Is Ethylene the Ripening Hormone

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Author’s contribution

The sole author designed, analyzed, interpreted and prepared the manuscript.

ABSTRACT

The fruits constitute a commercially important and nutritionally indispensable food commodity since they play a vital role in human nutrition by supplying the necessary growth factors essential for maintaining normal health. One of the limiting factors that influence their economic value is the relatively short ripening period and reduced post-harvest life. The fruit ripening involves a wide spectrum of coordinated biochemical and physiological processes that eventually leads to development of soft edible fruit with desirable qualities such as carotenoids, anthocyanin, color, sweetness, texture, firmness, flavor and aroma. The ripening is the phase of fruit development just before senescence, therefore the excessive tissues softening due to the high ethylene exposure leads to the spoilage upon the storage. Ethylene, a fruit ripening hormone can trigger many events of cell metabolism including ripening particularly in climacteric fruits even in minute amounts. As fruit mature, the rate of ACC and ethylene biosynthesis increases as well as the enzyme activities for ACC oxidase and ACC synthase enhance. However, the application of ethylene inhibitors such as 1-MCP, AVG and the ethylene remover proved to reduce the ripening where some quality attributes of ripening were reduced due to suppressed expression of the ripening hormone.

Keywords: Fruit; fruit ripening; ethylene; ethylene inhibitors; key enzymes.

1. INTRODUCTION

The fruit is highly specialized organs in the higher plants offering a great variety of aesthetic qualities with their complex delicate aroma, pleasant taste, exotic colors, succulence, flavor and texture [1]. Being part of the balanced diet, they play a vital role in human nutrition by

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supplying necessary growth regulating factors essential for maintaining normal health. One of the limiting factors that influence their economic value is the relatively short ripening period and reduced post-harvest life. The fruits are classified as tropical, sub-tropical and temperate and they are harvested in the maturity stage. In addition, they are self-sufficient with their own catalytic machinery to maintain an independent life, even when detached from parent plant. The ripening is a term that encompasses many processes which may occur simultaneously or sequentially and be independent or associated after the maturity stage. The fruit ripening is a highly coordinated, genetically programmed and an irreversible phenomenon involving a series of physiological, biochemical changes next the maturity stage that finally leads to the development of a soft edible ripe fruit with desirable quality attributes [1].

A wide spectrum of biochemical changes such as increased respiration, chlorophyll degradation, biosynthesis of carotenoids, anthocyanin, essential oils components, aroma, increased activity of cell wall degrading enzyme and a transient increase in ethylene production are some of major changes during the fruit ripening. Based on fruits respiratory pattern and ethylene biosynthesis during the ripening, harvested fruits can be further classified as climacteric and non-climacteric fruits [2]. The climacteric fruits which are harvested at full maturity can be ripened off the parent plant due to the respiration rate and ethylene formation though minimal at maturity, rise dramatically to a climacteric peak, at the onset of ripening after which it declines such as mango, apricot, peach, plum, banana, apple, pear, papaya, avocado and guava. On the other hand, the non-climacteric fruits are not capable of continuing their ripeness process once detached from parent plant such as grape, orange, pomegranate, pineapple and strawberry. Also, the non-climacteric fruits produce a small quantity of endogenous ethylene and do not respond to external ethylene treatment and show comparatively low profile and a gradual decline in respiration pattern and ethylene production throughout the ripening process.

Considering the complex nature of fruit ripening, in which changes in flavor, texture and color at least must be regulated and coordinated, it is perhaps not surprising to find that the process is under genetic control [3]. Furthermore, the ripening like other plant developmental processes is probably under the control of plant growth regulators because all the five major growth regulators effect on the ripening in one way or another if applied exogenously. In this concern, the auxin, gibberellins and cytokinins generally act to retard the ripening while ethylene and abscisic acid act to enhance the ripening process. Although some correlations can be found, only ethylene is routinely found to be associated with the ripening and hence has led to this plant growth regulator being considered the ripening hormone. In addition, the two key control enzymes for the biosynthesis of ethylene are ACC synthase and the ethylene forming enzyme also referred to as a ACC oxidase.

Ethylene, a fruit ripening phyto-hormone, in minute amount is generally thought to regulate fruit ripening by coordinating the expression of genes responsible for: conversion of starch to sugar, production of aroma, pigment synthesis, chlorophyll degradation, autocatalytic ethylene production and production of volatile compounds [4]. Meanwhile, the amount of endogenous ethylene produced by plant tissue generally increases auto catalytically at a specific stage of growth and development to initiate physiological response. Recently, the supplemental ethylene (exogenous) is commonly used to induce ripening of avocado, bananas, mangoes, tomatoes, de-green citrus (except lime) for fresh market and induce softening of freestone peaches and pears destined for processing.

Moreover, the supplemental ethylene may affect processes associated with quality such as color, firmness, texture, vitamins and chemical composition.

2. LITERATURE REVIEW

After seed development and fruit growth, the properties of the fruit change to make the fruit more attractive to potential consumers, such as animals, birds, and humans [5]. These changes include the most common ways by which we judge whether a fruit is ripe or not, including external features, such as softness to the touch, and internal features, such as sweetness. Fruits also change color as they ripen. This happens because of the breakdown of a green pigment called chlorophyll, along with the creation and accumulation of other pigments responsible for red, purple, or blue hues (anthocyanin), or bright red, yellow, and orange hues (carotenoids), to name a few.

Most fruits produce a gaseous compound called ethylene that starts the ripening process. Its level in under-ripe fruit is very low, but as fruit develop,
they produce larger amounts that speed up the ripening process or the stage of ripening known as the “climacteric.” The level of ethylene and rate of ripening is a variety-dependent process. Some apple varieties such as McIntosh, produce prodigious amounts of ethylene and are difficult to store once this occurs [5]. When harvested after the rapid rise in ethylene, they quickly soften and senesce in storage. Other varieties have a slower rise in ethylene and slower ripening rate. For apples that will be stored longer than two months, it is imperative to harvest them before the level of ethylene begins its rapid increase. Plums and peaches are also sensitive to ethylene and will continue to ripen after harvest in response to this hormone. Some varieties of plums, such as Shiro, ripen very slowly since ethylene production is suppressed. With these suppressed-climacteric types, fruit may remain under-ripe if harvested too early.

Other plum varieties such as Early Golden ripen very rapidly. In this case, harvest should be timed more precisely so that fruit are not overripe when they reach the consumer [6]. A major concern with ripened fruit is that it does not last very long before it begins to spoil. The loss of firmness and the production of sugars associated with ripening can also make the fruit susceptible to pathogens like bacteria and spoilage. Spoilage can be reduced by rapid transportation of fresh fruits, or by slowing down fruit ripening. There are several ways to slow down fruit ripening. One way to slow down ripening is by lowering the temperature. Another way to slow down ripening is by controlling the atmosphere around the fruit, primarily by increasing carbon dioxide levels and reducing oxygen levels. Fruit need oxygen to ripen, so if there is less oxygen in the atmosphere, the fruit will ripen more slowly. One final way to slow down ripening is to block the action of ethylene [7].

Ethylene is a gas and is known as the “fruit-ripening hormone.” Every fruit has a certain level of ethylene production throughout its lifecycle. However, in some fruits, ethylene levels shoot up when the fruit starts ripening. For climacteric fruit, exposure to an initial, small concentration of ethylene causes the fruit to produce greater quantities of ethylene until a peak concentration is achieved [7]. This increase in ethylene concentration triggers an increase in the fruit’s metabolism and causes the changes to the fruit that occur during ripening. Ripening of climacteric fruits can, therefore, be slowed down by reducing the amount of ethylene the fruits make or by blocking ethylene’s actions (www.frontlineservices.com.au/FrontlineServices). The methods we described above for slowing down ripening work in this way, because, in general, low temperatures reduce metabolism in fruit. Controlled atmospheres limit the amount of oxygen around the fruit, and oxygen is needed to make ethylene. Ethylene action is inhibited by carbon dioxide and by 1-MCP. Another method for slowing down ripening is to remove ethylene from the storage environment by using materials that absorb ethylene, such as potassium permanganate. Once the fruit reaches its destination, it can be ripened by exposure to ethylene gas.

The effect of ethylene on ripening is dependent on many factors. The fruits need to be mature enough to be able to respond effectively to ethylene. In highly sensitive species, like cantaloupes or bananas, ripening is immediately stimulated by ethylene, but the more immature the fruit, the greater the concentration of ethylene required to cause ripening. In the less sensitive species, like tomatoes or apples, ethylene treatment reduces the time before ripening occurs. Some fruits, such as avocados, do not ripen while attached to the tree and gradually increase their sensitivity to ethylene with time after harvest [8].

To elucidate the temporal relations between endogenous ethylene and color development, changes in ethylene concentration, fruit color, pigments and flavonoids were monitored at different interval during development and ripening of Pink lady apple fruits [9]. The concentrations of anthocyanin increased during maturation and ripening, coinciding with corresponding increase in percent red blush and endogenous ethylene concentration. Positive and significant correlation was found between ethylene and color development as well as between ethylene and total anthocyanin. Therefore, ethylene appears to be a key factor regulating anthocyanin biosynthesis and color development.

Saltveit [10] reported that ethylene biosynthesis rises prodigiously in ripening climacteric fruits and is thought to coordinate many ripening phenomena. In general ethylene enhances taste and flavor by stimulating fruit ripening. However, the total volatile developed in tomatoes picked mature green and ripened on the plant (Stern et al., 1994). For example, the most important aroma compound (2)-3-hexanal was 31% and 17% higher in fruit ripened on the plant...
compared to fruit harvested mature green and ripened with and without ethylene respectively. As with the other 31 tomato volatiles measure in the study, the total volatile was 12% higher in ripe fruit that were harvested mature green and treated with ethylene than in those ripened without ethylene.

Furthermore, ethylene treatment was also found to increase the desirable aroma in Honeydew melons in addition to stimulating flesh softening and enhancing external color [10].

Also, Apricot (Prunus armeniaca L) fruits are highly susceptible to flesh softening, loss of flavor and fruit decay particularly during post-harvest storage. Most of these quality changes observed during fruit ripening are under ethylene regulation [11]. In this regard, a study with objective of determining effect of 1-methycycloprene (1-MCP) and aminoethoxyvinyl-glycine (AVG) application on quality attributes of Modesto and Patterson apricot cultivars. The fruit quality evaluation was performed after 20-30 days of cold storage and after shelf life rate especially in cv. Patterson. The fruit softening and color development showed ethylene-dependent behavior with significant reduction for both cultivars in fruit treated with 1-MCP and AVG. The soluble solids concentration and titrable acidity showed ethylene independent pattern, thus, not affected by application of inhibitors. Among volatile compounds identified, ester and aldehydes showed ethylene-dependent behavior in both varieties [11].

In addition, the content of sugars, volatile compounds and organic acids, as well as color, shape and texture determine the sensorial properties of the fruit [12]. An important sensorial attribute is flavor with a direct effect on consumer acceptance is determined mainly by chemical sensations like smell and taste [13]. All these qualities of the fruit can be directly regulated by ethylene. During the growth and development period, there are many chemical and physical changes occurring that have an impact on fruit quality and ripening behavior after harvest. Ripening is the final stage of the maturation process when the fruit changes color, and develops the flavor, texture and aroma that makes up what we define as optimum eating quality. The biological agent that initiates this ripening process after the fruit is mature is naturally produced ethylene – this simple plant hormone described and understood over 40 years ago. While there are other factors involved in this “triggering” of the ripening process by ethylene, it is essentially a universal ripening hormone. When this internal concentration of naturally produced ethylene increases to about 0.1 – 1.0 ppm, the ripening process is irreversibly initiated. The process may be slowed, but it cannot be reversed once it is truly under way. So, here is the key point: additional and externally applied ethylene, provided prior to the time that the naturally produced internal concentration reaches the required 0.1 – 1.0 ppm level, will trigger or initiate – “promote” if you will – this natural ripening process at an earlier time.

Furthermore, the effective application of synthetic auxin 2, 4DP on fruit ripening of La France pears (Pyrus communis L) was examined. Pears generally fail to ripen on the tree. Cell wall synthesis is believed to continue on the tree and cell wall decomposition in fruit may be retarded while on the tree [14]. The buttery texture in pears is associated with cell wall degradation which is further promoted by ethylene [15]. The ripening is stimulated by relative high temperature about 20°C after being stored at about 5°C for 10 days. This is due to stress of low temperature which increases ethylene production in fruits.

The plant hormone ethylene plays a key role in climacteric fruit ripening. Studies on components of ethylene signaling have revealed a linear transduction pathway leading to the activation of ethylene response factors [16]. However, the means by which ethylene selects the ripening-related genes and interacts with other signaling pathways to regulate the ripening process are still to be elucidated. Using tomato (Solanum lycopersicum) as a reference species, the present review aims to revisit the mechanisms by which ethylene regulates fruit ripening by taking advantage of new tools available to perform in silico studies at the genome-wide scale, leading to a global view on the expression pattern of ethylene biosynthesis and response genes throughout ripening.

Overall, it provides new insights on the transcriptional network by which this hormone coordinates the ripening process and emphasizes the interplay between ethylene and ripening-associated developmental factors and the link between epigenetic regulation and ethylene during fruit [17].

As a developmental process, fruit ripening is coordinated by a complex network of endogenous and exogenous cues. Indeed, the making of a fruit is a genetically regulated
process unique to plants involving three distinct stages: fruit set, development, and ripening. Fruit development is characterized by a series of developmental transitions tightly coordinated by a network of interacting genes and signaling pathways. Among these, ripening has received the greatest attention from both geneticists and breeders. From the scientific point of view, fruit ripening is seen as a process in which the biochemistry and physiology of the organ are developmentally altered to influence the appearance, texture, flavor, and aroma [16]. Since most of the fruit sensory and nutritional quality traits are elaborated at the ripening stage, deciphering the key genetic and molecular factors regulating ripening becomes a major task toward improving overall fruit quality ([17]). In addition, the control of fruit ripening is also instrumental to maintain the quality attributes of the fruit during the postharvest shelf life.

In addition, for climacteric fruits, ethylene is generally thought to regulate fruit ripening by coordinating the expression of genes responsible. The ripening of paw fruit (Asimina triloba L) displayed an increase in ethylene production and respiration with maxima at 3 days after harvest [4]. Increasing ethylene evolution coincides with an increase in respiration and a rapid decline in firmness.

In a study conducted on Japanese plum cv. Red Rosa, the fruits were treated with 0.1 ppm 1-MCP for 20 hours at 20°C at harvest and then held at 20°C for ripening together with untreated fruit.

Another batch of plums were exposed to 15 ppm ethylene during 0°C storage and fruit ripening directly after 1-MCP treatment had lower ethylene production and softened slowly than untreated fruits [18].

Following storage both ethylene and 1-MCP treated fruits were low in ethylene production and softened more slowly than untreated. In Red Rosa plums, firmness loss was associated with the late increase in ethylene. At 6 days of ripening following harvest or storage, the ethylene was still very low in all treatment and no significant softening had occurred. Only after 14 days of ripening when control fruit had begun autocatalytic ethylene production was there major softening in the fruit from treatment while 1-MCP fruits remained much firmer. The ripening of fleshy fruits was the result of a series of biochemical, physiological and structural changes. It was concluded that the endogenous ethylene production has a continuing role in integrating the many metabolic changes associated with ripening [19].

In general, ethylene has long been regarded as the main regulator of ripening in climacteric fruits. The characterization of a few tomato mutants which are unable to produce climacteric ethylene and to ripe their fruits even following treatments with exogenous ethylene has shown that other factors also play a role in control of climacteric fruits ripening. In climacteric tomato and peach fruits it has been reported that concomitant with ethylene production, increase in the amount of auxin can also be measured. Besides the already known indirect activity on ripening due to its up-regulation of climacteric ethylene synthesis, it has been possible to show that auxin plays a role of its own during ripening of peaches. The study has demonstrated an existence of an important a cross-talk between auxin and ethylene, with genes in the auxin domain regulated by ethylene and genes in the ethylene domain regulated by auxin.

4. CONCLUSIONS

During the last decade, the implementation of advanced high-throughput technologies in genomics, metabolomics, and proteomics threw new light on the mechanisms by which ethylene regulates the ripening process. Although these studies confirmed ethylene as the main hormone regulating climacteric ripening, they provided evidence supporting the intervention of a complex network of interacting signaling pathways. Indeed, it is now clear that hormonal and developmental factors act in concert to tune the whole set of ripening-associated pathways. Ethylene exerts a strong influence on the ripening of fruits in which the onset of ripening corresponds to a sharp increase in ethylene production and respiration in climacteric fruits. The application of ethylene scavenger and inhibitors have proved ethylene participation as a regulator of processes that define the reported quality attributes such as the fruit texture, color, taste, firmness, sweetness, softness, vitamins and anthocyanin to name a few hence reduced ripening in fruits. It is indeed interesting to note that while ethylene significantly changed some of the studied attributes, thus dependence was partial, having been modified by diverse factors including doses of inhibitors. This shows the complexity of the fruit maturation process in which it is established that ethylene is only one factor among a great number. Therefore, ethylene is indeed yes a fruit ripening hormone.
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COMPETING INTERESTS

Author has declared that no competing interests exist.

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