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Special Issue Editorial

Advances in fruit development and ripening

Fruits originate from different tissues of the plant's reproductive organs. They have evolved primarily to protect the developing seeds from the environment, and to act to facilitate seed dispersal and subsequently plant propagation. In order to become attractive to seed-dispersing animals, fleshy fruits undergo changes in several physical and chemical properties including softening, flavour development, and pigment biosynthesis in a complex physiological syndrome known as ripening. The unique array of metabolites accumulated during ripening make fruits an indispensable component in any healthy diet. Hence, fruits are an excellent source of nutrients such as vitamins, carbohydrates, and minerals, as well as fibre. In addition, they accumulate a large set of healthy phytochemicals. From the breeding point of view, increasing visual, sensory, nutritional, and nutraceutical quality properties of fleshy fruits are currently important objectives.

From initial and pivotal investigations carried out on tomato up to the current time, there has been a growing understanding of the mechanisms that regulate development and ripening in many fruits. This special issue consists of 11 high-impact articles, including six reviews, two expert views, and three research papers that all address various aspects of fruit ripening. As reviewed by Zenoni *et al.* (2023), the physiological orchestration of ripening, and in particular the role played by hormones, defines fruits into two main categories, namely climacteric fruits, whose ripening is mainly regulated by ethylene, and non-climacteric fruits, whose maturation is to a great extent regulated by abscisic acid (ABA). The review highlights the fact that although these two types of maturation are governed by distinct and specific mechanisms, a common regulation of transcription, notably involving NAC transcription factors, might also be involved. However, regardless of the type of hormonal control, fruit ripening involves a common series of biochemical and physiological changes that make the fruit itself more attractive to seed-dispersing animals or consumers. One of the first, easily detected processes occurring during ripening is the change in colour of the outer epicarp, which is very important for consumer attraction. Denoyes *et al.* (2023) discuss the exploitation of genetic diversity of strawberry fruit colour and the identification of crucial genetic variability through the application of different types of strategies, from QTL mapping to haplotype phase genomic sequencing. Another non-climacteric species, grapevine, is investigated by Rodríguez-Lorenzo *et al.* (2023), who uncover the role of colour in berries by comparing a near-isogenic white line with a black-berried somatic variant. The study underlines the fact that a colour change can influence important physiological aspects in fruit. Thus, white berries show a higher expression of photosynthetic and light-response genes together with volatile precursor amino acids, while in black berries the functionality of *MYBA1* and *MYBA2* stimulate the accumulation of flavonol trihydroxylates (C_6-derived alcohol and esters and GABA) that are relevant for stress homeostasis. Several papers in this issue are focused on tomato, which is still the main model species for climacteric fruit. Ezura *et al.* (2023) review the processes leading to fruit set, an important aspect of development that ultimately leads to fruit yield, which is found to be coordinated by two main hormones, auxin and gibberellin. In tomato, *IAA9* and *DELLA/PROCERA* act as active repressors of these two hormones, thereby regulating downstream gene expression related to fruit set. Zuccarelli *et al.* (2023) use a multiomics approach to reveal that gibberellins play a pivotal role in fruit set, and hence ultimately in yield. They report that knock down or knock out of *S-nitrosoglutathione* (*SlGSNOR*), a gene involved in NO homeostasis, promotes shoot branching in tomato—with a consequent reduction in fruit size—through interference with the production and signalling of auxin, gibberellin, and cytokinin. Climacteric fruits are also known to accumulate starch for transient storage of carbon. Nicolas *et al.* (2023) show that a mutation in a gene encoding an ADP-glucose pyrophosphorylase reduces starch accumulation during growth. This change in carbon flux results in increases in contents of soluble sugars, readjusted lipid metabolism and growth, and protection against abiotic stress. Tourdot *et al.* (2023) review the endoreduplication process that occurs in a range of species including tomato, a mechanism that induces endopolyploidy and that could support rapid fruit growth. This special issue also sheds light on novel concepts regarding the functional distinction between climacteric and non-climacteric fruits. Thus, the review by

Pujol and Garcia-Mas (2023) deals with the ripening of melon, a species in which climacteric and non-climacteric cultivars coexist. Crossing such cultivars shows that the regulation of the climacteric response is controlled by a complex series of genetic loci that are quantitatively inherited. In recent years it has become increasingly evident that, acting via complex cross-talk with other important hormones, ABA is a key ripening regulator in non-climacteric fruit. The review by Perotti *et al.* (2023) focuses a discussion of two non-climacteric model species, namely strawberry and grape. Grape is also compared with apple, a typical climacteric fruit, and this leads to the proposal of a possible common mechanism as the basis of the control of fruit ripening. The review of Zenoni *et al.* (2023) also discusses how ripening control can have a practical impact on postharvest management, especially for apple. In addition, Nicolaï *et al.* (2023) present a reaction–diffusion model that is able to compute the spatiotemporal changes in the fruit metabolome during ripening and postharvest in climacteric fruit, a phenomenon that is significantly affected by the diffusion transport of gaseous molecules such as O_2, CO_2, C_2H_4, and NO.

All the information presented in this special issue represents a valuable source of knowledge for a better understanding of the regulation of fruit growth and ripening that can inform the improvement of fruit production and quality. As described by Gramazio *et al.* (2023) for eggplant, the exploitation of these traits within a genetic resource collection can be translated into new breeding programs leading towards a new Green Revolution targeted at improving fruit security and human health.

Keywords: Branching, climacteric, colour, fruit development, fruit set, non-climacteric, ripening, size, postharvest, yield.

Sonia Osorio[1,*], Fabrizio Costa[2,*], Yves Gibon[3], Björn Usadel[4] and Ariel Vicente[5]

[1] Department of Molecular Biology and Biochemistry, Institute of Mediterranean and Subtropical Horticulture 'La Mayora', Universidad de Malaga- Universidad de Málaga-Consejo Superior de Investigaciones Científicas (IHSM-UMA-CSIC), Malaga University, Málaga, Spain

[2] Center Agriculture Food Environment (C3A), University of Trento, Via Mach 1, 39098 San Michele all'Adige (Trento), Italy

[3] INRAE-Bordeaux, Villenave d'Ornon, Nouvelle Aquitaine, France

[4] Institute of Biological Data Science, CEPLAS, Heinrich Heine University Düsseldorf/(IBG-4), Forschungszentrum Jülich, Germany

[5] College of Agriculture, National University of La Plata - CONICET Argentina, La Plata, Argentina

[*] Correspondence: sosorio@uma.es or fabrizio.costa@unitn.it

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