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Review

# Proteomics as an approach to the understanding of the molecular physiology of fruit development and ripening

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ABSTRACT

Fruit ripening is a developmental complex process which occurs in higher plants and involves a number of stages displayed from immature to mature fruits that depend on the plant species and the environmental conditions. Nowadays, the importance of fruit ripening comes mainly from the link between this physiological process in plants and the economic repercussions as a result of one of the human activities, the agricultural industry. In most cases, fruit ripening is accompanied by colour changes due to different pigment content and increases in sugar levels, among others. Major physiological modifications that affect colour, texture, flavour, and aroma are under the control of both external (light and temperature) and internal (developmental gene regulation and hormonal control) factors. Due to the huge amount of metabolic changes that take place during ripening in fruits from higher plants, the accomplishment of new throughput methods which can provide a global evaluation of this process would be desirable. Differential proteomics of immature and mature fruits would be a useful tool to gain information on the molecular changes which occur during ripening, but also the investigation of fruits at different ripening stages will provide a dynamic picture of the whole transformation of fruits. This subject is furthermore of great interest as many fruits are essential for human nutrition. Thus far different maturation profiles have been reported specific for each crop species. In this work, a thorough review of the proteomic database from fruit development and maturation of important crop species will be updated to understand the molecular physiology of fruits at ripening stages.

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## 1. Introduction

The botanical definition of a fruit is a mature ovary and is, therefore, confined to the Angiosperms. Different parts of the flower can contribute to the final structure of dry and fleshy fruits; thus, the final form of the fruit is dependent upon the number and type of the floral organ components, the position of the contributing organs, and how the different tissues within them grow and differentiate [1]. Ripening is the final phase of fruit development, and involves deep metabolic changes in the biochemistry, physiology and gene expression of the fruit such as chlorophyll degradation and pigment (carotenoids and anthocyanins) biosynthesis, conversion of starch to simple sugars, accumulation of flavours and cell wall softening [2–4], ethylene receptor degradation [5], simple sugar and organic acid accumulation, volatile production and flesh softening [6,7]. The pathways involved in the processes of fruit development and ripening are exclusive for plants and vary between species. Thus, as an example, in the maturation of pepper fruits a series of important events takes place, as indicated in Fig. 1. During development and ripening of pepper fruits clear visible changes are manifested. Thus, mature green fruits shift to the final colour either red, yellow, orange or purple in a process that is accompanied by intense metabolism, emission of volatile organic compounds, destruction of chlorophyll and synthesis of new pigments, formation of pectins, synthesis of proteins, taste alteration and changes in total soluble reducing equivalents. Overall, developmental, physiological, anatomical, biochemical and structural differences contribute to the operation of unique pathways, genes and proteins [7].

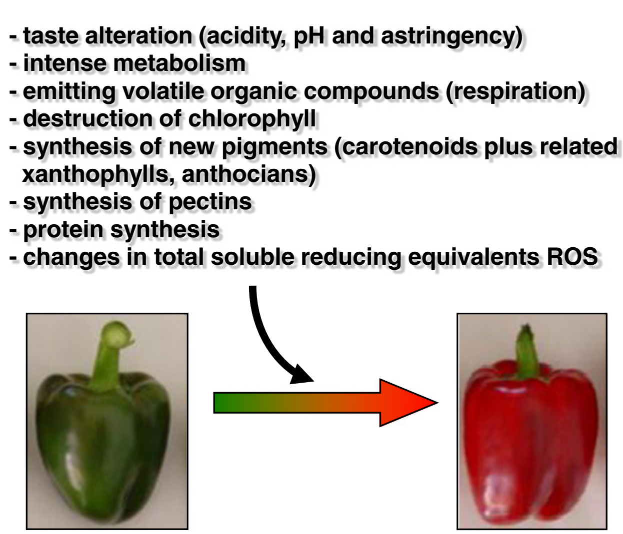


**Fig. 1 – Events which take place during ripening of pepper fruits.**

This developmental process seems to be also influenced by the type of fruit, either climateric or non-climateric, although no consistent data are available thus far to conclude this assert. In climateric fruits, which are characterised by a peculiar burst in the ethylene evolution and the respiration rate at the onset of ripening, these events are mainly regulated by the gaseous phytohormone ethylene, which is also involved in the decrease in flesh firmness typical of many economically relevant crops like tomato and peach [8]. On the other hand, ripening of non-climateric fruits such as pepper, citrus and strawberry is ethylene-independent, although similar major visual, texture, flavour and metabolic changes occur as in climacteric fruits. Many of the changes have been mainly characterised in climacteric-ripening fruits, whereas non-climacteric fruit ripening is still poorly understood. In Fig. 2, some climateric and non-climateric fruits are shown. Interestingly, this physiological behaviour is not linked to taxonomic groups. Species belonging to the same family, such as tomato and pepper (*Solanaceae*) display distinct response to ethylene. Thus, tomato is a climacteric fruit while pepper is not.

Taking into account the demand of consumers and agro-biotechnological companies, more attention was initially paid to the fruit set and development and post-harvest strategies than to the fruit maturation itself. In fact, a better comprehension of the genetic and molecular mechanisms responsible for fruit set and development has been gained due to the major impact of strategies for breeding and crop improvement in fruit bearing species. The impact of the model plant *Arabidopsis* in that field has been relevant, so genetic studies on this plant species have been proved to be very successful in the search for key regulatory genes acting in carpel and fruit development [9–13]. The study at molecular level of fruit ripening has been mainly accomplished from a genetic point of view [13]. The gene expression profiling of fruit development and maturation was recently examined [14–16]. Thus, an increasing number of data are now available from large-scale analysis of the gene expression during the climacteric or non-climacteric fruit development [17–22]. Also the evolution of a series of metabolites and other molecules during fruit ripening has been reported. Up until some years ago, only few data on fruit development proteomics were available [23,24]. However, the potentialities and the development of proteomics in the recent past years have triggered a scientific burst in all biological sciences and, consequently, the fruit proteomics is now a body of interest not only for biologists but also for agricultural companies.

Improved understanding of fruit maturation may yield benefits both for public health and agricultural economy. An important part of the human nutrition field to assess the safety of new crop plant varieties is the extensive compositional analysis, including the measurement of all key nutrients and antinutrients in a specific crop. The applicability of

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