

HANDBOOK OF **FRUITS AND FRUIT PROCESSING**

SECOND EDITION

Edited by

**Nirmal K. Sinha, Jiwan S. Sidhu, József Barta,
James S. B. Wu and M. Pilar Cano**



 **WILEY-BLACKWELL**

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Preface

Fruits are botanically diverse, perishable, seasonal, and regional commodities. They come in many forms, shapes and sizes, colors, flavors, and textures; and are an important part of a healthy diet. Some fruits have been billed as “superfruits” because of their unique nutritional properties and phytochemical composition. Low intake of fruits and vegetables has been suggested by the World Health Organization (WHO) as one of the risk factors for noncommunicable diseases such as various forms of cancers, cardiovascular diseases, diabetes, etc.

Besides vitamins, minerals, fibers, and other nutrients, fruits contain phenolic compounds having pharmacological potentials. Consumed as part of a regular diet these naturally occurring plant constituents are believed to provide a wide range of physiological benefits as antioxidants, antiallergic, anticarcinogenic, anti-inflammatory, etc. This new edition of handbook of fruits and fruit processing discusses these and other functional properties of fruits and fruit products.

According to the Food and Agriculture Organization’s (FAO) 2010 yearbook, the total production of fruits in the world increased from 470.4 million tons during 1999–2000 to 587.6 million tons in 2009. Fruits are important in global commerce. The total value of world’s fruit export and import increased from about \$45 billion during 1999–2000 to about \$105 billion in 2008. In the United States, approximately 60% fruits are consumed as processed products. The utilized production value of fruits in the United States according to USDA has increased from approximately \$10.5 billion in 2000 to \$15.02 billion in 2010. This shows the importance of fruits in agricultural productivity and growth. In most countries, there is an increasing emphasis on value-added agriculture and realization about the nutritional importance of fruits in the diet. The chapters on major fruits in this text highlight the leading fruit producing countries, production and consumption trends, and preservation and processing of fruits into various products.

Innovation, research, and development efforts in this field are aimed at improvements in production, postharvest storage and processing, safety and quality, development of new processes and products to increase demand and consumption

of fruits, and expansion of this sector. We believe a contemporary reference and source book such as this handbook, which can describe, distil, and disseminate important and relevant scientific information and advances in this field is valuable for the flow of such information. Our efforts in the second edition are to expand and improve the coverage of the original book published in 2006. Some of the major highlights of this new edition with 35 chapters include chapters on physiology and classification of fruits, horticultural biochemistry, microbiology and food safety (including HACCP, safety and regulation of fruits entering world trade), sensory and flavor characteristics, nutrition, and naturally present bioactive phenolics, postharvest physiology, storage, transportation and packaging, processing and preservation technologies (freezing, canning, aseptic processing, non-thermal technology, drying, etc.), and details on major fruits including tropical and superfruits, frozen fruits, canned fruit, jelly, jam and preserves, fruit juices, dried fruits and wines. This text is organized into five parts:

Part I: Fruit physiology, biochemistry, microbiology, nutrition, and health (five chapters)

Part II: Postharvest handling and preservation of fruits (seven chapters)

Part III: Product manufacturing and packaging (five chapters)

Part IV: Processing plant, waste management, safety, and regulations (four chapters)

Part V: Production, quality, and processing aspects of major fruits and fruit products (fourteen chapters)

This text is a joint effort of many individuals and signifies a remarkable cooperation and teamwork. The editorial team consists of five members from Asia, Europe, Middle East, and USA with expertise and experiences in this field. Four of these editors were part of the first edition. Dr. Wu with extensive teaching and industry experience specially in aseptic processing is a new editor. Each chapter has been contributed by dedicated professionals from across the globe

representing academia, government institutions, and industry. We hope this new edition with additional features would be a valuable source and reference book for students, professionals, product developers, scientists, and other professionals interested in this field. We sincerely hope this handbook addresses the needs of its readers and advances their understanding and knowledge of fruit science and technology.

We express our gratitude to all the authors and reviewers and thank them for their time and efforts. We acknowledge

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**Nirmal Sinha, Jiwan Sidhu, József Barta,
James Wu, M. Pilar Cano**

Part 1
Biology, Biochemistry, Nutrition,
and Microbiology

1

Physiology and Classification of Fruits

Kuo-Tan Li

- Introduction
- Development of a Fruit
 - Pollination and Fertilization
 - Fruit Set
 - Parthenocarpy and Stenospermocarpy
- Fruit Growth
 - Cell Division
 - Cell Enlargement
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- Drupe
- Pome
- Hesperidium
- Pepo
- Compound Fruits
 - Aggregate Fruit
 - Multiple Fruit
- Accessory Fruit
- Culinary Classification of Fruits
 - Fruits
 - Fruits used as Vegetables
 - Nuts
 - Cereals
- References

Abstract: Fruits are an essential part of human diet and culture. Various classification systems have been applied to fruits to meet various objectives. Physiological and morphological characteristics of a given fruit species or even a given cultivar affect its postharvest life and processing quality. This chapter provides a fundamental background on how a fruit develops in the field and how fruits are categorized in modern society.

INTRODUCTION

Fruits are indispensable in human diet to supply essential vitamins, for example, vitamin A, B₆, C, E, thiamine, niacin, minerals, and dietary fiber (Fourie 2001). Fruits are also savories that provide a pleasing taste. The majority of species of fruits that are grown and consumed in the modern world have been domesticated by the late Neolithic and Bronze Ages between 6000 and 3000 BC. In addition, a number of fruits that have been extensively collected from the wild by the native people were not domesticated until the early twentieth century (Janick 2005). Some other fruits, although commonly

utilized by the local people, remain exotic to the rest of the world. Nowadays, fruit production and processing are among the major industries in many countries, and the trading and distribution of fruits have become an important international economic activity. Although world production and consumption of fruits have increased significantly, most people's diets still fall short of the mark set by United Nation's Food and Agriculture Organization (FAO 2003).

Botanically, a fruit is the reproductive structure of a flowering plant in which seeds form and develop. In culinary arts, fruit normally refers to an edible, juicy, and sweet entity derived from a flower on any flowering plant. Among so many species of flowering plants with so much anatomical diversity, only a relatively small group of species and fruit types are common in human diet. Nevertheless, the physiological and morphological characteristics of a given fruit species or even a given cultivar affect its postharvest life and processing quality. Therefore, it is advisable to obtain a fundamental understanding on how a fruit develops in the field and how fruits are categorized in modern society.

DEVELOPMENT OF A FRUIT

A fruit is developed from a flower and its associate tissues. The onset of fruit development begins as early as the differentiation of flower by which the apical meristem on a shoot forms a flower or inflorescence instead of a leaf or a shoot. Anatomical changes begin at the edge of the meristem, first generating the calyx and the corolla, and later the androecium (male) and the gynoecium (female) tissues. The process of flower differentiation can be completed within a few days in annual plants to nearly a year in some perennial plants. The differentiation of gynoecium continues to form the carpel or pistil in which the ovule is hosted. A gynoecium may consist of a single carpel, multiple distinct (unfused) carpels, or multiple connate (fused) carpels. Inside gynoecia ovules, within one or more ovaries develop and later become seeds upon fertilization. When mature, gynoecia may function to attract pollinators through aroma or nectar. At bloom or in some instances prior to bloom, gynoecia receive pollen grains on their specialized surface structure called a stigma and in some cases actively select genetically different pollen grains so as to avoid inbreeding. Gynoecia may facilitate the growth of pollen tube to the ovule and the delivery of sperm to the egg. The gynoecium forms the pericarp. The pericarp in most fruits differentiates into three distinct layers. The outer layer is called exocarp and normally becomes the peel of the fruit. The middle layer is the mesocarp, the major edible part of most fleshy fruits. The inner layer is the endocarp, which directly surrounds the ovary and the seed.

POLLINATION AND FERTILIZATION

Most flowering plants will not set fruit without pollination or fertilization. Pollination is the process of transferring pollen

grains from anthers to stigmas. Pollination in some species occurs spontaneously at bloom due to their special structure of the flower or the specialized arrangement of their stigmas and stamens, for example, grapes and tomatoes. Pollination in most other species usually will not be completed without natural vectors, i.e., wind or insects (Stebbins 1970). The majority of common fruit crops require insect for pollination, and the pollination efficiency is usually improved by introducing bee (*Apis*) hives to the orchard during blooming season (Morse and Calderone 2000). Flowers of some tropical fruit crops, for example, mangos, are not attractive to bees. Instead, their major pollinators are native flies (Sung et al. 2006). In commercial production, their pollination can be benefited by introducing the oriental latrine fly (*Chrysomya megacephala*) to the orchard during bloom (Hu et al. 1995). Some fruits are dioecious, and pollen grains must be transferred from a male flower in a male plant to a female flower in a female plant to complete the pollination process. Examples of dioecious fruits include the wind-pollinated mulberries and the insect-pollinated kiwifruit (Hopping 1990). In monoecious fruit crops such as wind-pollinated chestnuts, walnuts, and pecans; and insect-pollinated lychee (Stern 2003), watermelons, and cucumbers, pollen grains must be transferred from a male flower to a female flower either on the same plant or on separate plants to continue the fertilization process.

Fertilization takes place after the germination of pollen grains on the stigma. A pollen grain after successful germination contains two sperm cells. Upon entering the ovule, one sperm cell fertilizes the egg cell and the other unites with the two polar nuclei of the embryo sac. The sperm and haploid egg combine to form a diploid zygote and later the embryo of the seed. The other sperm and the two haploid polar nuclei form a triploid nucleus and later the endosperm, a nutrient-rich tissue nourishing the developing embryo (Raghavan 2006). The ovary, which encompasses the ovule, develops into the pericarp of the fruit and helps to protect and disperse the seeds.

In self-fertilized fruit crops, for example, in most peach and nectarine cultivars, successful fertilization can occur within one flower, and pollen grains from other flowers or from other cultivars are not necessary (Weinbaum et al. 1986). On the other hand, fertilization in cross-pollinated fruit crops, for example, in most apple, pear, almond, and rabbiteye blueberry (*Vaccinium ashei*) cultivars, will not succeed with pollen grains from flowers of same cultivars or other cultivars with incompatible genetic background. Therefore, it requires the mixed planting of two genetically compatible cultivars in an orchard block to achieve a satisfactory yield (Visser and Marcucci 1984, Dedej and Delaplane 2003). In some fruit crops, for example, northern highbush blueberries (*Vaccinium corymbosum*), although self-pollination is possible to set fruit, cross-pollination by mixed planting two cultivars will increase the fruit size and quality (Huang et al. 1997, Ehlenfeldt 2001, Bieniasz 2007).

The embryo of the developing seed produces plant hormone gibberellins at early development stages to trigger the production of auxins and stimulates fruit growth (Ozga et al. 2002). In conclusion, pollination and fertilization are normally required to initiate fruit growth.

FRUIT SET

Fruit set refers to the retention of fruit on the plant after bloom. Most fruit crops produce numerous functional flowers but only a small percentage of the flowers continue to develop into mature fruits. Normally, less than 5% of apple flowers and less than 3% of orange flowers would continuously grow and mature by harvest.

In stone fruits, such as peaches, cherries, and plums, flowers will drop and fruits will not develop without a fertilized embryo. In some fruits, such as apples and pears, the fruit may set with few or no seeds, but the growth of the cortex exterior to a seedless carpel will be affected (Drazeta et al. 2004).

Flower or fruit drop may occur in various periods before full maturation of the fruit (Racskó et al. 2007). *Early flower drop* occurs before anthesis or petal fall, most likely when the flowers have not yet fully developed. Flower dropping shortly after anthesis, known as *late flower drop*, is a result of poor pollination or failure in fertilization. In most fruit crops, the fruit normally drops soon after bloom if fertilization has failed. In sour cherries, fertilization occurs in about 40% of flowers only (Lech and Tylus 1983). *Mid-season fruit drop*, often called *June drop* in the northern hemisphere, *December drop* in the southern hemisphere, or physiological fruit drop by plant physiologists, is a common phenomenon in which a significant portion of young fruits drop within several weeks after bloom. Mid-season fruit drop can be a delayed response to inadequate fertilization, involving the competition among fruits or between fruit growth and vegetative growth for resources (Agustí et al. 2002), environmental stress, or hormone imbalance (Racskó et al. 2006). Upon the completion of mid-season fruit drop, final fruit set is determined, and the remaining fruits usually continue to grow toward full maturity. In some instances, for example, “McIntosh” apples, a significant preharvest fruit drop may occur. The mechanism of this problem has yet to be fully explained (Ward 2004), but can be likely due to internal ethylene production (Blanpied 1972).

The growth and development of the fruits remaining on a tree is still influenced by many internal and environmental factors (Ho 1992). The presence of seeds is the major factor in the early fruit development stages. The growth and development of fruits in late stages are independent of seed development.

PARTHENOCARPY AND STENOSPERMOCARPY

Seedless fruits are often preferred by consumers. Some fruits can continue to grow without developing normal seeds in the

carpel. Seedless fruits can be a result of parthenocarpy or stenospermocarpy.

In parthenocarpic fruit set, a flower continues to develop into a fruit without pollination or fertilization. Parthenocarpy can be a natural event or induced by cultural practices (Gustafson 1942). Commercial banana and pineapple cultivars are naturally parthenocarpic, requiring no pollination (Simmonds 1953). Many citrus fruits will also set parthenocarpic fruits but require pollination to stimulate fruit growth. Seedless watermelons are commercially produced by cross-pollination between diploid and tetraploid parents (Terada and Masuda 1943). Parthenocarpy in watermelon can also be induced by the application of plant growth regulators (Terada and Masuda 1941) or by using soft X-ray irradiated pollen (Sugiyama and Morishita 2000).

In stenospermocarpic fruit set, both pollination and fertilization are required to initiate the growth of fruit, but the embryo aborts soon after fertilization, while the fruit continues its normal growth. Seedless grapes can be a result of natural stenospermocarpy as in the case of “Thompson Seedless” and “Flame Seedless” cultivars (Bharathy et al. 2005, Hanania et al. 2007) or artificially induced stenospermocarpy by plant growth regulators as in the production of seedless grapes in Japan (Shiozaki et al. 1998). Many lychee cultivars are liked for their shrivel seeds, a result of natural stenospermocarpy (Xiang et al. 2001).

FRUIT GROWTH

The growth of a fruit to reach its final size and weight involves an increase in cell numbers in the early stage and an increase in cell size and intercellular space in the late stage.

Cell Division

Fruit growth begins with a slow phase that is corresponding to cell division. During this stage, cell numbers are increasing, while the changes in fruit size and weight are not significant. The number of cells in a fruit is set upon the completion of cell division. The period of cell division and its contribution to the growth of entire fruit are not consistent among different fruit species (Carini et al. 2001). In *Ribes* (currants and gooseberries) and *Rubus* (raspberries and blackberries), cell division is completed by anthesis, and cell number of a berry will not change after bloom. Cell division in apple completes in about 4–5 weeks after bloom and accounts for about 20% of the total fruit growth period. Cell division in pears normally continues for 7–9 weeks after bloom and accounts up to 45% of the total growth period (Toumadje and Richardson 1998). In strawberries, cell division continues and the cell number increases up to harvest.

Cell Enlargement

A fruit enters the fast-growth phase upon the completion of cell division, and the sizes of individual cells and

intercellular air spaces start to increase. At bloom, intercellular air spaces are absent or very small. Concurrent with cell enlargement, air spaces increase to a maximum. When a cell enlarges, its vacuole increases in size and finally occupies most of the volume inside. The vacuolar, i.e., the cell sap inside a vacuole, contains mostly water and sugars with normally a small amount of organic acids and other compounds. During the cell enlargement stage, pigments may also form and accumulate in vacuoles in epidermis cells (Schwab and Raab 2004).

Seasonal Growth Curve

The durations of cell division and cell enlargement stages determine the seasonal growth rate and the final size of a fruit. Fruit size can be plotted against time. The resulted plot typically expresses a sigmoid or S-shape curve with various degrees of curvature depending on fruit species and environmental conditions in which the fruit develops. Fruits are generally categorized into two groups according to their seasonal growth patterns: that expressing a single sigmoid curve and that expressing a double sigmoid curve (Westwood 1995).

Single Sigmoid Growth Pattern A single sigmoid seasonal growth pattern begins with a slow initial growth rate followed by a phase of rapid linear increase in fruit size and then a declined growth rate when approaching full maturity. Examples of fruits expressing a single sigmoid growth pattern are apple, pear, strawberry, walnut, pecan, etc. Such fruits in the slow initial growth stage show few physiological changes but rapid morphological changes corresponding to the cell division phase. The mid-season fast growth stage corresponds to cell enlargement and rapid physiological changes. The declined final growth rate signals the maturation of the fruit.

Double Sigmoid Growth Pattern Some fruits express a double sigmoid seasonal growth pattern with two separate rapid size increasing phases linked by a slow-growth phase. Examples include stone fruits (peach, plum, cherry, etc.), and other fruits (grape, fig, etc.). Changes in fruit size are not significant during the slow mid-season growth phase while internal physiological and morphological growth proceeds. In stone fruits, the slow-growth phase is corresponding to the hardening of the endocarp and the formation of the pit (Dardick et al. 2010). In grape, development of the embryo inside the seed is almost completed by the end of the slow growth phase (Dokoozlian 2000).

MATURATION, RIPENING, AND SENESCENCE

Maturation, ripening, and senescence of a fruit are in a continuous process before and after harvest. This process involves numerous morphological, physiological, and metabolic changes as a result of gene transcription and enzyme generation (Giovannoni 2001).

Maturation of a Fruit

As a fruit continues to grow toward harvest, its palatability is improved by the morphological and physiological changes. Maturity and ripeness have different meanings. When a fruit reaches its full maturity, its size and weight reach a maximum and its growth rate decreases. A fully matured fruit is capable of continuing normal development to “ripen,” or to improve its palatability, after harvest. However, the development of maturity can only happen while the fruit is still attached to the plant.

Ripening of a Fruit

Ripening refers to the physiological and biochemical changes of a fruit to attain desirable color, flavor, aroma, sweetness, texture, and thus eating quality. The process of ripening usually does not occur until a fruit reaches its full maturity. Ripening of a fruit may occur on the plant or after harvest, depending on the species. A fully matured apple or mango fruit on the tree will continue to ripen (Bender et al. 2000), while European pears and bananas will not palatably ripen on the tree and are commercially harvested at full maturity and then forced to ripen for acceptable quality.

Senescence of a Fruit

When a fruit passes its maximum ripeness, it begins to breakdown and decay. Rather than a simple breakdown process, senescence is the final phase in ontogeny of a fruit, in which a series of normally irreversible physiological and biochemical events is initiated, which leads to cell breakdown and death of the fruit (Sacher 1973).

Physiological Changes of a Fruit toward Maturity

Color When a fruit grows toward its full maturity, many physiological changes in addition to its size and shape are happening simultaneously. Typically, the first noticeable change is the decline of chlorophyll in the chromoplast of the skin cells so the ground color of the fruit fades. Concurrently, attractive color of the skin and flesh develops due to the accumulation of anthocyanins, carotenoids, or flavones in vacuoles of epidermal cells (Fernández-López et al. 1992, Ikoma et al. 2001).

Seed Maturity Seeds in the fruit usually reach full maturity prior to the entire fruit does. The maturation of seeds is indicated by the darkened color of the seed coat.

Carbohydrate Profile For many fruits that accumulate starch during the cell enlargement stage, for example, apple, European pear, and mango, part of the stored starch is hydrolyzed to sugars during maturation. Major sugars in fruit are sucrose, glucose, and fructose (Brookfield et al. 1997).

For fruits that do not accumulate starch, for example, grapes, citrus, and peaches, a significant amount of sucrose is transported into the fruit during maturation and later partially transformed to glucose and fructose (Holland et al. 1999).

Acids The acid content in the fruit decreases accompanying the increase in sweetness during maturation. Major acids in the fruit are malic, citric, and tartaric. Most fully matured fruits contain less than 1% acid. Among the exceptions, lemon and lime fruits accumulate citric acid and increase acidity to more than 3% toward full maturity (Ramadan and Domah 1986).

Aroma and Flavor Compounds Aroma and flavor development occur when a fruit is reaching its full maturity. Aromatic compounds are generally volatile esters and alcohols (Gunata et al. 1985). Both aroma and flavor components accumulate up to full ripeness and then begin to decline as the fruits enter senescence phase. The desirable aroma and flavor may then be mingled with off-flavor materials. The accumulation of aromatic compounds during ripening and senescence is determined in large part by the genetics of the individual cultivar. However, environment, cultural practices, agrichemicals, and nutrition also have impact on flavor through effects on fruit development (Mattheis and Fellman 1999).

Firmness As a fruit is reaching its full maturity, cell walls become less interconnected due to pectin degradation and intercellular space expansion, resulting in reduced fruit firmness. Fruit softening and other textural changes in peach appear to have a number of stages, each involving a different set of cell wall modifications (Brummell et al. 2004). During maturation of grape, the cell walls in the skin lose structural polysaccharides and calcium continuously. Meanwhile, the incorporation of structural proteins and the cross-linking among phenolic compounds become active especially in the walls of epidermal and subepidermal cells (Huang et al. 2004).

Tannins In sweet persimmons (nonastringency persimmons), coagulation of tannins occurs when fruits are fully matured (Yonemori and Matsushima 1987). However, coagulation of tannins do not occur at full maturity in astringent cultivars, thus postharvest care is required to remove their astringency (Taira et al. 1992, Ben-Arie and Sonog 1993).

Respiration The rate of respiration normally increases when fruits are maturing. The degree of increment is dependent on the type of fruit (climacteric or non-climacteric) and differs among cultivars. Generally, early cultivars that mature in the early summer have a high respiration rate, short postharvest life, and early senescence. On the other hand, late cultivars that are harvested in the cool season have a low respiration rate and long storage life. Many berries, for ex-

ample, strawberry, mulberry, raspberry, and blackberry have very high respiration rate. On the other hand, nuts and dry fruits have very low respiration rate at harvest (Kader and Barrett 2005).

FRUIT CLASSIFICATION

Various classification systems have been applied to fruits to meet the objectives of classification. Fruits can be classified based on their origins (Kader and Barrett 2005), growth patterns (Westwood 1995), postharvest respiration rates and ethylene responses (Lelièvre et al. 1997), anatomical features (Spjut 1994), or the consumer's preference.

FRUITS CLASSIFIED BY THEIR ORIGIN

According to their origins and major production areas, fruits are commonly grouped into three types: temperate fruits, subtropical fruits, and tropical fruits. Most temperate fruit crops are deciduous and cultivated in regions with a period of chilling temperature in the winter for successful growth and yield (Westwood 1995). Temperate fruits include most common fruits from *Rosaceae* family and popular small fruit crops. Tropical and subtropical fruit crops differ from each other on the degree of tolerance to low temperature. Subtropical fruits include most citrus crops and some other evergreen species (Jackson et al. 2010). Tropical fruits mostly originated in tropical rain forests; they do not tolerate a temperature below 10°C. In addition to the well-known tropical fruits, for example, banana, mango, papaya, and pineapple, many other tropical fruits, fairly common and favored in specific regions, are rarely seen outside the tropics and therefore considered exotic for people living in the temperate and subtropical regions (Morton 1987). Examples of each fruit type are listed in Table 1.1.

FRUITS CLASSIFIED BY RESPIRATION RATES AND ETHYLENE RESPONSES

Many fruits at full maturity maintain a consistent, low respiration rate and are called *nonclimacteric* fruits. The respiration rate of such fruits responds primarily to temperature. On the other hand, fruits showing a remarkable increment in respiration rate in maturation are called *climacteric* fruits (Biale 1960). Examples of climacteric and nonclimacteric fruits are listed in Table 1.2. In addition to their distinctive respiration patterns, climacteric and nonclimacteric fruits also differ from each other in their response to ethylene (Lelièvre et al. 1997). When the climacteric fruit matures, a traceable amount of ethylene is produced, which triggers more ethylene production and a series of ethylene-related ripening and senescence processes. These responses can also be triggered by external application of ethylene to a mature climacteric fruit.

Ethylene production and reaction can be downregulated by the reduction in temperature (Cheng and Shewfelt 1998),

Table 1.1. Classification of Common Fruits by Their Origins and Main Production Regions

Temperate Fruits	Subtropical Fruits	Tropical Fruits
Apple, pear, peach, nectarine, plum, cherry, apricot, grape, strawberry, brambles (raspberry and blackberry), currants, gooseberry, blueberry, cranberry, kiwifruit, pomegranate, fig.	Citrus fruit (sweet orange, mandarin, tangerine, pummelo, grapefruit, lime, lemon, kumquat), avocado, cherimoya, lychee, loquat.	Banana, pineapple, mango, papaya, carambola (star fruit), guava, passion fruit, mangosteen, longan, jackfruit, durian, rambutan, sapota.

the increase in CO₂ content in the environment, the decrease in O₂ content (Kerbel et al. 1988, Gorny and Kader 1997), or the application of ethylene synthesis or reaction inhibitors such as aminoethoxyvinylglycine (Bregoli et al. 2002) and 1-methylcyclopropene (Blankenship and Dole 2003). These techniques have been commercially adopted to extend the postharvest life of climacteric fruits (DeEll et al. 2003).

BOTANICAL CLASSIFICATION OF FRUITS

Fruits can also be categorized into different types based on their anatomical origins. A fruit can be a simple fruit, derived from a flower, or a compound fruit, formed by many flowers. Either type of fruits can be further classified into subtypes.

Simple Fruits

A simple fruit is developed from a simple or compound ovary in a flower with only one carpel. Simple fruits can be dry or fleshy.

Simple Dry Fruits

A simple dry fruit is a fruit with dried pericarp. Simple dry fruits may be either dehiscent, i.e., opening to discharge seeds, or indehiscent, i.e., not opening to discharge seeds.

Table 1.2. Examples of Climacteric and Nonclimacteric Fruits

Climacteric Fruit	Nonclimacteric Fruit
Apple, banana, European pear, mango, papaya, persimmon, kiwifruit, cherimoya, avocado, guava, plantain, plum, peach, passion fruit, apricot, bread fruit, jackfruit, pawpaw, durian, feijoa, tomato, Indian jujube.	Grape, Asian pear, ^a orange, grapefruit, lemon, lime, pineapple, cherry, strawberry, lychee, blackberry, ^a blueberry, cranberry, raspberry, ^a pineapple, pomegranate, loquat, pitaya (dragon fruit), carambola (star fruit), rambutan, Chinese jujube.

^aAlthough these fruits are generally considered nonclimacteric, cultivars in the climacteric category have been reported.

Achene An achene is a dry single fruit formed from a single carpel (monocarpellate) and is not opening at maturity (indehiscent). Achenes contain a single seed that fills the pericarp, but the seed coat does not adhere to the pericarp. Achenes are most commonly seen in aggregate fruits. In strawberries, what we think of as the “seeds” on the fruit surface are actually achenes. A rosehip (or rose-hep), the fruit of rose, is in fact an aggregate fruit composed of many achenes (Genders 1966).

Capsule A capsule is a dry single fruit made of two or more carpels. Most capsules are dehiscent at maturity and the seeds within are exposed. A few exceptions are indehiscent, for example, the African baobab (*Adnsonia digitata*). Capsules of some species split between carpels, of others each carpel splits independently. Seeds are released through openings or pores that form in the capsule. In Brazil nut (*Bertholletia excelsa*), the upper part of the capsule dehisces like a lid and the seeds (“nuts” in commercial terms) are exposed (Rosengarten 1984). This type of capsules is called a pyxis.

Capsules may frequently be confused with the true nuts. The difference between a capsule and a nut is that a capsule splits when matures and the seeds inside are released or at least exposed, whereas a nut does not split or release seeds.

Caryopsis A caryopsis is a dry simple fruit resembling an achene. It is also monocarpellate and indehiscent. The only difference between a caryopsis and an achene is that in a caryopsis the pericarp is fused with the seed coat into a single unit. The caryopsis is commonly known as the grain and is especially referred to the fruit of *Gramineae* (or *Poaceae*), for example, corn, rice, barley, and wheat (Arber 2010).

Cypsela A cypsela is an achene-like simple dry fruit formed from the floret in a capitulum, the inflorescence or flower head of *Asteraceae*, for example, sunflowers. What we normally call a sunflower “seed” is a cypsela fruit. The husks of the seed are in fact the hardened pericarp of the fruit.

Fibrous Drupe A fibrous drupe differs from a typical drupe by its hardened, fibrous exocarp and mesocarp. Examples of fruit crops that bear fibrous drupes are coconut, walnut, and pecan. The shell of the coconut is derived from the exocarp

and mesocarp, while the meat is the edible inner layer of the hardened endocarp. The husks of walnut and pecan are produced from the exocarp and mesocarp tissues of the pericarp while the part known as the nut is developed from the endocarp (Rosengarten 1984).

Legume A legume fruit, or commonly called a pod, is a fruit in the family *Fabaceae* (or *Leguminosae*) in botany. It is a simple dry fruit that is developed from a simple carpel and usually dehisces on two sides (Tucker 1987). Peas, beans, and peanuts are examples of well-known legume fruits.

Nut A nut is a simple, indehiscent dry fruit containing one single seed protected by hardened ovary wall. The seed of a nut is usually intimately attached with the ovary wall at full maturity. In botany, nut refers to the fruit of *Fagaceae*, such as chestnut; or *Betulaceae*, such as hazelnut or filbert.

Simple Fleshy Fruit

Simple fruits in which the pericarp, whole or part of it, is fleshy at maturity are called simple fleshy fruits. In most simple fleshy fruits, the pericarp and the carpel are fused together.

Berry A berry is a simple fleshy fruit having seeds and pulp produced from a single ovary. The entire ovary wall of the berry ripens into an edible pericarp. Depending on species, a berry may usually have one or many seeds embedded in the flesh of the ovary. Similar to nuts, berries are ambiguously referred to many edible small fruits that are not true berries in botanical sense. Examples of true berries are grape, kiwifruit, banana, currant, gooseberry, tomato, etc. On the other hand, strawberries, raspberries, blackberries, and mulberries are not true berries because they are developed from multiple ovaries. A serviceberry or juneberry (*Amelanchier*) resembles a true berry but anatomically it is a pome.

Drupe A drupe is a fruit in which the exocarp and mesocarp, the outer and middle layers of the pericarp, are soft and fleshy but the endocarp, the inner layer of the pericarp, is lignified to form a hardened shell in which a seed is enclosed. A drupe is developed from a single carpel. Stone fruits, for example, peach, plum, cherry, apricot, etc., bear typical drupe fruits. Other common fruit crops bearing drupes include jujube, mango, coffee, olive, palm date, etc.

Some fleshy fruits contain a pit but the hardened shell of the pit is derived from the seed coat rather than the endocarp. Examples are lychee, longan, etc. By definition, these are not drupes.

Pome A pome is an accessory fruit developed from one or more carpels of a single flower and its accessory tissues. Pomes are exclusively referred to the fruit produced by *Maloideae* subfamily under *Rosaceae* (Aldasoro et al. 1998).

Examples of pome fruits are apple, pear, quince, loquat, etc. The cortex of a pome fruit is the main edible part and is derived from the receptacle (the enlarged section of a stem from which the flower develops) or the fused hypanthium (the fused bases of the sepals, petals, and stamens), the exocarp, and the mesocarp. The core of a pome is the fused leathery endocarp and carpels containing seeds.

Most pome fruits have a distinctive cortex and core. Some, for example, serviceberry or juneberry (*Amelanchier*), bear berry-like pome fruits with juicy flesh and indistinguishable core.

Hesperidium A hesperidium is a modified berry specifically referred to the fruit of the *Citrus* family (Ladaniya 2008). The exocarp forms the outmost layer of the tough, leathery rind of the fruit and is known as the flavedo. The flavedo contains pigments and essential oils. Underneath the flavedo is the albedo or pith that is derived from the mesocarp. The endocarp forms the fleshy part with separate sections (segments). The juicy sacs inside the segment are called juice vesicles and are actually specialized hair cells.

The rind of most hesperidia is usually not being consumed with the flesh. In some cooking styles, the flavedo of lemons or oranges is used as a flavor ingredient called zest. The rind of some hesperidia, for example, kumquat (*Fortunella margarita*), is tender and sweet and usually consumed together with the juicy sacs.

Pepo The term “pepo” is referred to a fruit from the melon (*Cucubitaceae*) family. A pepo is botanically a modified berry with hard, thick rinds derived from the exocarp. The fleshy inside is composed of mesocarp, endocarp, and ovary (Whitaker and Davis 1962). Most common pepo fruits, for example, cucumber (*Cucumis melo*), water melon (*Citrullus lanatus*), and pumpkin (*Cucurbita maxima*), contain many seeds. The chayote (*Sechium edule*) also belongs to the melon family but bears pepo fruit with only one large seed. The bitter melon (*Momordica charantia*) bears dehiscent pepo fruits that, when fully ripened, split into segments, which curl back dramatically to expose seeds covered in bright red pulp.

Compound Fruits

A compound fruit is a fruit derived from multiple ovaries within a single flower or from multiple flowers, each bearing a single ovary. The former is designated as an aggregate fruit and the latter a multiple fruit (Spjut and Thieret 1989).

Aggregate Fruit An aggregate fruit is developed from a single flower that has multiple pistils, each containing one carpel. Each pistil forms a fruitlet. Together, the fruitlets are called an aggregate or an etaerio (from French etaïrion, and from Greek hetaireia, association). Aggregate fruits can be etaerios of achenes, drupes, or berries. Strawberry bears aggregate fruits of achenes. Botanically, the “seeds” on a

strawberry are the true fruits and the fleshy part of the fruit is derived from the enlarged receptacle of the flower. A raspberry or blackberry is an aggregate of drupes each containing one pit. Annona fruits, for example, custard apple, cherimoya, and Atemoya, bear aggregates of berries.

Multiple Fruit A multiple fruit is derived from an inflorescence composed of multiple flowers. The ovaries of each individual flower are fused together to form a single fruit at maturity. There are different types of multiple fruits corresponding to different origins in the development. A sorosis, for example, mulberry, is a multiple fruit derived from the incorporated ovaries of the flowers. A coenocarpium, for example, pineapple and jackfruit (*Maclura pomifera*), is composed of the ovaries, floral parts, and receptacles of many flowers and the fleshy axis of the inflorescence. A fig fruit is also a multiple fruit developed from a syconium, a specialized inflorescence on *Ficus* plants.

Accessory Fruit

An accessory fruit is a fruit in which the fleshy part is mainly derived from the accessory tissues of the flower. Accessory fruits are also called false fruits or pseudocarps. For example, strawberries are aggregate fruits of achenes while are also accessory fruits because the fleshy part is the enlarged receptacle. Pome fruits with an enlarged fleshy receptacle fall in the same category. A fig fruit is another type of accessory fruit of which the enlarged hollow flesh part is the receptacle bearing multiple ovaries on the inside surface.

CULINARY CLASSIFICATION OF FRUITS

Botanically, a fruit means the structure on a plant developed from a flower and the accessories of this flower. In culinary practice and food processing point of view, edible fruits are grouped into four categories: fruits, fruits used as vegetables, nuts, and cereals.

Fruits

In culinary practice and food processing, fruits commonly refer to any edible part of a plant with a sweet taste and pleasant flavor, corresponding to most edible fleshy fruits in the botanical sense. However, some botanical fruits may not be palatable or sweet, for example, lemon, avocado, and cranberry, but are still considered as fruits in cooking or processing.

In some unusual cases, a plant part other than the botanical fruit may be accepted as a fruit in cooking or processing. For example, the fleshy and sweet petiole of the rhubarb (*Rheum rhabarbarum*) is considered a fruit in the United States.

Fruits used as Vegetables

Many fruits that are not palatable or sweet when consumed raw offer savory taste when cooked or processed and are recognized as vegetables in culinary sense. Crops that

Table 1.3. Common Culinary Nuts and Their Botanical Definitions

Culinary Nuts	Botanical Definition
Chestnut, hazelnut	True nuts
Almond, walnut, pecan, pistachio, macadamia nut	The kernel of a drupe
Brazil nut	The seed in a capsule
Peanut	The seed in a legume fruit
Cashew nut	The seed in a drupe
Lychee nut	A dried lychee fruit, the edible meat is the aril

are used as vegetables are mainly from the tomato family (*Solanaceae*), the gourd family (*Cucurbitaceae*), and the pea family (*Fabaceae*).

Some crops, for example, tomato, are mainly consumed as a vegetable in one region while commonly consumed as a fruit in another region.

Nuts

Although botanically only a few plant species in *Fagaceae* and *Betulaceae* produce true nuts, culinary nuts are a big group of dried seeds and fruits with diverse varieties. Many seeds and dry fruits producing oil-rich kernels within hardened pericarps or seed coats are all called nuts in food and processing industries (Rosengarten 1984). Examples of common culinary nuts and their botanical definitions are listed in Table 1.3.

Cereals

The dry fruit produced by *Poaceae* or *Gramineae* is botanically called a caryopsis, a type of dry fruit, but in culinary definition, those fruits cultivated for their edible parts are referred to as cereals or grains. Important cereal crops include wheat, rice, maize, etc. They are the major daily sustenance and unarguably the most important staple food in the world.

In addition to the caryopsis fruits from *Gramineae* family, a few species from other families bearing starch-rich seeds are also included in cereals, for example, buckwheat (*Fagopyrum esculentum*). Some oilseeds and oil-bearing materials are also considered cereals (Lusas 2000). Some cereal crops, for example, sweet corns, are used as vegetables when their fruits are young and tender.

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2

Biochemistry of Fruits and Fruit Products

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Abstract: Fruit ripening is a complex developmental process accompanying the last phase of fruit development and senescence. Ripening is a highly specialized and regulated process in which many of the physiological and biochemical changes occurring determine the nutritional and organoleptic quality of the fruit. Due to the tremendous commercial impact of fruit ripening on the consumers and society, considerable efforts have been made to understand the biochemical and molecular basis controlling the process. For many years, ethylene has been considered as the ripening hormone, but current evidences indicate that the classical classification between climacteric and nonclimacteric fruit is probably an oversimplification, and the hormone plays an essential role in the processes accompanying ripening in both types of fruit. In the present chapter, we summarize most recent findings of relevant changes taking place during ripening, as ethylene biosynthesis and regulation,

changes in pigment composition, aroma formation, carbohydrate, organic acids, and lipid composition. The main metabolic pathways of components of fruit quality are revised and critical assessments of molecular approaches influencing ripening are presented and discussed.

INTRODUCTION

Fruits and fruit products are good sources of vitamins, minerals, and many other components essential for human nutrition and health. Fruits of different plant species vary in size, shape, texture, color, flavor, organoleptic, and nutritional characteristics. The biological function of the fruit is to attract animals for seed dispersal, and throughout evolution, plants have adopted a diversity of features to make fruits attractive to natural predators. Fresh fruits are botanically diverse since the ontogeny and structure of both the capsule containing the seeds and the edible portion are highly different from fruit to fruit. Pome fruits such as apples and pears develop from the thalamus, while stone fruits develop from the ovary wall. Berry fruits such as tomato or grape are derived from the ovary, and strawberry or pineapple come from receptacle tissue. Citrus fruits are a modified hesperidium, in which the ovary walls develop a structure containing the locules of juice sacs. Despite the high diversity, many physiological aspects of fruit growth and development, and regulatory aspects of the biochemical and molecular changes during fruit ripening are somewhat similar. Changes in color, sugars, acidity, softening and loss of texture, synthesis of aroma and flavor components, and increased susceptibility to physiological disorders are prominent during fruit ripening. The fact that many of these processes are common in fruits of different plant species suggest that the regulatory mechanisms governing these transformations have been

at least partially conserved during evolution and the agromonomical domestication of the species. The biochemistry of fruit ripening has been the subject of comprehensive reviews (Paliyath and Murr 2006, Giovannoni 2004), and books (Seymour et al. 1993, Knee 2002). In this chapter, we summarize relevant biochemical changes during fruit ripening with emphasis on metabolic pathways of major components of fruit quality and molecular approaches influencing ripening.

REGULATION OF FRUIT RIPENING: THE ROLE OF ETHYLENE

The role of ethylene as the “ripening hormone” in regulation of fruit ripening has been recognized for many years. There are many ancestral practices for fruit manipulation and storage, which complement advance ripening, that are now known to be mediated by ethylene. The degreening of citrus fruits and bananas are two examples of ethylene-based postharvest technologies used worldwide. The notion of climacteric ripening was initially defined by Kidd and West as early as 1925 and is fundamental to understanding the physiology of the fruits and postharvest handling and storage. Fruits have been classically categorized as climacteric and nonclimacteric based on their ability to increase ethylene production and respiration rate at the onset of ripening. This climacteric behavior is invariably associated with an autocatalytic control of ethylene production. By contrast, fruits that do not produce elevated levels of both ethylene and respiration are referred to as nonclimacteric (Biale and Young 1981).

The increase in respiration and ethylene production accompanying the onset of ripening in climacteric fruit is not always coordinated. There are examples in which the rise in respiration rate precedes, or is concurrent or follow climacteric rise in ethylene production (Biale and Young 1981). Although the metabolic basis for the relationship between these two processes are still uncertain, evidences from transgenic fruits in which ethylene production has been genetically reduced indicate that ethylene is the trigger factor for the increase in respiration rate (Oeller et al. 1991).

However, this categorization is controversial and may depend on the experimental conditions. There are examples of different cultivars of plums with climacteric and non-climacteric ripening features (Abdi et al. 1997). The duration and intensity of the climacteric responses, either ethylene production or respiration rate, may also differ substantially among species and cultivars of the same species. Moreover, in nonclimacteric fruits, ethylene treatment enhances the ripening process. Therefore, categorization of fruit ripening in these two classical groups may be an oversimplification of the natural phenomena. However, in general, ethylene production appears to be a more reliable criterion for the distinction between climacteric and non-climacteric fruits (Watkins 2002).

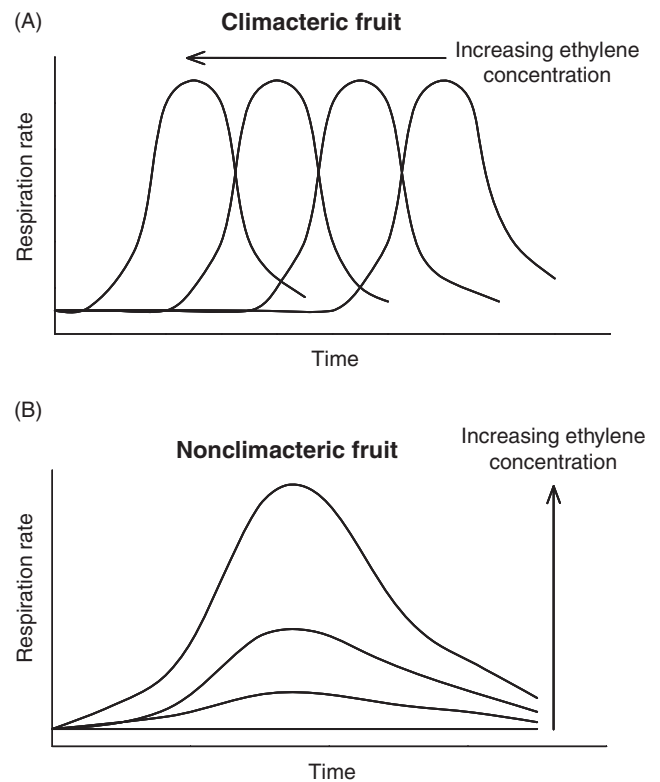


Figure 2.1. Effect of increasing ethylene concentrations on respiration of climacteric and nonclimacteric fruits.

Other important difference between climacteric and non-climacteric fruits is the response to exogenous ethylene. In climacteric fruit, ethylene deficiency affects the time to reach the maximum climacteric respiration but not its magnitude. This response is independent on the concentration of ethylene and is irreversible (Fig. 2.1A). Once a threshold of ethylene is achieved, it initiates autocatalytic ethylene production that irreversibly hastens the ripening process even if ethylene is removed. In nonclimacteric fruit, by contrast, ethylene increases the respiratory rate in a concentration-dependent manner (Fig. 2.1B). Since autocatalytic ethylene production is not operative, once ethylene is removed, respiration declines to basal levels, and the maturation rate is consequently delayed (Biale and Young 1981). These effects of exogenous ethylene are likely to mimic the endogenously produced and are of particular importance in the postharvest performance of the fruit. Ethylene may accumulate from nonbiological contaminants and also from ripening fruits, and the responses of stored fruit may be differentially affected and the storage-life reduced.

On the basis of the differences in the responses to ethylene and in the control of ethylene production, McMurchie et al. (1972) postulated the presence of two systems of ethylene production in plants. System 1 functions during

normal growth and development and in responses to stress conditions. This system is common to climacteric and non-climacteric fruits and to other tissues, and is regulated in a negative manner. System 2 is only present in climacteric fruits and is characterized by being stimulated by ethylene (autocatalytic). It was thought that ethylene production during the life span of the plants is produced by system 1, but only climacteric fruit would have the ability to stimulate system 2 once ethylene has reached a threshold and ripening would be initiated (Yang 1987).

Ethylene biosynthetic pathway in higher plants is now well defined, and regulation of ethylene biosynthesis during fruit maturation, especially in climacteric fruit, has been extensively studied. Excellent and comprehensive literature revisions have been compiled with recent findings and major breakthroughs (Giovannoni 2004, Barry and Giovannoni 2007, Cara and Giovannoni 2008, Bapat et al. 2010). Briefly, synthesis of *S*-adenosyl-L-methionine (SAM) from the amino acid methionine catalyzed by SAM synthase is the first step of the pathway. SAM is then converted to 1-aminocyclopropane-1-carboxylic acid (ACC) by the enzyme ACC synthase (ACS). Finally, ACC is oxidized to ethylene by an ascorbate-dependent ACC oxidase (ACO), which also generates carbon dioxide and hydrogen cyanide (NCH). Ethylene is produced in plants by many developmental and stress stimuli, and a large body of evidences indicate that ACS is the rate-limiting step in the pathway; even ACO is, to a minor extent, other regulatory factor. ACS and ACO are encoded by multigene families, which in the case of tomato are composed by eight ACS and five ACO genes (Cara and Giovannoni 2008). Differential expression of each member of these gene families in a tissue- and stimuli-dependent manner determines the timing and intensity of ethylene biosynthesis in different developmental processes. During tomato fruit ripening, it has been shown that *ACS1* and *ACS3* are expressed in green fruit, maintaining low levels of ethylene in the preclimacteric stage (system 1). *ACS2* and *ACS4* were expressed at the onset of ripening and are stimulated by ethylene, thus being responsible for autocatalytic ethylene production (system 2). Other members, such as *ACS6*, were expressed in green fruit but repressed by ethylene. Two ACO genes (*ACO1* and *ACO4*) were also induced during ripening and stimulated by ethylene (Nakatsuma et al. 1989, Barry et al. 2000, Yokotani et al. 2009). These results indicate that coordinated expression of specific ACS and ACO gene members in a specific and temporal manner regulate the transition from low (system 1) to high and autocatalytic (system 2) ethylene production during fruit ripening. Other factors such as ACS phosphorylation, ubiquitination, and ACO activity may also play a crucial role in modulating ethylene synthesis (Barry et al. 2007).

The role of ethylene in regulating fruit ripening has been clearly demonstrated in tomato and other plants by genetic manipulation of ethylene biosynthetic genes. Genetic engineering of ACS and ACO genes has been accomplished in several horticultural crops, such as tomato, apple, banana, or

melon (Barry and Giovannoni 2007, Matas et al. 2009, Bapat et al. 2010). In tomato plants transformed with an antisense ACS gene, fruit ripening was severely delayed and climacteric respiration failed to increase. Exogenous ethylene restored these phenotypes, indicating that ethylene is required to induce fruit maturation, including enhancement of respiration (Oeller et al. 1991). Other results with antisense ACO genes showed inconsistent results because delayed some ripening-associated processes (lycopene accumulation, loss of acidity), but other physiological processes were unaltered (Murray et al. 1993, Picton et al. 1993). Similarly, transgenic melon with reduced ethylene production displayed alteration in only some of the ripening-associated events (flesh firmness, rind coloration, aroma emission, among others) but not in others such as flesh coloration, sugar content, loss of acidity, or ACS induction (Guis et al. 1997, Pech et al. 2008). ACO-antisense transgenic apples also displayed a reduced aroma volatile emission, were firmer, and were with an extended shelf life (Dandekar et al. 2004). Together, these observations indicate that fruits from different species may have different requirements of ethylene production during natural ripening, which explain the variation of phenotypes observed in the low ethylene-producing transgenic plants. This further reinforces the notion that ethylene has only a limited role in regulating physiological and biochemical characteristics of fruit ripening (Barry and Giovannoni 2007).

Ethylene perception and signal transduction are also determinants in the ripening process of fruits. Major advances have been made in understanding how ethylene binds to plant receptors and how the signal is transduced to the nucleus, activating specific programs of gene expression. There is a high degree of divergence in plants, but in general, there are two families of ethylene receptors: subfamily I of receptors most homologous to histidine kinases and members of subfamily II lacking of this kinase domain (Kendrick and Chang 2008). In tomato, at least three members of each subfamily have been identified (Klee 2004). Expression of ethylene receptors during ripening has been also studied in climacteric (Takahashi et al. 2001, Rasori et al. 2002, El-Sharkawy et al. 2003, El-Sharkawy et al. 2007, Yin et al. 2008, Tatsuki et al. 2009) and nonclimacteric fruits (Katz et al. 2004, Trainotti et al. 2005, Wang et al. 2010). Tomato ethylene receptors have distinct patterns of expression during fruit ripening and in response to stress. *ETR1* and *ETR2* are constitutively expressed, but *NR*, *ETR4*, and *ETR6* are induced during ripening. Interestingly, loss of function in most of these genes did not produce altered ripening, but reduced expression of *LeETR4*-enhanced ethylene sensitivity and accelerated ripening. Reduced expression of *NR* was not associated with an altered ripening since *LeETR4* was overexpressed (Kevany et al. 2008). These results indicate a functional compensation between some of the ethylene receptors, and some of them function as negative regulators of ethylene response. Moreover, it has been shown that *LeETR4* and *LeETR6* proteins are degraded in response to ethylene during accelerated fruit ripening.

Current evidences are compatible with a model in which ethylene receptor is a major determinant of ripening initiation. As the receptors are negatively regulated by ethylene, their depletion would result in a progressive increase in hormone sensitivity and a consequent accelerated ripening (Kevany et al. 2007).

The classic concept of nonclimacteric ripening implies that the process proceeds with no changes in ethylene production. In strawberry, the use of the highly sensitive laser photoacoustic gas chromatography has revealed an increase in ethylene production that appeared to be autocatalytic and in respiration rate once the red color was developed (Iannetta et al. 2006). Interestingly, it has been also shown an expression of the ethylene receptors (*ERT2* and *ERT4*) in a ripening-dependent manner (Trainotti et al. 2005). This notion is also consistent with the effect of ethylene and of the ethylene action inhibitor, 1-MCP, in the evolution of different events during strawberry ripening (Villarreal et al. 2010).

The use of the 1-MCP has been important to understand the role of ethylene in grape ripening. In a series of experiments during ripening, it has been demonstrated that ethylene is required at the onset of ripening for anthocyanin accumulation and acid decline (Chervin et al. 2004). Several anthocyanin biosynthetic genes, including alcohol dehydrogenase (ADH), were also regulated by ethylene and repressed by 1-MCP (El-Kereamy et al. 2003, Tesniere et al. 2004). These results indicate that ethylene is involved in multiple aspects of grape development. Other classical nonclimacteric fruit like citrus, display several features suggesting that at least some ripening events may be controlled by ethylene. Inhibitors of ethylene action have been demonstrated to inhibit development of peel coloration (Goldschmidt et al. 1993). Ethylene by contrast, stimulated the expression of carotenoid biosynthetic genes, reproducing the naturally induced pattern of expression (Rodrigo and Zacarias 2007). It is interesting to mention that 1-MCP suppressed the expression of carotenoid biosynthetic genes of fruit on the tree (Carmona et al., in press), indicating that this hormone is involved, at least in the induction of peel coloration, during natural fruit ripening. Analysis of ethylene biosynthesis during the reproductive development of orange fruit has shown that ethylene production in immature fruits is autocatalytic, whereas mature fruits evolve a negative feedback regulation of ethylene production (Katz et al. 2004). Collectively, ethylene also appears to be involved in the ripening process of non-climacteric fruits, although the mechanisms may be different from the climacteric fruits. It is conceivable that other unknown biochemical and molecular systems may have developed in nonclimacteric fruit to sense and coordinate the ethylene signals in spite of the reduced levels of ethylene production during ripening, suggesting the possibility of new pseudo-climacteric mechanisms.

Early studies in tomato fruit stored under controlled atmosphere pointed out to the occurrence of ethylene-dependent

and -independent processes during fruit ripening (Watkins 2002). Transgenic fruits, especially melon, tomato, and apple, with reduced ethylene production, and the use of 1-MCP have proved to be valuable to examine ripening events under ethylene control. In *ACO*-antisense melon fruit, it was observed that the initiation of climacteric ethylene (ACS activity and ACC content) was under developmental or environmental control, but the rate of the process may be ethylene-dependent. Those fruits displayed altered rind yellowing, softening of the flesh, development of the peduncle abscission zone, aroma formation, and climacteric respiration, indicating that they are totally or partially ethylene-dependent. Other processes such as pulp coloration, accumulation of sugars, and loss of acidity were ethylene-independent processes (Ayub et al. 1996, Guis et al. 1997). Fruit softening was substantially affected in the *ACO*-antisense melon, but the activation of a subset of cell wall hydrolytic enzymes demonstrated the presence of components dependent and independent of ethylene (Hadfield et al. 2000). Other studies have demonstrated that fruit softening still occurred in fruit with a small residual ethylene production (antisense-*ACO* tomato and apple fruit) or in 1-MCP-treated kiwifruit (Koukounaras and Sfakiotakis 2007), suggesting the implication of ethylene-independent components.

Emission of volatile compounds and aroma formation is one of the effects more severely affected in fruits with reduced ethylene production or sensitivity. A genomic analysis in *ACO*-antisense apple fruit demonstrated that ethylene only regulates a reduced number of genes in the different ripening-associated processes. Ethylene-dependent genes are essential in the case of aroma production and predominantly in the final steps of the biosynthetic pathways (Schaffer et al. 2007).

CARBOHYDRATE METABOLISM

Biochemical changes during fruit development and maturation are the key determinants of fruit quality. In plants, photosynthesis produces organic compounds from inorganic carbon by using energy from the sunlight. In fruits, however, the contribution of photosynthesis to total carbon requirements declines during growth and maturation. Photosynthetically active tissues in fruit lose this capability during development as chlorophyll (Chl) is progressively lost. Contribution of photosynthesis to reproductive development varies across species. However, in many fruit trees, it ranges from 5% to 15% (Fleancu 2007).

In general, sugar accumulation in fruit is due to translocation of sucrose from leaf and bark and is stored as starch. Sucrose, the major form of transport sugar, is synthesized from glucose-1-phosphate. In some cases, sucrose is not the main transporting sugar in fruits, since it can be converted into glucose and fructose in a reaction catalyzed by the enzyme invertase. Sugar alcohols, mannitol and sorbitol, may be