 35° C. In general, more nitrate is present in green tomatoes than in riper fruits.[296,298,299]

Only small amounts of nitrite have been found in tomato fruit, ranging from negligible quantities[86,298] to 1.3 ppm.[305]

Table 24
THE NITRATE-NITROGEN CONTENT OF TOMATO FRUIT, AS mg NO$_3$-N/100 mℓ EXPRESSED JUICE, IN RELATION TO NITROGEN AND PHOSPHATE NUTRITION

Nitrogen level	Phosphate level		Nitrogen level means
	P$_1$	P$_2$	
N$_1$	0.81	0.99	0.90
N$_2$	1.15	1.58	1.37
N$_3$	1.85	2.75	2.30
Phosphate level means	1.27	1.78	

Note: Each value is the mean of 12 observations.

From Davies, J. N., *Annu. Rep. Glasshouse Crops Res. Inst. 1967,* 1968, 131. With permission.

C. Ammonia

The small amount of information available on the ammonium-nitrogen content of tomato fruit suggests that it forms a considerable proportion of the alcohol-soluble nitrogen, perhaps between 10 and 15%. Yu et al.[283] suggested that the marked fall in the ammonium concentrations as tomato fruit (cv. V. R. Moscow) ripened was a reflection of the deamination of amides, glutamine, and asparagine. This could account for the rapid increase in the concentrations of aspartic and glutamic acids that accompanies ripening. As is shown in Table 25, there is a rapid decline in the NH$_4$-N content of both the locular juices and outer walls as ordinary tomatoes ripen, and the fruit of the currant tomato, *L. pimpinellifolium,* show a similar trend. As might be expected, nitrogen deficiency is accompanied by a decrease in the NH$_4$-N content of the fruit.[298] In contrast, accumulation of ammonium ions occurs when potassium nutrition is inadequate, presumably to compensate for the shortage of cations.[536]

XIV. CELL WALL CONSTITUENTS, PROTEINS, AND ENZYMES

The cell wall is properly regarded as the fraction of material remaining after the cell has been broken open (most easily by freezing[306,307]), gently triturated with buffer to remove the cytosol, followed by extraction with chloroform/methanol and then acetone to remove lipids, starch, and water.[307,308] More commonly, that fraction insoluble in 70% propan-1-ol[309] or about 80% ethanol[98,102,224,306,310,311] is used, but the coprecipitation of cytoplasmic material probably leads to inflated results.

Fiber is a mixture of lignin and polysaccharides from plant cell walls which is not hydrolyzed by the secretions of the human digestive tract, and forms the bulk of the alcohol-insoluble solids (AIS). Available figures show the fiber content to range between 0.82 and 1.02 g/100 g for fresh yellow-green tissue,[313] and between 1.4 and 1.5 g/100 g for fresh ripe tissue.[61,312] Woodmansee et al.[309] found 0.50 to 0.56% of fiber in "unripe" tomatoes, and there was little change during development of the fruit to overripeness. The values found obviously depend very much on the method of assay, but 0.6 to 0.7% fresh weight would seem to be a reasonable compromise (see Figure 4).

In a study of the AIS of various parts of detached tomatoes kept at 20°C, Hall[310] demonstrated that at the turning stage, the AIS in the placental tissue was higher than that in the walls. During ripening, the content in the placentas fell sharply, probably

Table 25
AMMONIUM-NITROGEN CONTENT OF TOMATO FRUIT AT DIFFERENT STAGES OF RIPENESS AS mg/100 g FRESH TISSUE

Species	Stage of ripeness					Significance P	L.S.D. between means $P = 0.05$
	Mature green	Green-yellow	Yellow-orange	Orange	Red		
Lycopersicon esculentum (cv. Craigella)							
Locular juice	25.2	16.2	13.2	10.2	8.4	<0.001	5.2
Outer walls	13.8	10.2	11.0	11.4	9.2	<0.05	2.8
Lycopersicon pimpinellifolium							
Whole fruit	92.9	78.1	68.7	64.9	53.2	<0.001	9.1

Note: Each value is the mean of five observations.

Data from Reference 536.

because of the intense metabolic changes associated with the formation of the semiliquid material in which the seeds are embedded. Further work by Davies[224] on whole fruit, outer walls, and the locular contents confirmed the fall in AIS in the placentas, with a more restrained decrease in the outer walls. Table 26 quotes typical values for the AIS in representative members of the subgenera *Eulycopersicon* and *Eriopersicon,* together with comparative figures for both British and American varieties. The method used by Stevens and Paulson[311] for determining AIS is unique to them and thus does not allow direct comparisons to be made with other results. Brown and Stein[314] also looked at this component in seven variously shaped tomato varieties over more than one season. They found an average of 1.53% AIS, with 25.8% of it as protein.

Schemes for fractionating the AIS from tomato fruit are available,[98,311] as well as procedures for the isolation of cell walls from tomatoes[308] and other fruits.[306,307] The main constituents of tomato cell walls are pectic substances, hemicelluloses, cellulose, and protein. The results of three investigations are given in Table 27, and a wide variation in composition is apparent. Details of the way in which the components in sycamore cell walls are spatially arranged[315] may well provide a model for fruit walls as well.

A. Pectic Substances

The pectic polymer in tomato fruit is a complex mixture of polysaccharides composed mainly of galacturonic acid residues with much smaller amounts of galactose, arabinose, and rhamnose.[308] Xylose, ribose,[314] glucose, and mannose[311] have also been reported as constituents. Cell wall models propose a rhamnogalacturonan main chain consisting of an α-1,4-galacturonosyl polymer interspersed with regions rich in 2-linked rhamnosyl residues. In tomatoes, a neutral polysaccharide is linked to the main chain and has been found to be a combination of an araban and a galactan.[308] Evidence from sycamore cells suggests that the arabinosyl residues are in the form of a branched chain, while the galactosyl residues are present as a linear polymer attached at its reducing end to the main chain through the C-4 of the rhamnosyl residue.[315] In addition to the essentially homogeneous arabans and galactans, a highly branched polysaccharide containing both arabinose and galactose may well be a third component of the pectic substances.

A further variable in the structure of pectin is that some of the carboxyl groups on the galacturonosyl residues are present as methyl esters. The remaining unesterified groups

Table 26

AIS CONTENT IN WILD AND CULTIVATED SPECIES OF RIPE (EXCEPT WHERE STATED) TOMATO FRUIT AS g/100 g FRESH WEIGHT

Species/variety			Significance P	Least significant difference $P = 0.05$
L. pimpinellifolium — B34	4.98			
— B6009	4.39	4.76		
L. esculentum var. *cerasiforme*	4.92		<0.001	0.26
L. hirsutum f. *glabratum*	3.26			
f. *typicum*	4.74	3.87		
L. peruvianum var. *typicum*	3.63			

	Color stage						
	Mature green	Green-yellow	Yellow-orange	Orange	Red	Significance P	Least significant difference $P = 0.05$
L. esculentum							
Craigella							
Walls	2.76	2.40	2.19	2.15	1.87	<0.001	0.27
Locular contents without seeds	1.28	0.97	0.98	0.85	0.80	<0.001	0.14
Whole fruit	3.03	2.71	2.56	2.38	2.22	<0.001	0.30
Moneymaker							
Whole fruit	2.87	2.28	2.23	2.12	1.92	<0.001	0.20
"Blotchy" walls	2.12				1.88	<0.01	0.13
Marion							
Whole fruit	1.83		1.40		1.25		
Indian River							
Whole fruit	1.42		1.15		1.08		
Brookston							
Whole fruit	2.65				2.04		
Valiant							
Whole fruit	2.05				1.69		

Based on References 224, 257, 309, 310, and 536.

are thought to be involved in the formation of intermolecular bridges with calcium. This metal ion is the ideal size to cross-link with the carboxylate side-groups on the polymer, and the stability of the complex is enhanced by the occurrence of homogalacturonan sequences of more than about 20 residues.

Largely water-insoluble in unripe tomatoes, pectic components become increasingly soluble during ripening,[309,317] and various schemes for following these changes have been used.[98,311,314] The pectic fraction comprises up to 60% of the cell wall in the pericarp tissue of mature green tomatoes, giving figures between 0.27 and 0.34 g/100 g unripe fruit tissue,[309,318] and between 0.16 and 0.34 g/100 g for ripe tissue,[309,318] but Stevens and Paulson[311] found up to 0.67 g in half-ripe fruit. These estimates assume that pectin is composed exclusively of galacturonic acid residues, and this is clearly not so.[319]

In an analysis of the components of the pectic substances in tomato cell walls during ripening, Gross and Wallner[308] reported that galactose, arabinose, and galacturonic acid all declined in concentration, whereas xylose, noncellulosic glucose, mannose, cellulose, and protein either remained the same or showed some increase, probably because of the disproportionate removal of uronic acid.

Table 27
ANALYSIS OF CELL WALL MATERIAL FROM RIPE
TOMATO FRUIT AS mg/100 mg

Constituent	Kakhana and Arasimovich[316]	Gross and Wallner[308]	Williams and Bevenue[98]
Lignin	6.4—6.6	—	—
α-Cellulose	26.4—28.9	30	17
Pectic substances	13.1—19.2	38[a]	22
Hemicelluloses	26.0—26.6	7.0[b]	12—21[b]
Proteins	9.5—18.6[c]	3.8	17
Araban and galactan	—	9[d]	21

[a] From combined total of galacturonic acid (assuming 50% of the carboxyl groups methylated), rhamnose, arabinose, and galactose.
[b] From combined total of xylose, mannose and noncellulosic glucose.
[c] From total amino acids.
[d] From combined total of arabinose and galactose (already included in the pectic substances figure).

Increased solubilization of the pectic substances, progressive loss of tissue firmness,[320] and rapid rise in the activity of polygalacturonase (PG)[321] accompany the normal ripening of tomato fruit. As the pectic polymers only begin to acquire solubility after PG becomes active,[321] it is possible that this enzyme is involved in the breakdown of the insoluble complex, perhaps by reducing the length of the chains cross-linked by calcium, thus weakening the stability of the bonding. Certainly, cohesion in the middle lamella, which is particularly rich in pectic substances, is dependent on ionic rather than covalent bonds, and bound calcium decreases substantially during ripening.

The precise mechanism whereby solubilization of pectic substances is achieved is still obscure. However, the components are de-esterified by pectin-esterase[318] to form a preferred substrate for PG. In addition, the activity of PG is much higher using polymers that have very high galacturonic acid contents such as rhamnogalacturonans with restricted side-branching. The erosion of the pectic substances is directly related to the loss of tissue firmness, but PG is not the only enzyme involved, assuming that pectinesterase is present in nonlimiting amounts. Although the decline in galactan or arabinogalactan found in both apples[322] and tomatoes[308,323] probably has only a minor effect on fruit firmness, it is possible that the presence of these chains could regulate PG action by restricting access to the substrate in the cell wall.[308]

B. Hemicellulose

The classical hemicellulose fraction of plant cell walls consists of xylans, arabinoxylans, mannans, glucomannans, and galactoglucomannans. These polymers constitute an important fraction of cell wall material.[306,324] Thus cell walls of pear fruit contain xylan residues with side chains of D-glucuronic acid,[325] while mannose is also found in cell-wall hydrolysates of many fruits, and is probably associated with glucose in the form of glucomannans.[323] During ripening, the hemicellulose fraction from tomatoes shows no loss (indeed, an apparent gain probably due to a progressive loss of water-soluble material) in xylose, mannose, and noncellulosic glucose,[308,323] and little or no degradation is apparent.

Experiments with sycamore cells indicate that under dissociating conditions after pretreatment with PG, fragments of the pectin chain and a xyloglucan are released.[326] The xyloglucan consisted of a β-(1 → 4)-linked glucan with frequent xylosyl side chains

attached to C6 of the glucosyl residues. It has been suggested that the xyloglucan is noncovalently bound to the cellulose fibrils of the wall, and covalently linked to the pectin polysaccharides,[326,327] thus interconnecting the microfibrils and the pectic substances. Whether a similar situation obtains in the tomato is unknown.

C. Cellulose

Analyses of the primary and secondary walls of fruit[98,306,308,316] and other plant[315] cells confirm that cellulose is a major constituent. The linear glucan molecules in the primary cell walls are thought to be bound together by hydrogen bonds to form very elongated elementary fibrils which aggregate into larger units in secondary walls. The bulk of the primary wall consists of amorphous material surrounding the fibrils and binding them together.

Although cellulase is active in many fruits,[332] including the tomato, and instances of extensive erosion of micelles coincident with softening have been found, there is no convincing evidence that the crystalline fibrils are degraded by cellulases in the tomato[308,330] or other fruit. Although unripe pear tissue required both PG and cellulase to transform the appearance of the cells to that of naturally ripened tissue,[328] an alternative explanation to the one suggesting erosion of the fibrils by the cellulase could be that the enzyme is acting as a glucanase, functioning in conjunction with PG in the ripening sequence. The involvement of wall hydrolases other than PG in tomato ripening has been put forward.[323]

D. Proteins

Cell walls appear to contain an intrinsic amount of protein. In sycamore cells, there is evidence that wall protein, particularly rich in hydroxyproline, is glycosidically attached through a serine residue to a galactose chain substituted with arabinose, in turn attached to a rhamnogalacturonan. Other protein appears to have arabinosyl tetrasaccharides glycosidically attached to hydroxyproline residues.[329,334] Estimates based on the N content of the tomato gave a range of from 3.1% protein in cell wall material from immature green fruit to 3.8% from ripe tissue.[308] Hence, on a fresh weight basis, this is equivalent to a cell wall protein content of 0.03%.

Total protein in whole fruit has been reported to be between 0.42 and 0.46% for unripe and 0.48 to 0.55% for ripe tomatoes.[309] Mean values for the protein content of 13 varieties of tomato analyzed over two seasons averaged 0.87% for "breaker" fruit and 0.92% for ripe fruit,[56] while according to Watt and Merrill[53] green fruit contained 1.2% protein; ripe, 1.1%. Some of the difficulties of ensuring that protein estimates are not invalidated by the protein combining with polyphenols are hinted at by Hulme and Jones,[335] but protein estimations based on preliminary precipitation with trichloroacetic acid, perchloric acid, phosphotungstic acid, or hot alcohol must produce rather different answers.

Information about the release of proteins from plant cell wall fractions by fungal endo-PG may have a parallel in tomato fruit tissue. Strand et al.[336] found that the rupture of the galacturonide linkages was sufficient to release some of the proteins from the cell wall matrix of potato, carrot, and cotton. Exo-PG and cellulase were not effective. Differences in the composition of the proteins obtained from these tissues suggest that the linkages which attach proteins to the cell wall matrix vary either in the type of linkage-carbohydrate involved or in the accessibility of these linkages to pectolytic enzymes.

Endo-PG and endo-pectic lyase from fungal sources were able to release galacturonides, neutral sugars, and proteins during the maceration of potato tuber tissue.[337] When pectolytic activity begins in fruit tissue, some of the components released could be wall-bound enzymes involved in the furtherance of ripening. A "conditioning" event has been

suggested by Tigchelaar et al.[338] as important in the genetically controlled process that induces tomato fruit to undergo the multiple changes associated with ripening.

E. Proteins as Enzymes

One of the most convenient ways of examining the proteins from tomato fruit is to purify and concentrate them by forming acetone-insoluble powders, and after solubilization in salt solutions to separate them by disk-gel electrophoresis.[339] Protein stains are able to show up at least 30 of the major constituents, and these must be regarded as structural or storage proteins. In addition, there must be several hundred metabolically active proteins present in smaller quantities, some of which can be detected using their properties as enzymes to produce a colored product. Many enzymes (perhaps all) exist in two or more multimolecular forms. Table 28 lists most of those enzymes whose activity has been demonstrated in tomato fruit and the available information about any isoenzymic diversity that they may show.

F. Pectic Enzymes

Two excellent reviews, one partially and the other totally concerned with the pectic enzymes, have appeared recently.[340,341] Enzymic de-esterification of pectin appears to proceed linearly along the chain of the molecule resulting in blocks of free carboxyl groups being left. Of the two endo-PGs found in tomato fruit,[345] one of 44,000 mol wt randomly splits glycosidic bonds while the other, almost twice this size, is thought to release oligogalacturonides, but the degradation is not of the terminal cleavage type.

G. Cellulase

The high activity in young green tomato fruit decreases during growth until a minimum at the mature green stage is reached,[333] after which the activity rises again towards full ripeness. Pharr and Dickinson identified two isoenzymes,[348] but other work has suggested that there are two endocellulases, an exocellulase and a β-glucosidase,[331] making four components for the complex.

H. Amylase and Phosphorylase

Eight bands showing amylase activity have been reported for the tomato.[349] After electrophoretic separation, phosphorylase may be detected by either of two methods,[350,351] and a single zone of activity was detected with tissue from small green fruit.[537] In immature pericarp tissue the activity was weak, and absent in ripe tissue,[352] whereas it was strongly active in tissue of the *rin* mutant at comparable ages.

I. Invertase

In whole fruit, acid invertase in the cultivated tomato was highest at the overripe stage.[133] Fruit of *L. pimpinellifolium* were particularly rich sources of the enzyme, with activity more than 20 times that in the cultivated form. Activity in the locular walls of normal varieties reached a maximum with full ripeness of the fruit and then declined somewhat.[133] Green fruit probably contain an inhibitor, and its disappearance together with *de novo* synthesis of the enzyme during ripening is thought to account for the activity rise.[356]

J. Pentose Phosphate Pathway

Evidence for the operation of the pentose pathway in fruits has been well summarized by Dilley.[357] The activity and number of isoenzymes of 6-phosphogluconate dehydrogenase and phosphoglucomutase in the tomato were at a maximum at the mature green stage,[339,358] while phosphohexose isomerase and glucose-6-phosphate dehydrogenase were uniformly active throughout development, only decreasing towards overripeness.

Table 28
ENZYMES AND ISOENZYMES FOUND IN TOMATO FRUIT

	Reference for quantitative method of assay	Maximum number of isoenzymes
Pectic enzymes		$2,^{345}\ 3^{347}$
Endopolygalacturonase	321, 345, 346	$4,^{342}\ 5,^{344}\ 8^{343}$
Pectinesterase	318, 342	$2,^{348}\ 4^{331}$
Cellulase	331, 333, 346	8^{349}
Amylase	349	1^{352}
Phosphorylase		$2,^{354}\ 3^{355}$
Invertase	133, 353	
Pentose phosphate pathway		4^{355}
Glucose-6-phosphate dehydrogenase		6^{355}
Phosphoglucomutase		6^{355}
6-Phosphogluconate dehydrogenase		10^{355}
Phosphohexose isomerase		
Glycolytic pathway		$2^{339,355}$
Aldolase	361	$4^{355,358}$
Phosphofructokinase	359	
Citric acid cycle		
Citrate synthase	365	
Fumarase		5^{355}
iso-Citrate dehydrogenase		$2^{339,355}$
Malate dehydrogenase	23, 362	$4,^{339}\ 5,^{352,355}$
NADP$^+$-malic enzyme	355, 360, 362, 363	$4^{339,355}$
2-Oxoglutarate	23	
Succinic dehydrogenase	23, 365	
Phosphatases		$2,^{368}\ 7,^{367}\ 8^{339}$
Acid phosphatase	366, 367, 368	6^{358}
ATPase		3^{355}
β-Glycerophosphatase		
Miscellaneous enzymes		
Acyl hydrolase	383, 384	
α-Alanine aminotransferase	393	
Alcohol dehydrogenase	390	
Aromatic alcohol dehydrogenase	369	
Carboxypeptidase	392	
Catalase	374	
Chlorophyllase	391	
p-Coumarate CoA ligase	369, 389	
Esterase		$5,^{352}\ 13^{355}$
α-and β-Galactosidase	386, 387	
β-1,3-Glucanase	387, 388	2^{355}
α- and β-Glucosidase	386	
Glutamic acid decarboxylase	375	
Glutamate dehydrogenase	375	6^{355}
Glutamate-oxaloacetate transaminase	26, 364, 365	4^{355}
Glycolate oxidase	374	
Hydroperoxide cleavage enzyme	384	
Hydroxycinnamyl transferase	369, 389	
Hydroxypyruvate reductase	374	
Indoleacetic acid oxidase	376	1^{377}
Leucine aminopeptidase	355	4^{355}
Leucine aminotransferase	393	
Lipoxygenase	382, 383, 384, 385	
α- and β-Mannosidase	386	
NADH$_2$-diaphorase		12^{355}

Table 28 (continued)
ENZYMES AND ISOENZYMES FOUND IN TOMATO FRUIT

	Reference for quantitative method of assay	Maximum number of isoenzymes
Peroxidase	371, 372, 373	$4,^{355}$ $6,^{372}$ 8^{371}
Phenylalanine ammonia lyase	369, 370	
Phosphoenolpyruvate carboxylase	362, 378, 379	
Phospholipase D	384	
Ribulose bisphosphate carboxylase/ oxygenase	362, 374, 378, 379	
Superoxide dismutase	380	2^{380}
Tyrosinase	69, 369	4^{355}
α- and β-Xylosidase	386	

K. Glycolytic Pathway

Phosphofructokinase assayed both after separation on polyacrylamide gel[355,359] and spectrophotometrically[360] was found to be almost as active in ripe fruit as in mature green tomatoes. Aldolase, also analyzed qualitatively[339,355] and quantitatively,[361] behaved similarly.[537]

L. Citric Acid Cycle

The total activity of fumarase was at a maximum at the mature green stage, and polyacrylamide gel separation indicated that the enzyme existed in five isoenzymic forms.[339] Malate dehydrogenase can also be separated into several isoenzymes.[339,352,355] Both mitochondrial[23] and whole tissue studies[355] suggest that maximal activity occurs at fruit maturity and does not change much during ripening. Enzyme activity is reduced by potassium deficiency.[364] Malic enzyme activity reached a peak at maturity and then decreased,[355] but further studies have not substantiated this.[360] Isocitrate dehydrogenase increases in activity during ripening,[339] but 2-oxoglutarate dehydrogenase remains steady.[23] Succinate dehydrogenase has variously been reported as having uniform[23] or falling activity.[365] Citrate synthase has also been found in tomato fruit mitochondria.[365]

M. Phosphatases

Crude extracts of small tomato fruit gave eight sites of activity after they had been separated on polyacrylamide gel, but only three retained activity at the overripe stage.[339,355] Overall activity decreased steadily during ripening[366] to reach a level only 25 to 40% of that of extracts of immature green fruit.[367] Two major phosphatases were separated and purified by Chen et al.[368] Electrofocusing suggests that there are four isoenzymes in immature fruit, and during ripening the contribution by the nonparticulate fraction to the total activity decreases.[352] The acid phosphatases also display some activity when β-glycerophosphate or ATP is used as substrate, but certain of the phosphatase isoenzymes act specifically on p-nitrophenyl phosphate.[339,367] Both β-glycerophosphatase and ATPase show isoenzymic proliferation and diminishing activity with ripening.[339,355]

N. Miscellaneous Enzymes

Tyrosinase activity is at a maximum when the fruit are close to maturity,[69,369] and four isoenzymes are detectable at this stage.[355] In this laboratory, peroxidase also showed four isoenzyme bands which persisted throughout ripening,[355] but Ku et al.[371] and Ogura et

al.[372] reported even more. Experimenters have generally found that the enzyme activity increases with ripening,[352,355,371] but Ogura et al.[372] and Kokkinakis and Brooks[373] suggested that the opposite was the case. Peroxidase from tomatoes has a very low indol-3-ylacetic acid (IAA) oxidase activity.[373] Catalase, which has some peroxidase-like activity, rises to a peak of activity in half-ripe fruit and then decreases rapidly towards full ripeness.[374] Esterase, $NADH_2$-diaphorase, glutamate dehydrogenase,[355] and glutamic acid decarboxylase[375] all show greatest isoenzyme diversity at the mature green stage, whereas leucine amino peptidase[355] increases, and glutamate-oxaloacetate transaminase[26,355] decreases in activity throughout normal development. This last enzyme has four molecular forms, and activity is found in both the mitochondrial and cytoplasmic fractions.[26] The mitochondrial contribution was increased by potassium deficiency.[364]

IAA oxidase can be obtained from tomato fruit in two forms according to the extraction conditions; one form has about five times the molecular weight of the other. At present, it is thought that the bigger molecule is the native form, the activity of which rises somewhat with ripening.[376] Frenkel also indicated that IAA oxidase activity intensifies during ripening.[377]

Among the enzymes examined by Willmer and Johnston,[362] Bravdo et al.,[378] Laval-Martin et al.,[379] and Martin et al.,[374] ribulose-1,5-bisphosphate carboxylase was shown to decrease during ripening,[374,378] but the associated oxygenase component as a proportion of the carboxylase activity was variously reported to remain the same,[374] or rise to a peak,[378] as the fruit became half ripe. Phosphoenolpyruvate carboxylase decreased in activity during ripening of both cultivated[378] and "cherry" tomatoes.[379] Glycolate oxidase and hydroxypyruvate reductase generally decreased in activity during tomato fruit development, although this trend was temporarily checked during the climacteric respiration rise.[374] Superoxide dismutase was resolved into two isoenzymes, but the total activity did not alter much during the ripening period.[380]

Whereas the glycolipid content of tomato fruit during ripening did not change significantly, the phospholipids decreased, probably because of lipid peroxidation. It has been suggested that a combination of a transaminase, "lipoxygenase", and a peroxidase is capable of forming ethylene from methionine or its derivatives,[381] but a much more efficient pathway involving l-aminocyclopropane-1-carboxylic acid is present in tomato fruit.

A system from tomato fruit homogenates containing lipoxygenase in association with acyl hydrolases reacted with the polyunsaturated fatty acids linoleic and linolenic.[383] The main products were characterized as the 9-hydroperoxides of the fatty acids and the volatile carbonyls hexanal and hexenal from linoleic and linolenic acids, respectively. A more complete scheme whereby hydroperoxide cleavage enzymes are invoked in the final step has been proposed.[384] Lipoxygenase has been found to rise to a peak in activity coincident with the onset of the respiration rise.[382,385]

A survey of the nitrophenylglucosidases bound to the cell walls of tomato fruit revealed activities of α- and β-galactosidase, also both forms of glucosidase, mannosidase, and xylosidase.[386] The β-glucosidase and α-galactosidase were associated with purified cell wall fragments. Since all these enzymes remained constant in activity or actually decreased during fruit development, they are thought not to be involved in fruit softening.[386] Of the glycosidases investigated by Wallner and Walker,[387] β-galactosidase and β-1,3-glucanase activities were the highest, and they remained fairly constant throughout ripening. Alternative possibilities are that β-glycosidases promote cell wall dissolution such as occurs in the locular cavity during ripening, or that action by these enzymes allows subsequent transformations by PG to proceed.[387]

In the leaves of *Nicotiana glutinosa* infected with TMV,[388] also in tomato fruit similarly affected,[537] the activity of β-1,3-glucanase was considerably enhanced compared with uninfected tissue. Both hydroxycinnamyl transferase and phenylalanine

ammonia transferase increased when tomato fruit were chilled,[369] but other enzymes of phenylpropanoid metabolism did not react to low temperatures in the same way. Alcohol dehydrogenase isolated from tomato fruit transformed *trans*-2-hexenal to *trans*-2-hexenol.[390] Chlorophyllase activity increased during ripening until the fruit exhibited a full red color, and then decreased.[391] Whereas leucine aminopeptidase exhibited maximal activity in ripe fruit,[355] a similar enzyme, carboxypeptidase, reportedly reached maximum activity early on in the ripening period.[392] Both mitochondrial and soluble cell extracts contained α-alanine aminotransferase, but leucine aminotransferase was confined to the soluble fraction and appeared to be much lower in activity.[393] A number of amino acids have been shown to act as substrates in the production of carbonyl compounds, and some of the volatile products may contribute to tomato aroma.[394] Many of the transformations involved in the biosynthesis of tomato pigments have been summarized by Khudairi,[395] and some additional ones are referred to in the following section.

XV. PIGMENTS

As there are a number of general reviews[396-398] of this complex subject, as well as other accounts dealing more specifically with tomato fruit,[1,3,395] we intend to confine this account to indicating the changes that take place in the various pigments during ripening, their concentration range in normal ripe fruit, and how the concentration varies in different parts of the fruit. Illustrations of how oxygen tension, light levels, and temperature changes are able to influence pigment concentrations are also included in this section.

The structures of the various carotenoids and their division into acyclic (e.g., lycopene) and alicyclic (e.g., β-carotene) carotenes, in contrast to the oxygenated carotenes (the xanthophylls), may be found elsewhere.[396-399] The influence of the mutant genes that alter the normal balance between pigments or induce the formation of novel pigments, upon which much emphasis has been placed in elucidating the mechanisms of pigment synthesis, has also been extensively reviewed,[3,395,396,399] and will not be enlarged on here. Changes in the carotenoid pigments during the ripening of the variety Homestead[400] are illustrated in Figure 6. The colorless pigments phytoene and phytofluene, together with γ-carotene, δ-carotene, and lycopene, all increase in concentration throughout ripening, a finding that was generally confirmed by Rabinowitch et al.[401] and Watada et al.[402] Both α- and β-carotene often reach peak concentration prior to full ripeness.[400] In contrast, the xanthophylls, which constitute more than half the total carotenoids in immature fruit,[401] are at a minimum during incipient ripeness, and consist of a number of oxygenated carotenoids.[3,403] The balance between the epoxides of lutein and zeaxanthin with the original xanthophylls is considerably affected by light levels.[401] Other data for changes in carotenes and xanthophylls during ripening have been summarized by Herrmann.[3]

Carotenoid pigments in ripe fruit of six tomato varieties (all American in origin as we failed to find comparable data from fruit grown in other countries) show quite a wide variation in concentration, as is illustrated in Table 29. Lycopene is, not unexpectedly, the most abundant in ripe fruit, but it is difficult to subscribe to the levels reported by Salunkhe and his co-workers[2,103,104] which seem to be about 20 times too high. Although there is considerable evidence in certain varieties that β-carotene, the second most prevalent pigment, reaches peak concentration prior to full ripeness,[103,104,400-402] the maximum values in the results from Salunkhe's laboratory[2,103,104] are about 400 times those generally quoted (see Table 29). Nor do we feel that there is any evidence to substantiate the suggestion[103] that as ripeness
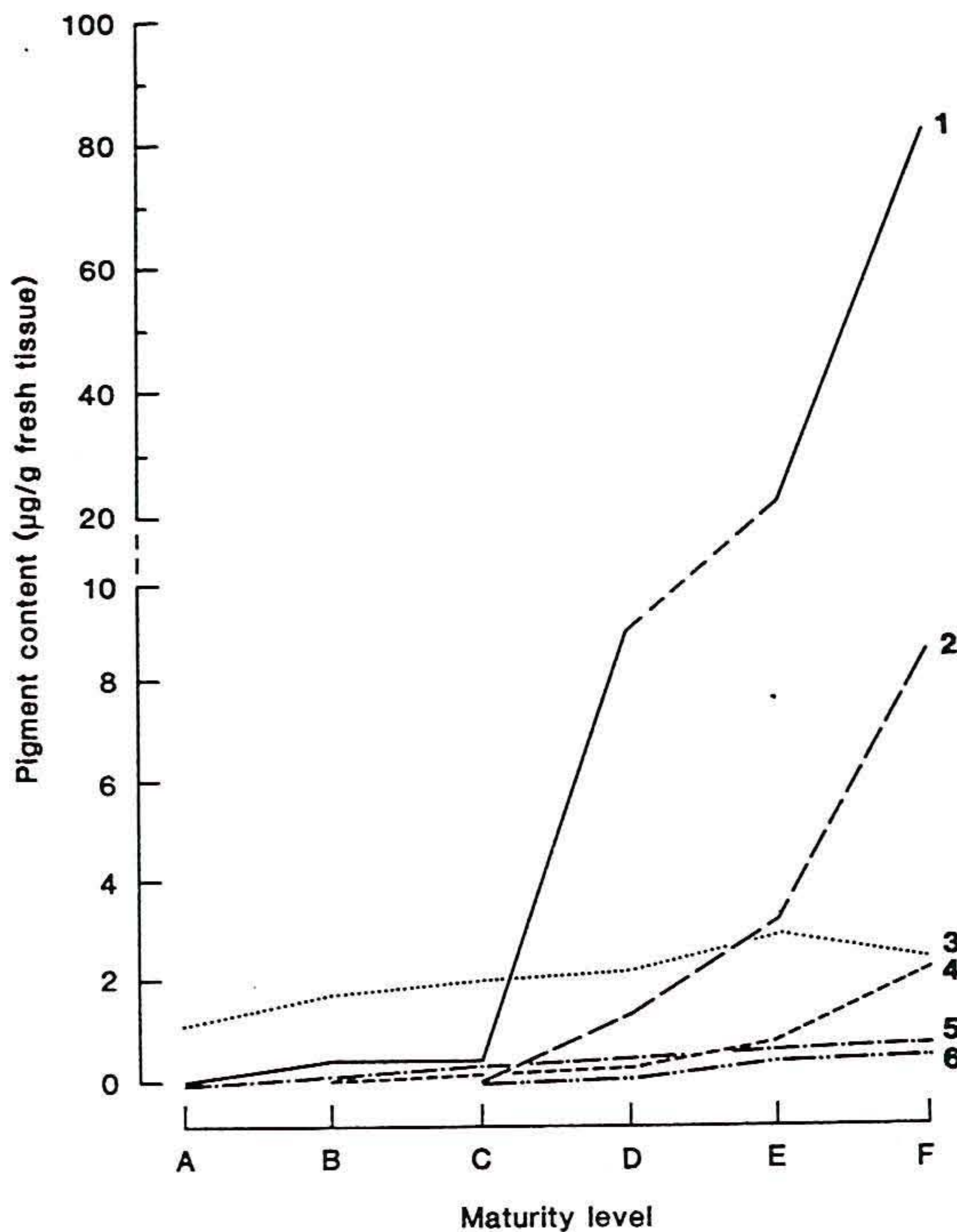
FIGURE 6.   Changes in the concentration of tomato fruit pigments during ripening (cv. Homestead). 1, lycopene; 2, phytoene; 3, β-carotene; 4, phytofluene; 5, γ-carotene; 6, δ-carotene. Stages of maturity: A, mature green; B, breaker; C, turning; D, pink; E, light red; F, red. (Adapted from Reference 400).

approaches, β-carotene is transformed into lycopene, as this would involve reopening the terminal β-ionone rings.

The distribution of β-carotene, lycopene, and the total amount of carotenoid pigments in the fruit is shown in Table 30. Whereas β-carotene is more concentrated in locular tissue than in pericarp tissue,[404,405] the reverse is true for lycopene.[404]

Chlorophyll decreases rapidly with the onset of ripening. It is generally agreed that in normal unripe tomatoes, the content of chlorophyll "a" is higher than that of "b".[408,411,412] The total chlorophyll concentration quoted by Salunkhe and his group[2,103,104] of about 450 μg/g fresh weight would appear to be some ten times too high. Also, their results showing chlorophyll rising to a peak in concentration just before ripening[103,104] are at variance with those of other workers which indicate a steady decline with growth.[1,402,411,412] Immature *rin* and *nor* mutant fruits contain fairly normal levels of chlorophyll,[408,412] but with continuing development it disappears at a very much slower rate than normal. Chlorophyll "a" is preferentially lost in such mutant fruit compared with those of the parental lines.[408,412] Chlorophyll formation is a light-dependent reaction,[406] and the pigment does not decompose in the absence of oxygen unless the fruit are illuminated.[413] An account of the transformation of chloroplasts to chromoplasts during ripening has been given by Khudairi,[395] while Simpson et al.[412] have highlighted differences between the rate of chromoplast formation in normal fruit and in certain of the ripening mutants. From a study of the ultrastructure of chromoplasts, Spurr[414] has observed that lycopene accumulates on the extended membrane systems of the chromoplast, whereas β-carotene is concentrated in the lipid globules.

Table 29
CAROTENOID PIGMENTS IN RIPE TOMATO FRUIT IN $\mu g/g$ FRESH WEIGHT

Pigment	Sunrise[a] [406]	Rutgers[b] [407]	Campbell 146 [399]	Fireball × Cornell 54 — 149 [408]	Fireball[c] [409]	Early Red Chief[d] [410]
Phytoene	9.8 ± 2.1	29.0 ± 14.0	24.4	27.76 ± 16.55	15.54 ± 0.90	23.05
Phytofluene	8.3 ± 1.6	8.2 ± 2.0	2.1	15.49 ± 4.85	5.10 ± 0.08	7.87
α-Carotene			0			0.02
β-Carotene	7.4 ± 0.9	4.9 ± 1.5	1.4	11.91 ± 0.77	2.72 ± 0.05	2.18
δ-Carotene	1.8 ± 0.6		0		1.0 ± 0.04	1.70
γ-Carotene	0.6 ± 0.2	1.4 ± 0.1	1.1	2.60 ± 0.62	1.58 ± 0.09	0.51
Neuro-sporene	0.15 ± 0.06		0			0.32
Lycopene	78.3 ± 7.5	43.6 ± 9.2	43.8	181.20 ± 26.84	55.9 ± 2.57	57.68

[a] Recalculated assuming a dry matter percentage of 6.25.
[b] Maturation temperature 23.5°C.
[c] Mean of analyses from plants receiving 2 to 10 meq K/ℓ nutrient solution.
[d] Samples analyzed 14 days after initial coloration, the plants being kept between 17.8 and 25.6°C.

XVI. THE "NONRIPENING" MUTANTS

The use of breeding programs designed to improve the desirable aspects of the composition of tomato fruit as an alternative to, or in conjunction with, environmental or nutritional regimes are being widely undertaken.[114] However, it is proving difficult to combine the major genes for disease resistance with both high yields and good quality as, to some extent, these attributes seem to be mutually exclusive. Until more is known about the constraints involved, much of the work on selections designed to improve yield without sacrificing quality must be somewhat empirical.

Genetic mutants provide excellent tools for elucidating metabolic pathways, and they have been widely exploited in studies on interconversions between the various tomato fruit pigments.[395,407] In order to examine the effects of mutant genes in isolation, it is desirable to introduce each of them into a common genotype, especially where quantitative assessments are being made, and a backcross method has been extensively used. A list of over 100 genes so treated has recently been published.[28] A few of the genes affect changes that normally occur as tomatoes ripen, and lines containing them have become known as the "nonripening" mutants.

In tomato trials being carried out by Professor L. L. Morris in 1950, one line was observed in which part of a fruit colored and softened much more slowly than usual.[8] This retardation of ripening was due to the presence of a dominant allele, "Never ripe" (*Nr*), and further investigation indicated that the dominance was incomplete.[422] Thus the solubilization of the pectic substances did not proceed as far in the heterozygote (*Nr nr*) as in the parental line, a finding that is in keeping with a partial failure in the synthesis of the pectic enzyme endopolygalacturonase.[423]

A further gene mutation, a recessive named "ripening inhibitor" (*rin*),[424] was discovered in breeding material of Professor H. M. Munger at Cornell University. Many aspects of the normal ripening pattern are affected and the storage life of fruit containing the recessive alleles is very long.[338,425] A somewhat similar mutant was noticed by Dr. E. A. Kerr in Ontario, Canada,[426] and the gene involved, also a recessive, is called "nonripening" (*nor*). Varieties containing other mutant genes such as "evergreen", "green flesh",[425] and "Snowball"[427] appear to have less extensive effects on the ripening mechanism of the fruit than the genes "Never ripe", "ripening inhibitor" and "nonripening".

The physiology and growth regulator content of fruit of *Nr*, *rin*, and *nor* tomatoes have been reviewed by Tigchelaar et al.,[338] together with the ways various investigators have attempted to induce such mutant lines to ripen. Some of the effects that the introduction of these genes have on the composition and behavior of the fruit have been brought together in Tables 31 and 32. More recently, Davey and van Staden[428] have suggested that high levels of endogenous cytokinins in *rin* fruit could be involved in preventing the fruit from ripening normally. However, it has been pointed out[429] that although cytokinins can affect the rate of ripening, their concentration need not be at a minimum when ripening commences. Following a study of the concentrations of abscisic acid, phaseic acid, and gibberellin during the growth and senescence of both normal and *Nr*, *rin*, and *nor* mutants, McGlasson and Franklin[430] concluded that these growth substances and similar compounds are related more closely to ripening and senescence than to growth. This is in keeping with McGlasson's previous conclusion[431] that since the hormone levels and their rate of turnover vary so widely within the nonripening mutants, these factors are secondary to some other genetic control system.

The exceptionally slow rate at which fruit from the nonripening mutants senesce and deteriorate endows them with a very long shelf life. Considerable efforts have been made

Table 31

PHYSIOLOGICAL AND COMPOSITIONAL CHANGES BROUGHT ABOUT IN NORMAL TOMATO FRUIT BY THE INTRODUCTION OF SLOW-RIPENING ALLELES

	Mutant introduced		
	Nr Nr	*rin rin*	*nor nor*
Respiratory climacteric	Half normal or less[432,435]	None[425,432,433]	None[436]
Associated C_2H_4 production	Half normal or less[425,432,435]	None[425,432,433]	None[436]—12%[437]
Storage life	50% increase[438] over normal	3—5 times normal[438]	3—5 times normal[438]
Firmness	Increased[360,422,432]	Much increased[439-441]	Much increased[436]
Dry matter	Very low[360,422]	Low[360]	
Soluble solids	Low[8,432]	Low[432,441]	
Titratable acidity	High[360,432]	Low[360,432]	Normal[442]
Total acidity	High[240,360]	High[360]	
Potassium in the sap	Very low[360]	Low[360]	
pH of the sap	Low[360,432]	Normal[360]	
Reducing sugars	Low[360,432]	Low[360,432]	
Total sap solids	Very low[360]	Low[360]	
Pigments in ripe fruit or of comparable age as $\mu g/g$ fresh weight			
Phytoene (5^{436}—29^{407})[a]		Normal[408,443]	Very low[436]
Phytofluene (2^{400}—15^{408})		Very low[408,443]	Very low[436]
β-Carotene (3^{400}—12^{408})		Very low[408,443]	Very low[436]
γ-Carotene (1^{410}—3^{408})		Low[408,443]	
Lycopene (44^{407}—181^{408})		Very low[408,443]	Trace[436]
Chlorophyll "a" (not present)		Present[408,412]	Present[412]
Chlorophyll "b" (not present)		Present[408,412]	Present[412]
Eventual color of the fruit	Orange-red	Yellow	Light orange

[a] The figures in parentheses give the general concentration range for each of the pigments in normal red fruit.

to induce the mutants to ripen, as this would not only provide insight into the ripening mechanism and its control, but might also allow commercial exploitation. Methods have usually centered around the use of exogenous ethylene or propylene, which temporarily stimulate respiration but do not affect endogenous ethylene production.[338,425,432,433] Combinations of high light and enhanced oxygen tensions have also been used (see Reference 338), illustrated by the work of Buescher and Doherty[434] in connection with carotenoid synthesis in *rin* and *nor* material in which it was found that light and ethylene were the most important factors. Thus it appears that the capacity to develop normal pigmentation is present in mutant fruit but is suppressed. The almost complete restoration of ripening in *rin* tomatoes induced by ethephon or ethylene gas which was reported by Mizrahi et al.[441] has not been repeatable by other laboratories.

The search for explanations of the altered behavior of the mutants in failing to ripen, and in resisting senescence and senescence-inducers such as ethylene, has led to investigations of the water-permeability of tomato cells.[445] The usual increase in this property towards the end of development failed to occur in *rin* tissue. Further observations[446,447] have indicated that high levels of bound divalent cations in the absence

Table 32
ALTERATIONS IN THE ACTIVITIES OF ENZYMES IN THE FRUIT BROUGHT ABOUT BY THE INTRODUCTION OF NONRIPENING ALLELES INTO NORMAL TOMATO VARIETIES

	Mutant introduced		
Enzyme activity[a]	*Nr Nr*	*rin rin*	*nor nor*
Pectinesterase	Normal[360,422]	High[444]/low[360,440]	High[444]/normal[338]
Polygalacturonase	Very low[360]	Absent[360,440,444]	Trace[436]
Phosphofructokinase			
Mature green fruit	Normal[360]	Normal[360]	
Age equivalent to ripe "wild-type" fruit	Low[360]	Very low[360]	
NADP$^+$-malic enzyme			
Mature green stage	Normal[360]	Normal[360]	
Age equivalent to ripe "wild-type" fruit	Very low[360]	Very low[360]	
Hydroxypyruvate reductase		Slightly low[374]	
Catalase		Low[374]	
Glycolate oxidase		Small increase[374]	
Cellulase		Normal[440]	

[a] In tissue of such an age that "wild-type" (i.e., normally ripening) fruit would have been ripe, except where mentioned otherwise.

of polygalacturonase probably endow mutant fruit with exceptional longevity. There is now good evidence to show that ethylene in plant systems is derived from methionine via S-adenosylmethionine and l-aminocyclopropane-1-carboxylic acid (ACC).[448] The *rin* mutant fruit contains similar levels of both ACC and of the ACC-forming enzyme to those usually found in "wild-type" tomatoes at the mature green stage.[449] However, ACC is as ineffective as ethylene in promoting the ripening of *rin* fruit.

Although it is not at present possible to induce mutant fruit to ripen to any great extent, there is considerable commercial potential in the use of F_1 material resulting from hybridizing normal and nonripening lines.[338] Fruit resulting from these crosses show an intermediate rate for many of the processes involved in ripening, and some examples are given in Table 33. Because of the adverse effect of the *Nr* allele on tomato composition in producing high acid, low sugar fruit, even when the character is present in heterozygous (*Nr nr*) form, it has little or no commercial potential.[360] The results in Table 33 suggest that the *rin* character in heterozygous form confers only a small increase in shelf life and firmness, although the color of the fruit is little altered. With *nor* hybrids, the effects are somewhat more pronounced and the shelf life is considerably extended. The detriment to composition is minimal, and modest increases in both "field-holding" ability[338] and processed juice viscosity[442] have been demonstrated. Further advantages from the introduction of the *nor* allele in hybrid combination could lie in the improvements in acidity and yield of fruit.[436] Also, the increased storage life would allow the harvesting of riper fruit than is at present possible, with consequent improvement in quality.[43]

Where double mutant hybrid material (e.g., *Rin rin Nor nor*) has been investigated, the effect of each of the alleles appears to be roughly additive to the behavior of the genotype.[438,450] In all these genetic manipulations, however, the choice of female parent may affect the eventual composition of the resultant fruit. Differences in the composition of fruit between reciprocal hybrids involving *rin* and normal parents have been

Table 33

PHYSIOLOGICAL, COMPOSITIONAL AND ENZYMIC CHANGES IN THE FRUIT OF F_1 HYBRIDS BETWEEN ISOGENIC LINES CONTAINING THE NEVER RIPE (*Nr*), RIPENING INHIBITOR (*rin*), AND NONRIPENING (*nor*) MUTANTS AND THEIR RECURRENT PARENTAL LINES

	Mutant introduced		
	Nr nr	**Rin rin**	**Nor nor**
Respiratory climacteric		Delayed but normal[444,450]	Delayed, 50% of normal[436,450]
Associated C_2H_4 production		26[425]—47%[450] of normal	10[444]—48%[450] of normal
Increase in storage life at 20°C in days (50% of the fruit unacceptable)		4[451]	27[451]
Softness as % of the normal figure for fruit of the same age	79[422]	79[451]—81[452]	49[451]
Water-soluble pectin as % of total (comparable figure for normal fruit shown in parentheses)	13 (45)[422]	36 (42)[451]	31 (42)[451]
Pectinesterase activity as % of normal fruit of comparable age	100[422]	82[360]—87[451]	75[451]
Polygalacturonase activity as % of normal fruit of comparable age	4[422]	35[450]—65[360,451]	25[450]—39[451]
Phosphofructokinase activity as % of normal fruit of comparable age		64[360]	
NADP$^+$-malic enzyme activity as % of normal fruit of comparable age		52[360]	
Carotene levels 5 days after respiration peak as % of normal		55[450]	55[450]
Pigments in ripe fruit or of comparable age as μg/g fresh weight[a]			
Phytoene		10—30 (28)[408]	3 (5)[436]
Phytofluene		7—10 (15)[408]	3 (5)[436]
β-Carotene		8—10 (12)[408]	4 (4)[436]
γ-Carotene		2.1—2.5 (2.6)[408]	1 (2)[436]
Lycopene		130—132 (181)[408]	24 (49)[436]

[a] The figures in parentheses in this section of the Table give the concentration for each of the pigments in comparable ripe parental lines.

reported,[408,425] and it seems likely that cytoplasmic factors cause this phenomenon. Some diversity in the effects of nonripening mutants as heterozygotes must be expected, and this is already apparent.[360,408] The main disadvantage in using any of the nonripening genes as heterozygotes is in the lack of pigmentation in the ripe fruit, and the introduction of genes such as "high pigment"[438] or "old gold crimson"[28] which affect carotenoid levels may be an answer.

XVII. VOLATILE CONSTITUENTS

In 1970 we summarized much of what was known about the components of tomato fruit aroma.[1] Although at that time relatively few individual constituents had been

identified, the main classes into which the compounds fell had been recognized. Progress since then has been rapid. Johnson et al.[453] listed over 150 individual volatile constituents, while additional components have been enumerated in subsequent reviews.[3,454] A detailed Hungarian catalogue of no less than 285 compounds reportedly present in tomato aroma was published in 1977 (cited in Reference 290).

Despite the wealth of qualitative data, quantitative results are relatively scarce, but some values can be found.[455-459] Only a small number of components are regarded as dominant in the aroma profile, and of those perhaps *cis*-3-hexenal,[458,460-464] 2-isobutylthiazole,[292,458,461,463] and β-ionone[399,458,461] have attracted most attention. In addition, the odor thresholds of many compounds normally found in the aroma of tomatoes have been established.[461]

A typical volatile fraction from field-grown tomatoes has been found to consist of 58% esters, hydrocarbons and long-chain alcohols, 32% carbonyls, and 10% C_3 to C_6 alcohols.[457] However, many of the esters reportedly identified in this investigation[457] and in similar studies[465,466] have not been encountered subsequently.[461,463] Minamide and Ogata[467] found that whereas the aliphatic carbonyl and volatile fatty acid fractions of tomato fruit increased markedly during incipient ripeness, the unsaturated fatty acids decreased rapidly. This was thought to be due to the involvement of lipolytic acyl hydrolases and lipoxygenase in the production of volatile substances during this phase of ripening, causing a temporary fall in the concentration of unsaturated fatty acids. Maceration of tomato tissue results in the rapid degradation of the phospholipids and galactolipids by hydrolytic and oxidative enzymes to give free fatty acids as the first product.[384] The C_6-aldehydes form an important part of tomato flavor,[462] but their absence in heat-processed products[458] suggests that an enzymic pathway is responsible for their synthesis. The mechanism proposed by Galliard et al.[384] is that tomato acyl lipids are hydrolyzed by phospholipase D or hydrolase enzymes to give the free fatty acids, reported to be mainly palmitic, linoleic, and linolenic, although other acids would also be expected (see Reference 458). Lipoxygenase then converts lineoleic and linolenic acids to their hydroperoxides, predominantly the 9-hydroperoxy isomers.[383] However, only the smaller quantities of the 13-hydroperoxy isomers were cleaved to produce volatile carbonyl compounds.

Analyses of the volatile components of field and greenhouse-grown tomatoes provide some indication of the relative quality of the fruit that are produced. Although no absolute differences between tomatoes grown in the two locations could be found, almost invariably the concentration of alcohols, aldehydes, and esters was higher in the field-grown fruit.[465,466] Shah et al.[457] reported that short-chain (C_4 to C_6) compounds were more concentrated in artificially ripened fruit, while longer-chain (C_9 to C_{12}) carbonyls and terpene esters predominated in field-ripened fruit. The latter compounds were thought to be important components of ripe tomato aroma. The amounts of compounds with "high olfactory interest" in three tomato varieties, one grown outdoors in the Canary Islands and two grown in greenhouses in Belgium, have been determined.[463] The outdoor variety showed a much higher content of 3-hexen-1-ol which was considered to be one of the key components.

In taste panel tests, tomatoes ripened on the plant were preferred to fruit picked green and then ripened, but no specific differences in composition were detected.[177] In other similar studies,[43,468] tomatoes picked at defined stages of ripeness were ripened to a standard color and then assessed by a taste panel. Premature harvest resulted in the fruit being regarded as less sweet, more sour, less "tomato-like", and having more "off-flavor" than those picked when ripe. Differences in sweetness were related to variations in reducing sugars, and sourness was negatively correlated with both reducing sugars and pH.

Richter[469] compared normal and parthenocarpic tomato fruit, but was unable to show any qualitative differences between the two types of fruit in their content of volatiles. Modifications in taste were thought to be due to a reduction in the proportion of material in the locular cavities, resulting in a higher sugar but lower organic acid content.

Various attempts[84,468,470] to relate "off-flavor" with individual chemicals have met with limited success except in the case of the variety "Cal Ace" where hex-trans-2-enal, in particular, appears to be closely related to the taint.[43] Later work indicated that the chemical was probably 2-methyl-2-butenal.[470] Seven other volatile components appeared to have some impact on the "off-flavor" characteristic when three varieties in addition to "Cal Ace" were considered.[468]

Certain pure compounds have been added to tomatoes in an attempt to assess their contributions to flavor. Thus, the addition of 2-isobutylthiazole and citric acid to one tomato juice sample compensated for the flavor differences between it and another sample.[84] In other experiments,[43] the overall flavor was most frequently affected by the additions of fructose, glucose, citric acid, and the volatile compound n-hexanal.

It has been suggested that some of the intermediates in normal pigment formation in tomatoes also contribute to the volatile components of tomato flavor.[399] The polyene-carotenes were particularly implicated, and were thought to account for some of the flavor differences between tomato varieties.

The possible identity of the precursors in aroma formation, and the changes that accompany mechanical disruption and heating have been discussed.[454] It has been shown that during the production of tomato juice, a series of C_6-alcohols are formed from fatty acids,[464] confirming Stevens' finding that carotenoid intermediates were the basis for a range of aroma compounds.[399] Sieso and Crouzet[471] followed the modifications to the volatile compounds during the production of canned juice and tomato paste. In juice preparation, only short-chain constituents such as C_6-aldehydes and alcohols decreased, whereas paste production caused more widespread degradation of normal components leading to the formation of a number of artifacts. The volatile amines in tomatoes and its products have also been examined.[290] The major volatiles in tomato juice, in a concentrate of volatile compounds and in an essence, were separated and characterized by Lever and Matthews,[459] and consumer preferences for each of the modified preparations were assessed.

Although further reports of the incidence of additional minor components will continue to add to the total picture of the tomato volatiles, the relative merits of the various systems used to extract and concentrate them have not been critically assessed, although Herrmann[3] lists the extraction procedures used in connection with a number of investigations. A long and impressive list of the constituents of tomato aroma has thus emerged, but some doubt must still be attached to isolated reports of small amounts of volatile substances until they have been confirmed.

XVIII. ALKALOIDS

Alkaloidal glycosides, bitter to the taste, are common throughout the Solanaceae, and on acid hydrolysis yield steroidal bases and a mixture of sugars. The alkaloid most commonly found in tomato plants is α-tomatine, the basic structure of which[1,472] consists of the aglycone tomatidine and a tetrasaccharide composed of two molecules of glucose and one each of galactose and xylose. The biochemical, biological, and toxicological aspects of α-tomatine have been comprehensively reviewed by Roddick,[472] and more briefly by Herrmann.[3]

In the genus *Lycopersicon*, tomatine and/or one of its derivatives is usually the only steroidal alkaloid present. It is widely distributed throughout the tomato plant, and is in soluble form in the cell.[473] More tomatine was detected in the fully open flowers (0.93 to

2.2% of the dry weight) than in other parts of the tomato plant, but not too dissimilar concentrations (0.86 to 1.9%) were also reported in the leaves.[474] Some 0.09% on a fresh weight basis was found in mature green tomatoes,[475] but concentrations declined rapidly with ripening[475,476] to half that amount in red fruit,[475] and only traces could be detected in tomatoes ripened for a further two days.[475] The enzyme responsible for the breakdown is tomatinase, which is highly specific for tomatine.[477] There is some disagreement about whether ripe tomatoes are completely tomatine-free or whether small amounts of the alkaloid persist (see Roddick[472]).

Species other than *L. esculentum* often contain more tomatine than the cultivated tomato.[472] Hence, when crosses with wild species are included in tomato breeding programs, concern has occasionally been expressed over the possibility of transferring the potential for the synthesis of excessive quantities of tomatine and other glycoalkaloids together with the desired disease-resistance factors. Whereas the leaves of wild species of tomato may contain fairly high quantities of tomatine,[478] results from the investigations of both Courtney and Lambeth[479] and Davies[480] confirm that the amounts in the fruit at the mature green stage are not excessive, and are likely to fall to even lower levels as development continues.

XIX. STORAGE

A. Low-Temperature Storage

In 1931, now almost 50 years ago, $10°C$ was considered to be the optimum temperature for storing both green and red tomatoes.[481] Many years later, work in the Netherlands suggested a minimum storage temperature of $16°C$ for green fruit and $8°C$ for red fruit, allowing them to be kept for from 3 to 4 weeks,[482] while in Canada it was recommended that mature green tomatoes should be stored at $10°C$ ripened at $21°C$ for 2 to 6 days, and then held at $10°C$ for a further 8 to 10 days.[483] Subsequently, it was reiterated that $21°C$ was the optimum for ensuring even ripening and high quality without serious losses from disease.[484] More recently, low-temperature regimes for storing a wide range of vegetables and soft fruits have been established.[485] At a temperature of $8°C$ and 80 to 90% R.H., "quarter-ripe" tomatoes could be kept for 7 to 10 days with a subsequent shelf life at $20°C$ of 4 to 5 days. The tolerance of different tomato cultivars to cold storage has been studied minimally, but small-fruited varieties may have an intrinsically longer shelf life than large-fruited ones.[486] Certainly the susceptibility of tomato fruits to chilling injury varies according to their stage of ripeness.[487-491] In general, the ability to withstand low temperatures without harmful effects on fruit quality increases with ripeness.

Low-temperature storage of mature green tomatoes has been found to inhibit the usual decline in acidity during ripening,[492,493] while a decrease in firmness and an increase in color as the fruit ripened occurred when the storage time at $7°C$ was extended.[492] Previously, the adverse effects of low temperature on firmness, color, and susceptibility to decay had been pointed out.[494] In the U.K., storage of orange-red fruit for 2½ weeks at temperatures of between 7 and $13°C$ had little deleterious effect on fruit quality apart from an initial decrease in acidity and fruit firmness.[495] On the other hand, American work in which tomatoes at the "breaker" stage were stored at $2°C$ for up to 21 days, followed by ripening at 20 or $24°C$, showed that titratable acidity of the fruit increased and the pH fell.[496,497] Malic acid in the pericarp decreased during chilling, while citric acid accumulated.[497] On ripening, fruit that had been chilled for 3 weeks contained considerably more citric acid than those chilled for shorter periods, but glucose and fructose concentrations were substantially lower.

Whereas Lewis and Workman[498] found that the capacity for phosphorylation declined rapidly in mature green tomatoes after only 2 days at $0°C$, Buescher and Dostal[499] showed that adenosine-5'-triphosphate and uridine-5'-triphosphate increased in similar

fruit during the first 2 weeks at 2°C. However, within 2 days of transfer of the fruit to 20°C, after 3 weeks of chilling, there was a dramatic decline in the concentration of these nucleotides.

In the low-temperature storage experiments quoted in this account, the marketable quality of the resultant fruit is not mentioned except in one case[496] where more than 80% of the fruit were decayed after chilling for 20 days. The risk of chilling injury appears to be far too high to justify the use of temperatures as low as 2°C for storage of tomatoes.

The effect of chilling on the ultrastructure of tomato fruit has been examined by Moline,[330] who concluded that tomatoes stored at 2°C for 10 days failed to ripen normally, due, in part at least, to interference with the conversion of chloroplasts to chromoplasts. After 15 days, plastids and mitochondria swelled and degenerated, while in fruit stored for 21 days at 2°C, only very few organelles were at all distinguishable. Stenvers and Stork[500] concluded that as the storage period at or below 12°C was increased, the longer was the ripening period on transfer to 19°C, but the greater was the incidence of decay.

Sugar losses under storage conditions of 12°C and 85% R.H. have been reported to be much less rapid in fruit of two TMV-resistant cultivars than in those of two nonresistant varieties.[501] However, the introduction of TMV-resistance had no apparent effect on the losses of citric and malic acids, which were most rapid during the first week of storage for all four cultivars.

B. High-Temperature Storage

Temperatures in excess of 30°C inhibit the synthesis of lycopene, and tomatoes stored under such conditions end up a yellow or orange color rather than red.[502,503] Japanese workers[202] claimed that storage of mature green tomatoes at 33°C for about 12 days (thus inhibiting lycopene formation), followed by ripening at room temperature, restored lycopene production and greatly extended the shelf life to over 200 days, although there was a weight loss of over 40% during this time! It would also seem unlikely that sufficient lycopene would be formed under these circumstances for the fruit to be regarded as good quality.

C. Controlled Atmosphere Storage

Studies of the effects of controlled atmospheres on stored tomato fruit have proliferated since 1933, when Kidd and West[504] found that a mixture of 5% O_2 with 5% CO_2 at 12°C retarded ripening and fungal growth in tomatoes. Subsequently it was noted that holding tomatoes for 28 days at 13°C in the gas mixture recommended by Kidd and West gave better quality fruit than when higher CO_2 levels were used.[505] A somewhat lower temperature of 10°C was considered by Tomkins[506] to be advantageous, while more than 5% CO_2 delayed the onset of ripening and also increased disease. In another study,[507] storage at 13°C in 2.5% O_2 and 5% CO_2 was found to be the most effective mixture for delaying tomato ripening. However, 2.5% O_2, combined with the same percentage of CO_2, resulted in the minimum incidence of decay. In contrast, later work in the U.S.[508] showed that mature green tomatoes held at 13°C for 6 weeks kept better in 3% O_2 in the absence of CO_2 than they did in air. Increasing the CO_2 concentration to between 3 and 5% did not affect the incidence of rotting, and sometimes resulted in CO_2 injury. Morris (cited in Reference 509) found that at 13°C, "breaker" and pink tomatoes were best stored in atmospheres containing between 4 and 8% O_2, and between 1 and 2% CO_2. Moreoever, ripening was retarded and storage life increased thereby. Atmospheres containing less than 4% O_2 and more than 4% CO_2 caused the fruit to ripen unevenly. It has also been observed[508] that mature green tomatoes held at 13°C in air ripened to a full red color after 6 weeks, but 65% of them were decayed. In contrast, those held in 3% O_2 for a similar length of time had only reached the pink stage of ripeness, and only 3.5% were

decayed. Although direct comparison of fruit stored under the two regimes was not possible because of the high incidence of decay in those that were air-stored, flavor was judged to be unimpaired in those held under low oxygen conditions. Other investigators[510,511] have also claimed that O_2 concentrations within the optimum range of 3 to 5% had no significant effect on the major taste components. In contrast, mature green tomatoes stored at CO_2 levels of between 3 and 5% tended to be more acid after ripening than those held in a CO_2-free atmosphere.

It was shown by Parsons et al.[512] that storage in nitrogen generally retarded ripening. Thus, fruit previously held in 99% N_2 and 1% O_2 on transfer to air at 21°C ripened slowly without marked deleterious effect on either flavor or appearance. In contrast, fruit stored for longer than 4 days in 100% N_2 acquired an abnormal flavor and ripened atypically. Salunkhe and Wu[511] also reported that low oxygen concentrations inhibited tomato fruit ripening and increased the storage life at 13°C. With "green-wrap" tomatoes, a storage life of 62 days was obtained in 10% O_2 and 90% N_2, while in an atmosphere of 3% O_2 and 97% N_2, 76 days was claimed. An additional 10 days of storage life was obtained by a further reduction of the oxygen concentration to 1%. These low levels of oxygen inhibited chlorophyll and starch degradation and delayed the synthesis of lycopene, β-carotene, and sugars. A similar temperature (12.5°C) has been used in combination with 2.5 to 4% O_2 and 4% CO_2 to store mature green tomatoes of various varieties.[513] These conditions were shown to inhibit pigment changes associated with normal ripening, but some cultivars continued to undergo compositional changes.

Little information is available on the effect of controlled atmospheres on fruit firmness. Anaerobic atmospheres generally preserved firmness,[512] while in another study[514] softening and ripening were delayed more by an atmosphere containing 2.5% O_2 than by one having double that amount. Atmospheres of 3 to 5% CO_2 combined with more than 5% O_2 were effective in delaying fruit softening,[500] especially with fruit more than half ripe.

It is well known that high CO_2 levels can inhibit fruit ripening,[515] and a recent study[516] has explored the effects of various partial pressures of CO_2 in the presence of 20 to 22% O_2 on tomatoes at the turning stage while kept at 20°C. Concentrations of CO_2 in excess of 20% were required before ripening was retarded, and exposure to atmospheres containing more than 10% CO_2 for as short a time as 4 days was deleterious to fruit quality.

Until recently, the term "controlled atmosphere storage" has been used to indicate a modification of the atmosphere with respect to either (or both) oxygen and carbon dioxide concentrations. Recently, a third gas, carbon monoxide, has been used, and has been observed to mimic the effects of ethylene on fruit ripening,[517,518] but there is little information on its possible use for controlling decay. Kader et al.[519] have shown that 5 to 10% CO added to 4% O_2 can be effective in reducing the incidence of *Botrytis* on mature green fruit stored for up to 14 days. There were no undesirable effects on either ripening behavior or on composition. The favorable effect of CO on the sugars and acids in the fruit during storage merits further attention, but its high mammalian toxicity may prevent the widespread use of the gas for such purposes. It is of interest in this connection that CO, apparently a minor natural metabolite of tomatoes, is not given off, and small concentrations (about 30 to 40 $\mu\ell/\ell$) occur in the internal atmosphere of the fruit during ripening.[520]

Claims for increased storage life for tomato fruit must be set against losses due to decay or physiological disorder, but even if after storage the fruit are still marketable, their flavor may well be impaired. Despite the development of fairly satisfactory systems for controlled atmosphere storage of tomatoes, there is relatively little incentive for investment in its use for fruit intended for the fresh market since rapid transport now allows the freshly harvested product to be widely available throughout the year.

D. Low-Pressure (Hypobaric) Storage

The storage of perishable fruit and vegetables at subatmospheric pressures[521] was first referred to as "hypobaric storage" by Tolle[522] in 1969, who defined it as ". . . refrigerated storage of produce under gas pressures totalling less than 760 mm of mercury. . .". The point has been made that it would seem preferable to refer to the system as "low pressure" rather than "hypobaric" storage, not the least because the term can be abbreviated to LPS (Lougheed et al.[523])! The main principles and applications have been described elsewhere,[523-528] as have some of the problems and dangers of the system.[523] Although LPS has been the subject of much academic discussion and of experimentation mainly on a laboratory and pilot-plant scale, its commercial application is still relatively restricted. The consequences of LPS may be summarized as follows: initially the reduction in oxygen supply slows down respiration and the synthesis of ethylene. Secondly, ethylene diffuses from the stored product and is removed. Finally, other volatile substances such as CO_2, acetic acid, and acetaldehyde (all of which may contribute to various physiological disorders) are removed continuously. The success of LPS in retarding fruit ripening has been attributed to a reduction in the intracellular ethylene,[515] a lowered partial pressure of oxygen,[523,529] or both.[530-532] For example, maximum delay in the ripening of mature green tomatoes was observed when both the oxygen partial pressure and the atmospheric pressure were reduced.[521] Different subatmospheric pressures had little effect on fruit behavior during storage when oxygen pressures were held constant. Subsequent work has confirmed these observations and has shown that the onset of tomato fruit ripening under LPS conditions is controlled by oxygen pressures, and that ethylene concentration under such conditions has no effect provided that it is not allowed to rise excessively.[529]

Streif and Bangerth,[532] however, showed that some ripening processes in the tomato, such as the decline in fruit firmness, lycopene synthesis, and increased activity of the pectic enzymes, could be accelerated if sufficient ethylene were introduced into the storage atmosphere even at oxygen pressures as low as 20 mm Hg.

Wu et al.[533] found that whereas "green-wrap" tomatoes stored at 13°C ripened under normal atmospheric pressure (646 mm Hg in Utah) in 35 days, those stored at 471 and 278 mm Hg ripened in 65 and 87 days, respectively. An even lower pressure (102 mm Hg) completely prevented ripening, but the fruit deteriorated after 100 days in these conditions. However, if the fruit were restored to normal conditions after these 100 days, they ripened in seven days and were of typical appearance. The results clearly show that as the pressure at which the fruit were stored was lowered, the remaining content of volatile flavor components on subsequent ripening at atmospheric pressure was smaller, and the flavor of the product must thereby be impaired.

Evidence is accumulating to suggest that many of the effects of LPS on tomato fruit can also be produced by low oxygen levels at atmospheric pressure.[523] In fact, Lougheed et al.[523] do not consider that LPS using either mature green or ripe tomatoes merits serious consideration as a storage system. The high cost of LPS facilities must militate against their widespread adoption for the storage of tomatoes, although they may well find applications in other horticultural fields.

XX. CONCLUSION

With reviews on tomato fruit composition appearing every few years,[1-3] we have endeavored to make this text complementary to previous accounts rather than merely repetitive. Thus we have only dealt briefly with some topics that have been adequately and recently summarized, and more extensive coverage given to others according to the availability of reliable data and our judgment of the importance and appropriateness of the subject.

The tomato is still growing in popularity as a crop, with increasing emphasis on outdoor production and on mechanical harvesting, but in our opinion the quality of the fruit still leaves much to be desired. The clear message from trials in many parts of the world that it is possible to produce high-quality tomatoes in high yield with but little additional effort and expense over growing for yield alone, is still largely ignored. Moreover, we continue to be dismayed by the innumerable papers on the composition and storage of tomatoes that totally disregard the effect of the experimental conditions on the palatability of the resulting crop. In fact, reports on taste-panel assessment of tomatoes from replicated trials of any kind are rare. It is only the continuing efforts of research workers, growers, and those concerned in marketing that will make available to the consumer high-quality, full-flavored tomatoes, attractive both to the eye and to the palate.

ACKNOWLEDGMENTS

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