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Review

Multi-Omic Approaches to Investigate Molecular Mechanisms in Peach Post-Harvest Ripening

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Abstract: Peach post-harvest ripening is a complex developmental process controlled by a plethora of genetic and epigenetic factors. Specifically, it leads to protein, lipid and nucleic acid degradation, all resulting in cell death. Substantial research has been directed at investigating peach regulatory mechanisms underlying genomic, metabolomic and transcriptomic modifications occurring during this stage, and much progress has been made thanks to the advent of Next Generation Sequencing technologies. This review is focused on the latest multi-omics studies, with the aim of highlighting the most significant results and further investigating the regulation of the key genes involved in peach post-harvest processes and related physiology. By offering an exhaustive overview of peach omics profiles, it provides a comprehensive description of gene expression changes and their correlation with ripening stages, including some post-harvest treatments, as well as with volatile organic compound modifications. However, the present work highlights that, due to the complexity of the process, recent investigations do not elucidate all underlying molecular mechanisms, making further studies still necessary. For this reason, some key points for future research activities and innovative peach breeding programs are discussed, relying on trusted multi-omic approaches.

Keywords: gene expression; genomics; metabolomics; omics; *Prunus persica*; ripening; transcriptomics; volatile organic compounds



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1. Introduction

Peach (*Prunus persica* (L.) Batsch) and its variant nectarine (*p. persica* (L.) Batsch var. nectarina) are fruits belonging to the Rosaceae family. Peach has become an important model plant due to its small (227.4 Mb) and publicly available doubled haploid genome, whose structure is similar to that of other important fruits such as apricot (*p. armeniaca*) [1]. Although it has excellent production potential, its consumption is still lower than other popular fresh fruits such as bananas and apples [2]. An effective strategy to promote its consumption could be to enhance its aroma, as well as its quality, which both tend to be affected during extended storage periods, along with its firmness and colour.

Peach ripening is a complex developmental process controlled by a plethora of genetic and epigenetic factors [3]. Its underlying mechanisms lead to structural changes of the fruit that acquires desirable organoleptic qualities and becomes edible. It is a coordinated process requiring a change in the expression levels of hundreds or even thousands of genes to modify a wide range of biochemical and physiological signals such as carbohydrate and organic acid metabolism, chlorophyll breakdown, anthocyanin accumulation, ethylene production, cell wall restructuring, small metabolite and volatile organic compound (VOC) biosynthesis [3]. Abbreviations used throughout the manuscript are also listed in Table 1.

Table 1. List of abbreviations used in this manuscript.

Abbreviations	Definition
1-MCP	1-Methylcyclopropene
AATs	Alcohol acyltransferases
ABA	Abscisic Acid
ACC	Aminocyclopropane-1-carboxylic acid
ADHs	Alcohol Dehydrogenases
AVG	Aminoethoxyvinylglycine
BAC	Bacterial Artificial Chromosome
CA	Controlled Atmosphere
CBF	C-Repeat Binding Factor
cDNA	complementary DNA
CI	Chilling Injury
CKs	Cytokinins
CNA	Correlation Networks Analysis
CRISP/Cas9	Clustered Regularly Interspaced Short Palindromic Repeats/CRISP associated protein 9
CS	Cold Storage
DEG	Differentially Expressed Gene
EST	Expressed Sequence Tag
GAs	Gibberellins
GC-FPD	Gas Chromatography-Flame Photometric Detection
GC-MS	Gas Chromatography–Mass Spectrometry Techniques
GC-O	Gas Chromatography-Olfactometry
GWAS	Genome-Wide Association Study
HPLs	Hydroperoxide Lyases
HS-SPME	Headspace Solid-Phase Microextraction
Jas	Jasmonates
LC-MS	Liquid Chromatography–Mass Spectrometry Techniques
LOXs	Lipoxygenases
MET	L-methionine
MJA	Methyl Jasmonate
NGS	Next Generation Sequencing
NMR	Nuclear Magnetic Resonance
QTL	Quantitative Trait Loci
qRT-PCR	Real Time or Quantitative PCR–Polymerase Chain Reaction
SAM	S-Adenosyl Methionine
SMRT	Single Molecule Real-Time
SNPs	Single Nucleotide Polymorphisms
SVs	Structural Variants
TD	Thermal Desorption
UV	Ultraviolet
VOC	Volatile Organic Compounds

VOCs are generated in the maturation process through the degradation of compounds such as fatty acids, proteins and carbohydrates and their production varies in different conditions and developmental stages [2]. VOC profiles change during ripening [4,5], during cold storage (CS) [6,7], as a result of post-harvest treatments [5], as well as amongst differing germplasm [8] and the compound distribution characterizes the different parts of the fruit [9]. In some species, like strawberries, a single compound may be largely responsible for the typical aroma of the fruit, but this rarely happens [10]. The highly specific aroma of a given fruit generally depends on a mixture of different compounds, as highlighted in tomato and peach [11]. Around 110 VOCs, belonging to different families, such as aldehydes, esters, ketones, lactones and phenols have been described to date from the peach volatilome [7]. Among them, more than 30 aroma compounds have been identified [2,12]. Differences in aromatic profiles have been observed among different cultivars as well as between peaches and nectarines [13].

Fruits can be classified into two categories: climacteric, such as tomatoes, apples, peaches and bananas, where the ripening process is characterized by an increase in respiration rate and ethylene production, and non-climacteric, including grapes, strawberries and citrus fruit, where during ripening respiration and ethylene do not increase [14,15]. In climacteric fruits, the observed increase in ethylene levels induces significant changes in colour, aroma, texture, flavour and other biochemical and physiological parameters. Instead, in non-climacteric fruits, the changes occurring during the ripening process are ethylene-independent, governed by incompletely understood regulatory mechanisms [16,17].

Once fruits are removed from the plant and before they are consumed, a time interval known as post-harvest ripening can occur, whose effects depend on the specific fruit metabolism and maturation state at the time of harvest. Post-harvest ripening leads to protein, lipid and nucleic acid degradation, all ultimately resulting in cell death [18]. Furthermore, peach fruits are characterized by a rapid deterioration at room temperature [19,20]. The post-harvest degradative processes eventually impact fruit quality characteristics, like texture, taste and aroma. For this reason and in order to extend fruit shelf life, different post-harvest strategies, depending on the specific fruit, are applied. Cold storage (CS) treatments are commonly used for enhancing their shelf-life [21], even though CS can lead to chilling injury (CI), including changes in texture, and a decline in aroma quality [22]. The cold induces changes in gene expression, and an increased expression of the C-repeat Binding Factors (CBFs), related to plant cold acclimation and tolerance, has been reported in many species, including peach [23,24]. Post-harvest treatments such as controlled atmosphere (CA; a high CO₂ concentration and low O₂) are used under cold conditions to avoid this CI. A significant reduction of CI was also observed after pre-storage with a high-CO₂ treatment [25]. In peaches, treatments with 1-methylcyclopropene (1-MCP) can also prevent CI [26]. Ultraviolet (UV) light irradiation and specifically UV-B and UV-C treatments, causing a reduction of ethylene levels and therefore a maturation delay, also have become common recently [27,28]. Many other post-harvest treatments have been applied to peach fruit and it has been found that nectarines have a better resilience to storage conditions than peaches [29].

Innovative research tools based on omics technologies have already provided new insights into the mechanisms behind fruit development and ripening [30] as well as opportunities to expand this knowledge to post-harvest processes, including effects of treatments. Substantial advances have been made since the introduction of Next Generation Sequencing technologies (NGS). Nevertheless, the existing studies do not completely elucidate all these molecular aspects and further investigations are still necessary. In fact, although a large amount of data has been produced, some aspects of the ripening process in post-harvest situations are not fully understood.

In this context, we collect and discuss here the most relevant recent findings and studies in the field, focusing on omics and above all multi-omics approaches. With the term ‘multi-omics’, we refer to a method of applying the principles of several omics sciences to analyse a given problem, such as transcriptomics and metabolomics. However, since, to date, it is quite hard to integrate the very heterogeneous data obtained [31], the method is not necessarily based on merging them in a narrow sense. Moreover, to the best of our knowledge, in the agricultural field multi-omics studies based on a heterogeneous network of data obtained by integrating information from different kinds of omics science are not available yet. In this work, we focus on metabolomics, genomics and transcriptomics approaches.

Our first preliminary survey is already available as part of the 1st International Online Conference on Agriculture—Advances in Agricultural Science and Technology-IOCAG2022.

Compared to this previous overview, here we discuss in much greater detail topics already covered, also referring to a more extensive literature. Furthermore, issues, both related to the peach ripening process and to changes in VOCs, are discussed together with data reported on gene expression, offering an in-depth analysis of the molecular mechanisms involved. In addition, peach omics profiles are discussed, and we include

a comprehensive description of gene expression changes and their correlation with the ripening stages, including some post-harvest treatments. Repercussions and perspectives are also examined, suggesting some key points for possible future studies.

2. The Peach Ripening Process

2.1. Compounds Involved

Although every fruit species and cultivar shows a specific response to hormones, it has long been recognised that in those belonging to the genus *Prunus* the integrated action of auxins, cytokinins (CKs) and gibberellins (GAs) plays a fundamental role in the regulation of several fruit traits. In addition, abscisic acid (ABA) and ethylene are also important during fruit ripening in all *Prunus* species [32,33].

Auxin effects are different in climacteric and non-climacteric fruits: in the former, auxin seems to accelerate the maturation process, while in the latter, auxin may negatively regulate it. A genomic approach has shown that many genes involved in auxin responses including auxin response factors (ARFs) and *Aux/IAA* increased in expression during peach ripening, highlighting how the hormone plays a key role in this process [34]. Other IAA-related genes seem to be up-regulated during the pre-climacteric/climacteric transition: particularly, two putative *TIR1* genes, encoding auxin receptors, and one *PIN1* gene, encoding a putative auxin efflux facilitator protein. *PIN1* expression was found to be mainly induced by exogenous ethylene. This finding shows how in peach a dynamic cross-talk between auxin and ethylene is significant for ripening regulation. This evidence was further supported by changes in the expression of *ACS1* and *ACO1*, two key ethylene biosynthesis genes, during treatment with both of these hormones. In fact, the expression of *ACO1* is mostly up-regulated by ethylene, while the highest up-regulating effect on *ACS1* was the result of auxin activity [34,35].

Endogenous levels of CKs play a crucial role during plant growth, through the stimulation of cell division, but they can also partially inhibit auxin responses and be responsible for an increase in fruit size [36].

GAs seem to enhance the fruit development process, promoting cell division and enlargement, and delaying peach ripening by decreasing ethylene production [37].

Ethylene signalling is associated with a complex transduction pathway involving genes related to traits associated with fruit maturation, such as aroma, colour, firmness and post-harvest shelf-life [33]. The levels of this hormone depend on three enzymatic reactions: L-methionine (Met) is converted into S-adenosyl-L-methionine (SAM) by the enzyme S-adenosyl-L-methionine synthetase (MAT), 1-aminocyclopropane-1-carboxylic acid (ACC) synthase (ACS) converts SAM to ACC; and, finally, ACC oxidase (ACO) oxidizes ACC to produce ethylene (Figure 1).

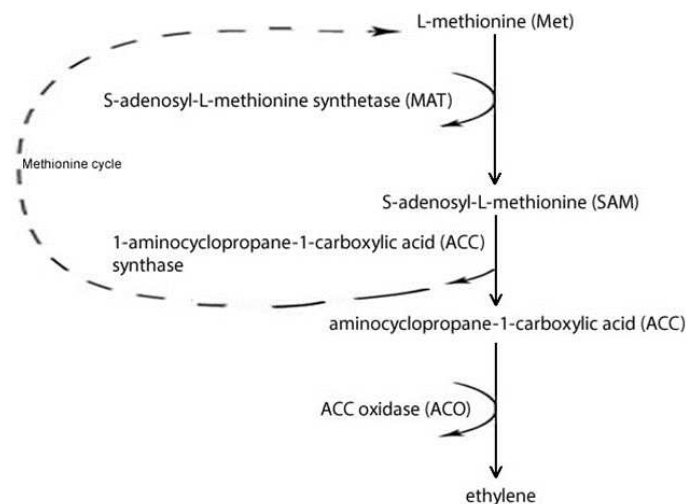


Figure 1. Ethylene biosynthesis in peach [38].

This ethylene formation is oxygen-dependent, while under anaerobic conditions ethylene production is not observed [33,38]. Aminoethoxyvinylglycine (AVG) acts as a competitive inhibitor to the conversion of SAM into ACC, by stopping ACS activity and slowing down the softening process in peach post-harvest without an effect on its quality traits [39]. Conversely, the use of ethephon, resulting in a persistent ethylene release, was found to enhance fruit ripening and cause abscission [40].

The hormone ABA interacts with ethylene, the cell wall and auxin-related genes in peach [41]. In climacteric fruits, it accumulates before ethylene production and reaches maximum levels in fully ripe fruits. Furthermore, ABA enhances anthocyanin and sugar accumulation, promotes softening and is associated with increased ethylene biosynthesis [41].

Fatty acids (FAs) are another compound category whose composition changes during peach fruit ripening and has an important influence on aroma production. FA biosynthesis relies on enzymes including lipoxygenases (LOXs), hydroperoxide lyases (HPLs), alcohol dehydrogenases (ADHs), alcohol acyltransferases (AATs) and fatty acid desaturases (FADs) [5]. LOXs catalyse oxidation of polyunsaturated fatty acids, like linoleic and linolenic acids, which accumulate during fruit ripening. Concentrations of linoleic acid were found to increase after peach harvest and then decrease during storage at 20 °C. Linolenic acid increased during the post-harvest ripening phase, especially after about one week. Conversely, palmitic acid showed a two-fold decrease over the same period, while the concentrations of other fatty acids, such as stearic and oleic acid showed no major changes [5].

LOX is responsible for catalysing the hydroperoxidation of polyunsaturated fatty acids to start the synthesis of oxylipins [42]. In particular, jasmonates (JAs) are a class of oxylipins that slow down the peach ripening process, often considered as a reference to investigate the effects of this hormone [43], and they are also responsible for an interference between ripening and stress defence genes [44]. Alterations in the ripening physiology may be related to effects of MJA (Methyl JAsonate) treatment, often used to delay natural fruit decay [45], to prevent CI after harvesting [46] and inhibit pathogens [47]. Specifically, MJA causes a reduction of the expression levels of the genes responsible for the ripening process and that are found at high levels in this phase, with some also involved in ethylene biosynthesis (e.g., *ACO1*) [35].

Flavonoids such as anthocyanins and flavonols, play a crucial role in fruit colour and health benefits. They vary during peach fruit growth and ripening and *R2R3 MYB* transcription factors regulate their biosynthesis [48]. In fact, flavonoids are synthesized in a pathway regulated by genes belonging to the *MYB* and *bHLH* families.

Carotenoids, besides their role as photosynthetic accessory pigments, are norisoprenoid precursors that are found in the 10fruits of many plants [49]. Norisoprenoids are characterised by peculiar aromatic properties along with a low odour threshold [50] and many of them are key compounds in the final peach aroma, with levels increasing during fruit ripening [4].

In peaches, violaxanthin is the predominant xanthophyll both in the skin and in the flesh. It can be found in amounts up to three times higher than other carotenoids [51]. Carotenoid levels are highly influenced by post-harvest treatment, including temperature and CA composition [52]. In fruits stored at 20 °C, β -cryptoxanthin was found to increase, while violaxanthin and β -carotene levels decreased. Refrigeration at lower temperatures resulted in a slowed down carotenoid biosynthesis [53].

Vitamin C (ascorbic acid and dehydroascorbic acid) was found in similar amounts in peaches and nectarines. Higher levels depend on post-harvest ripening progression [54], and ascorbic acid concentration decreases with storage at low temperatures [52,55].

Overall, the phenolic profile resulting from ripening changes significantly among cultivars and with maturation stage at harvest, even though no general rules can be established [54,56,57]. However, peach cultivars are generally characterized by a higher antioxidant content compared to nectarines, with a similar trend observed for late-harvested versus the early-harvested cultivars [58].

2.2. Volatilome and Profiling Techniques

VOCs are a major fraction of the plant metabolome, and being main contributors to fruit aroma and flavour, and thus to fruit quality, have proved to be of particular biological interest.

Two lactones, γ - and δ -decalactone are considered to be the most relevant compounds to the final peach aroma [59–61]. Particularly, γ -decalactone is the major lactone compound of peach VOCs and it is widely used as a flavour and fragrance agent in the food industry [2,62–66]. Another lactone showing a peach-like odour is γ -jasmolactone, first detected in peach juice [67]. A few other VOCs, including δ -octalactone, δ -dodecalactone and 6-pentyl- α -pyrone, are also major contributors of the overall peach aroma [64].

C6 aldehydes and alcohols, such as *n*-hexanal, (E)-2-hexenal and (E)-2-hexenol are also partly responsible for peach aroma, but not to the same extent. Similarly, esters, such as (Z)-3-hexenyl acetate, partially contribute to the flavour [62].

Most typical peach VOCs are produced during fatty acid biosynthesis and an involvement of LOX, ADHs and FAs has been proposed [68]. Specifically, six carbon aldehydes and alcohols are synthesized from linoleic and linolenic acids through LOX-catalysed reactions [5]. The pathway produces hydroperoxide isomers of both linoleic and linolenic acids, which are then split by HPLs to hexanal and hexenal, respectively. Through a reduction reaction, aldehydes can then be converted into related C6 alcohols by ADHs. Finally, AATs catalyse the production of esters [5].

All lactones derive from saturated fatty acids, through several steps, including dehydrogenation, epoxidation, hydration, hydroxylation, shortening by β -oxidation and then internal esterification with hydroxyacetyl-coenzyme A [69,70].

Amongst the VOCs, only a small sub-set impacts the final aroma which increases during fruit ripening. However, VOC production in peach is not a static process, since their level changes dramatically during this stage and flavour compound patterns are different among tissues, species and cultivars, depending on post-harvest conditions [4,5,71,72]. In particular, it has been demonstrated that the aromatic profile and organoleptic properties are influenced by both pre-harvest factors, such as growing conditions and maturity stage of the fruit, as well as post-harvest factors, including storage temperature, controlled atmosphere composition, ethylene modulation and the presence of wax coatings [16,73,74]. Overall, some broad trends in VOC changes have been observed. For example, aldehydes tend to decline, and esters to increase in peach fruit over their shelf-life [75]. Linalool is a terpene which is reported to be present in peaches at harvest and to rapidly decrease under cold storage [74]. CS induces the production of esters and lactones, two compounds typically related with advanced ripening stages [5], that increase during storage at 20 °C after cold treatment [75,76].

A crucial factor affecting the number and the species of VOCs identified in peach aroma is method choice for detection and analysis. Older studies [62] used steam distillation and hexane extraction from frozen samples which is unlikely to reflect the aroma profile of fresh fruit due to changes elicited by the heating. In recent years, pathway analysis and metabolite identification skills have improved [77] thanks to the technological advances and to the new platforms adopted. State-of-the-art volatilomics encompasses analytical techniques such as gas chromatography and liquid chromatography–mass spectrometry-based techniques (GC–MS and LC–MS) and nuclear magnetic resonance (NMR) spectroscopy. GC–MS applications mainly concern volatile and thermally stable molecules, while LC–MS is also used to identify a wider compound set, including plant secondary metabolites [78]. Headspace solid-phase microextraction (HS-SPME) is largely used to extract volatile compounds before a further GC-MS analysis is employed for the VOCs separation [79,80], however the SPME fibers can become saturated and are not easily transportable.

A wide range of techniques are now available for the analysis of flavour and aroma in both foods and processed food products. Examples of these techniques and VOCs analysed using them were recently reviewed [81]. Each technique has its own advantages and disadvantages such as speed, selectivity, dynamic range and ease of use. For example, NMR

is characterized by low sensitivity compared to MS, but it provides more reliable metabolite structure and does not require destructive sample preparation [82]. This platform makes it possible to monitor changes in both primary and secondary plant metabolites, and can be useful to study VOCs and metabolic changes occurring during post-harvest fruit ripening [83]. It has also been used in peach, for instance, to investigate the metabolite profile of varieties differing in their susceptibility to medfly attack and to detect VOC precursors that may be important in resistance [84].

MS along with GC, LC and NMR are the most widely used methods to study the plant metabolome, including its modifications after fruit harvest [81]. HS-SPME combined with GC-MS has been widely used in peach volatile profile studies. For example, this method was successfully adopted to investigate the volatile profile of about 40 peach cultivars [85] leading to identification of significant differences in the flavour volatiles across the cultivars. Recently, peach VOCs obtained from five peach cultivars were analysed through GC-O (GC-olfactometry, which enables a sensorial assessment in parallel with chemical analysis), GC-MS and GC-flame photometric detection (FPD) revealing 40 odour-active VOCs [12]. An approach using multiple techniques was also adopted to investigate peach volatiles, using HS-SPME, solvent-assisted flavour evaporation (SAFE), GC-O, GC-MS and FPD [86]. Applying these methods it is possible to define a library of aroma compounds resulting from chromatography in specific peach cultivars that can be used to evaluate their quality.

The use of thermal desorption (TD) tubes for the collection of VOCs from fruit [87] is more versatile than SPME, enabling storage and transport of VOCs on the TD tubes. Coupled with the high sensitivity of ToF-MS VOCs can be directly captured from whole or minimally processed samples with enhanced sensitivity, reducing problems associated with saturation by dominant VOCs found with SPME. Recently, an enhancement of thermal desorption gas chromatography time of flight mass spectrometry (TD-GC-ToF-MS), referred to as TD-GC \times GC-ToF-MS, has been used to assess aroma profiles in peach [7] that improves chromatographic resolution enabling clearer identification of additional different compounds. Detection of aroma from whole peaches [7,88] is very helpful in support of consumer studies since purchasing relies on aroma from whole fruits.

3. Omics Advances in Rosaceae

Several genomes of Rosaceae species are now available and accessible from the Genome Database for Rosaceae [89] and from the Phytozome portal [90]. This website also hosts useful bioinformatic resources, such as retrieval of orthologous genes, as well as many sequenced and annotated plant genomes. Integrated data such as genetic information, annotated sequences of genomes and transcriptomes, can be found in specific online portals and databases, providing added value to each type of data and making the use of genomic information relating to each species easier. Other genomic and genetic data about the Rosaceae are available and include BAC (Bacterial Artificial Chromosome) libraries, ESTs (Expressed Sequence Tags), genetic maps and molecular markers used for mapping and genotyping activities [91,92].

Over the last decade, the advent of NGS, such as pyrosequencing, 454 and Illumina, have made it possible to generate large-scale plant transcriptome and genome sequences, and bioinformatic packages are now an essential part of this technological era. A large amount of data, including annotated whole-genome sequences, transcriptome and expression data, as well as metabolomic data have been generated and their effective use and integration are supported by bioinformatic tools and databases. Initially, the main limitation of the early NGS technologies was the relatively short lengths of their reads, and, as a consequence, the resulting plant genomes contained a substantial number of unassembled sequences. Moreover, the potential to identify structural variants (SVs), specifically located in the repetitive regions of plant genomes was often limited [93]. Subsequently, long-read sequencing technologies, the so called third generation methods, allowed high-quality assemblies to be made for several plant genomes. Among these new methods, the most

relevant are the Single Molecule Real-Time (SMRT) sequencing of Pacific Biosciences and the Oxford Nanopore technology (ONT) [94].

The use of NGS technologies to successfully obtain cDNA (complementary DNA) sequences has been a significant advance in transcriptomic studies, allowing not only an analysis of the expression levels of previously chosen genes, but also of low-level transcripts, investigating their allelic expression and splice-variants [95].

In peach, since 2013 a significant number of important studies revealing the complexity of its transcriptomes have been carried out. The analyses involved different parts of peach tissues, resulting in the identification of new transcripts and making it possible to improve the current genome peach annotation [96]. Moreover, more than 9500 SNPs (Single Nucleotide Polymorphisms) have been detected across six peach genotypes providing a useful resource for investigating further peach horticultural traits.

These omics technological advances have also allowed a detailed analysis of the peach post-harvest ripening process and of the CS treatments effects, such as CI symptoms. The latter were investigated and discussed in a recent review [97], where it was highlighted how genomics and transcriptomics approaches have allowed the discovery of genes responsible for different chilling injury symptoms.

3.1. Genomic and Transcriptomic Peach Profiles

Genes related to fruit quality traits have been characterized and mapped to the peach genome for several years now, proving how a significant amount of the phenotype depends on a limited number of genes [98]. Since then, a peach reference genome has been developed within a project initiated in 2008 by the International Peach Genome Initiative. The first version (Peach v1.0) was released in April 2010 and was followed by the Peach v2.0.a1 (approximately 227.4 Mb arranged in 191 scaffolds), based on the DNA from the doubled haploid cultivar 'Lovell' (PLOV2-2N), that made it possible to assemble the genome consistently and accurately. This release, composed of eight pseudomolecules representing the eight peach chromosomes, has a total of 99.2% mapped sequences [99].

Alongside this accurate peach genome, many resources, including peach EST databases and NCBI (National Center for Biotechnology Information) entries have accumulated, and many new genes have been characterized, investigated and clustered. Of particular relevance to peach aroma are those involved in fatty acid production. Cross genome comparisons have shown, for example, that the peach *PpAAT1* sequence is approximately 86% identical to apricot *PaAAT1* [5].

Over this period, technological progress has allowed us to improve our knowledge about genetic mapping and quantitative trait loci (QTL) identification. These have then been adopted as strategies for the detection of candidate genes related to peach characteristics of agronomic interest and to the ripening process. These genomics approaches can now be used in post-harvest biology for marker assisted breeding, finding the genes responsible for specific fruit quality traits, understanding gene networks regulating phases of fruit development, and identifying external factors influencing post-harvest resilience [100,101].

At the same time, advances in bioinformatic analysis have created many new tools to deal effectively with these complex data sets and to investigate hundreds of putative genetic markers simultaneously. Consequently, many omics applications based on QTL analyses have recently been designed and developed for a wider range of fruit bearing species, including peach, targeted at quality traits such as flesh texture, colour, sweetness, acidity and other organoleptic properties. For instance, the identification of peach candidate genes associated with maturation stages and with mealiness, a fruit texture defect where juice is absent in the flesh due to CS at 0–5 °C, was obtained by using QTL analysis and deep sequencing [102]. A QTL analysis for peach quality traits and CI symptoms was also carried out in a study representing one of the first QTL studies specifically aimed at identifying quality traits and CI symptoms through the use of a high-density SNP map [103]. Results detected significant QTLs for mealiness, flesh bleeding and flesh browning.

Genome structural variations (SVs) have also been associated with fundamental traits in a large range of agronomically important species [104]. A total of 129 peach accessions have been used for a comprehensive genome-wide association study (GWAS) of 12 key agronomic traits (texture, taste, shape, etc.). Using cultivated peaches and wild species, specific genome regions related to fruit aroma have also been defined [105]. Recently, by using 336 peach genomes, an integrated map was generated and a number of candidate causal variants was detected [106]. This result is an important starting point for future peach genomic research aiming to investigate the associations between SVs and the most important volatiles.

Peach transcriptome profiling and especially gene expression analysis during ripening was initially based on microarrays. In particular, the Italian Consortium for Genomics studies in Rosaceae species (ESTree Consortium) developed the first peach microarray (named μ PEACH1.0) including about 4800 probes for genes involved in fruit development [107]. To investigate the relationships between peach maturation/post-harvest physiology and ethylene, μ PEACH1.0 was used to evaluate the effect of propylene and ethylene treatments with a duration of 24 h in peach fruit at the pre-climacteric stage, demonstrating the existence of the already mentioned cross-talk between auxin and ethylene [34]. Furthermore, a microarray of about 850 unique ESTs from a ripe peach cDNA dataset was used to investigate the molecular mechanisms underlying woolliness [108]. A database called CHILLPEACH, about 8000 cDNAs from both sensitive and tolerant peach varieties, was also developed and the related CHILLPEACH microarray [109] made it possible to identify peach cold-responsive genes [110]. By using these resources, microarray data analyses highlighted how an ethylene receptor complex protein (*Pp-ETR2*), homologous to the tomato *Le-ETR4*, appeared to be involved in the pre-climacteric to climacteric transition [35].

Subsequently, a new peach microarray was developed to investigate transcriptomic changes at different ripening stages, revealing over 1800 transcripts differentially expressed during ripening and between two genotypes, previously selected for their contrasting aromas [111].

Only in 2016, a transcriptomic analysis based on RNA-Seq (RNA-Sequencing) technology was performed to investigate different peach fruit maturation stages, including post-harvest ripening [112]. Two peach varieties, “Zhongyou9” (a nectarine; *Prunus persica* L. Batsch) and its mutant “Hongyu” were analysed including two ripening stages at 20-day intervals, and 180 up- and 234 down-regulated genes were found. Many differentially expressed genes were related to aroma and flavour volatiles, as well as plant hormones. In this study, two genes linked to aroma production: *Ppa003798m*, encoding a putative FAD-linked oxidase and *Ppa007757m*, a putative gene belonging to the ADH super-family, were both significantly down-regulated during ripening.

Mechanisms involved in the effect of CA on CI prevention during peach post-harvest ripening, were also investigated and transcriptomic changes in “Red Pearl” nectarines were analysed through RNA-Seq [113]. Nectarines refrigerated and subjected to a CA treatment developed a less mealy texture. Differentially expressed gene (DEG) analysis showed that low O₂ combined with CS significantly slowed down the metabolic ripening processes, more than CS alone.

In another study, RNA-Seq was used in the analysis of peaches stored at high temperature (35 °C) and room temperature (25 °C) after pre-storage at 5 °C for 2 days [114]. Genes associated with membrane stability, such as those encoding peroxidases and lipoxygenases, appeared down-regulated when exposed to the higher temperature, as well as pectinesterase, polygalacturonase, pectate lyase and pectin methylesterase.

The RNA-Seq approach was also adopted to analyse DEGs in ‘Madoka’ peach fruit treated with 1-MCP and high CO₂, and stored at 0 °C for 12 days [115]. The results showed how this treatment caused CI delay, as observed by comparing parameters such as firmness and total pectin. Moreover, *beta-amylase 3, chloroplastical (BAM3)*, a gene encoding starch degrading enzyme, was up-regulated in both CS + 1-MCP and CS + CO₂ as compared to CS alone. However, respiration and ethylene production rates showed no significant

differences among CS, 1-MCP + CS and CO₂ + CS [115] suggesting that the mechanism for the changes in texture and gene expression were not related to ethylene biosynthesis.

Further advances have been made in understanding the biosynthetic pathways of compounds contributing to fruit flavour, and some of the genes involved have been identified. In particular, a small set of peach genes related to sweetness and acidity flavour were detected [116]. Furthermore, on the basis of the high-quality *p. persica* reference genome (257.2 Mb) of Longhua Shui Mi, it was shown that *PpALMT1* (aluminium-activated malate transporter 1) contributes to an increase in malate levels (the predominant organic acid in peach) and that *PpERDL16* (Early Response to Dehydration 6-Like 16) is responsible for higher fructose levels during peach development, contributing to greater sweetness for the fruit [117].

Recently, RNA-Seq showed that UV-C treatment inhibits the expression of the *ACS* gene and of the ethylene receptor in peach fruit, contributing to the reduction of ethylene production and thus delaying ripening [28]. Results showed that several genes related to antioxidant and defence mechanisms under this treatment are up-regulated while those involved in cell wall breakdown are down-regulated. However, more evidence is needed about the influence of UV-C treatment on gene expression regulating peach senescence and softening processes.

3.2. Metabolomic Peach Profiles

To study the relationships between VOCs and metabolites, methods based on correlation networks analysis (CNA) have been used. The first CNA application was carried out in tomato showing that VOCs deriving from the same biochemical pathway were highly interconnected, unveiling important information about the underlying biological systems [118–120].

In peach, metabolic networks have been investigated mainly through GC-MS and expression levels of key regulatory enzymes have been evaluated in many studies through qRT-PCR (Real time or Quantitative PCR–Polymerase Chain Reaction) [121]. To combine these datasets PCA (Principal Component Analysis) has been applied and has uncovered metabolic changes during post-harvest ripening. A decrease in amino acid levels correlated with transcripts encoding enzymes involved in amino acid and organic acid catabolism, was found during fruit ripening, in agreement with a function for the amino acids in support of cell respiration [121]. Furthermore, sucrose cycling seems to play a role in peach post-harvest ripening and variations in sugars have not been found to be particularly pronounced, except for a slight decrease in 1-O-methyl-glucoside and in the fucose cell wall, glucoheptose and Fru-6-*p* at the last maturation stages [121].

A combined approach based on hierarchical cluster analysis and metabolomic CNA was adopted to study the consequences of treatments applied pre- and post-harvest on VOC production [2]. Peach volatiles were clustered considering the compound family or well characterized biosynthetic pathways. VOC clusters including similar families were identified (i.e., lactones, non-cyclic esters, carboxylic acid and long-chain aldehydes) as well as those belonging to specific metabolic pathways (i.e., lipid-derived metabolites and terpenoid biosynthesis). Lactones, such as γ -hexalactone, γ -heptalactone, γ -octolactone, γ -decalactone and δ -decalactone, were highly correlated with one another. Furthermore, lactone synthesis during peach post-harvest ripening seemed to be regulated by the first enzyme of the β -oxidation metabolic pathway (acyl-CoA oxidase) [122].

γ -Jasmolactone levels did not show a high correlation with ethanol and its ester (ethyl acetate) that generally characterize the over-ripening process. Lipid-derived volatiles, such as pentanal, hexanal, 2-hexanal, furan 2-pentyl and furan 2-ethyl appeared highly correlated with each other [2]. Long-chain aldehydes, such as octanal and nonenal, and carboxylic acids, like pentanoic acid and hexanoic acid, showed a weak correlation with other volatile clusters [2].

Compounds important for organoleptic properties (organic acids, amino acids and sugars) of different peach varieties have also been investigated during post-harvest ripen-

ing [123]. GC–MS was used, showing differences across varieties in amino acid levels as well as in metabolic pathways. In particular, different sugar levels were compared among peach varieties, and the content of sucrose and fructose were quite similar. Conversely, the relative levels of sugar alcohols, maltitol and galactinol varied considerably amongst different samples.

Quite recently, in several peach varieties subjected to CS conditions a drastic decrease in the content of sugars and sugar alcohols, as well as in several amino acids was found in woolly when compared to juicy fruit [76]. Changes in peach proteome composition were also found, as well as increased free radical production, suggesting that the wooliness defect may be caused by an oxidation process.

Importantly, intact peaches, sampled immediately after CS, showed different aromatic profiles when compared with fruit stored for three additional days at 20 °C [124], indicating that the recovery period following CS influences the final peach aroma. Intact peaches were also the subject of other post-harvest studies [7] in which the VOC profiles and the expression of about 10 crucial genes involved in VOC pathways from six cultivars were analysed before and after storage at 1 °C for seven days. A total of 115 VOCs were identified, and a subset of 15 VOCs showed differences between cultivars and between nectarines, in agreement with other previous studies [13].

Other interesting investigations into metabolomic fruit changes happening during post-harvest storage were reported in a recent review focused on the identification of key metabolites involved in organoleptic and health-benefit traits, such as sugars, acids, polyphenols and carotenoids [125]. The review points out the difficulties of fully understanding fruit post-harvest storage changes, however, in peach, two primary metabolites, raffinose and galactinol, often increasing during cold acclimation, were shown to be important antioxidants, to mediate stress responses, and were proposed as potential markers for plant cold tolerance [126].

4. Peach Gene Expression and Correlation with VOCs

FADs are undoubtedly key enzymes influencing VOC production, but surprisingly their specific role in plant VOC synthesis has not yet been completely elucidated.

In peach, *ppFAD1* was reported to be involved in the formation of a precursor of lactones/esters [127]. Real-time quantitative polymerase chain reaction (qPCR) analysis showed that two ω -3 FAD genes, *PpFAD3-1* and *PpFAD3-2*, may be important in peach VOC biosynthesis since in ripe fruit *PpFAD3-1* was high while expression of *PpFAD3-2* was low. Instead, high *PpFAD3-2* and low *PpFAD3-1* transcript levels characterized young fruit [127].

The FAD gene family expression during peach ripening and in particular the transcript abundance of *PpFAD1* seems to increase in the first days after harvest [5]. In contrast *PpFAD2* is found at low levels for one or two days, and then increases together with ethylene and linolenic acid during post-harvest ripening [5].

FADs and their related genes also play a significant role in the changes in lipid membrane fluidity, which is typical of cold-responsive fruits [128]. The transcriptional regulation of these genes, in peach, has been associated with metabolic changes occurring during CI [19]. Both in several peach cultivars and nectarines, *PpFAD4* gene expression was found to decrease under CS, showing, however, very distinctive differences among peach varieties before and after CS [7].

In peach *PpLOX1* and *PpLOX4*, *PpLOX2* and *PpLOX3*, are associated with the synthesis of lactones and of C6 aldehydes [5], and recently differences in expression of these genes amongst cultivars and in response to storage conditions have been shown [7]. Specifically, *PpLOX1* expression increased following cold storage in three different nectarine cultivars, whereas in peach cultivars its gene expression fluctuated. Conversely, at the same temperature, *PpLOX2*, *PpLOX3* and *PpLOX4* showed a down-regulation with no significant differences among cultivars [7].

The expression of members of the epoxide hydrolase gene family, *PpEPH2* and *PpEPH3*, were found to be involved in the formation of γ -decalactone [66,70] and to be down regulated during CS in different cultivars [7]. However, the alcohol acyltransferase *PpAAT1*, which catalyses the biosynthesis of this lactone [129,130] appeared significantly up regulated after cold exposure in different nectarine cultivars [7]. A recent study, comparing transcriptomes and metabolomes of high and low aromatic cultivars confirmed the role of *PpAAT1* in the biosynthesis of γ -decalactone [129]). *PpAAT1* expression was found to correlate with ester formation in peach as well [131]. Overall, AAT1 gene family members seem to be associated with aroma production during peach post-harvest ripening [5,131].

PpTPS1 terpene synthase, whose expression was found to decline significantly in different peach cultivars after CS [7] is localized in plastids and its expression during cold storage was correlated with the linalool production, while the isoform *PpTPS2* was shown to be responsible for (E,E)- α -farnesene (a common biotic-stress-induced plant volatile) biosynthesis in the cytoplasm [132]. Under UV-B light treatments, RNA-Seq showed altered transcript levels for these two terpene synthases in peach [132], with a decrease of 86% of *PpTPS1* and an 80-fold increase of *PpTPS2*. The reduction of the volatile linalool suggests that the levels of compounds contributing to flavour in peach fruits can be regulated by this ultraviolet treatment.

In relation to the production of alcohol VOCs, in CS post-harvest peaches, *PpADH2* gene expression seems to depend on the specific cultivar more than on the treatment [7], thus an examination of the other genes related to ester biosynthesis should be evaluated across different cultivars to assess whether they also show cultivar-specific responses.

Therefore, VOC profile, gene expression and changes in their response to CS appear to be cultivar specific, and to obtain a complete picture there is the need to test these parameters across a wider range of cultivars.

5. Multi-Omics Approaches and the Peach Post-Harvest Ripening Process

NGS technologies have revolutionized plant biology and have been extended widely to non-model systems with very low costs [30]. At the same time, combined approaches, based on the relationship amongst genomics, transcriptomics and metabolomics methods, have been developed to exploit these inter-related datasets.

Multi-omics applications have been carried out for a wide range of different fruit species and have provided a powerful tool for identifying correlations between different biological components controlling plant functions and metabolic pathways. For instance, a combined analysis of metabolites and transcripts revealed the metabolic shifts underlying tomato fruit development and new associations between specific transcripts and metabolites were identified [133]. Similar approaches have been successfully applied to study candidate genes involved in tomato fruit ripening [134,135] and in other fruit e.g., grape berry development [136–138].

In peach, combined omics approaches were applied to identify relationships between fruit VOCs and QTLs for a better understanding of the gene regulation mechanisms behind the biosynthesis of the compounds. For instance, thanks to the availability of an annotated peach genome, QTLs were detected for 23 VOCs and associations between candidate genes and QTLs were established [139].

Furthermore, QTLs associated with characters of agronomic interest both to pre-harvest and post-harvest ripening across several *Prunus* species have been assembled through genotyping with many DNA markers distributed across the entire genome [140]. For peach this has been particularly challenging due to the restricted genetic diversity of cultivated peaches, but nevertheless hundreds of QTLs have been identified and related to fruit VOCs.

Other combined genomics and metabolomics approaches have investigated pre- and post-harvest ripening processes and confirmed specific loci that control peach aroma [141]. By using GC-MS, compounds associated with aroma were also analysed and a correlation-based analysis of these datasets was developed, revealing that the peach volatilome is

organized into modules composed of compounds from the same biological pathway or having similar chemical structures.

A QTL approach was applied to a very heterogenous peach pedigree, always using the recently available reference peach genome [142]. Thanks to use of this genome, the intrachromosomal positions of several QTLs showed differences compared with those previously reported in peach and the mapping quality was generally enhanced. The results of this study provided new insights for a model study for pedigree-based analysis in several peach breeding programs.

The validation of genes localized in QTLs through gene expression analysis (RNA-Seq and qPCR) has been recently tested as an approach in peach, in a study aimed at identifying candidate genes involved in fruit softening rate [143]. The results, suggesting that auxin may be important in rapid fruit softening, helped to improve our understanding of the genetic mechanisms involved in this process both in peaches and nectarines, and could lead to the identification of molecular markers associated with softening rate.

Further multi-omics studies, based on transcriptomic and metabolomic analyses, identified new candidate genes impacting aroma volatiles in pre-harvest and post-harvest conditions in two peach cultivars [70]. In this investigation, datasets from microarrays and qRT-PCR analyses were combined with VOCs detected using HS-SPME-GC-MS. The combined dataset was analysed through a correlation-based approach (using CNA) to identify the genes showing a correlation with the major aromatic compounds, including lactones, esters and phenolics. The results showed a core set of genes, including alcohol acyl transferase, fatty acid desaturases and transcription factor genes, that are highly related with peach fruit VOCs and could be useful for future biotechnological activities.

In another study, parallel metabolomic and transcriptomic analyses were carried out to characterise the response of peach to CI [19]. A set of peaches after harvest were exposed to cold treatment (40 days, 0 °C) and another group was pre-conditioned (48 h, 20 °C) previously to low temperature exposure. Results highlighted that the pre-conditioning suppressed CI symptoms and led to a more pronounced ethylene production than that observed in other treatments. Metabolite differences were also highlighted in relation to the different treatments used. Metabolomic and transcriptomic data suggested the involvement of valine and/or isoleucine in the CI response.

Recently, levels of the monoterpene linalool were investigated at different peach developmental stages and across cultivars [144]. The relationships between metabolome and transcriptome were explored through Pearson correlation analysis, and in particular the gene, *PpUGT85A2*, associated with an enzyme showing linalool glycosylation activity, was detected. Metabolomic analysis was performed through GC-MS, and transcriptomic investigation through RNA-Seq technology. Results also showed that treatments with exogenous ethylene stimulated *PpUGT85A2* transcription and linalyl- β -D-glucoside accumulation. Conversely, treatments with the ethylene signalling inhibitor 1-MCP, in addition to reducing ethylene production, led to a down-regulation of the *PpUGT85A2* transcript, linalyl- β -D-glucoside, and a decrease in linalool content. Furthermore UV-B irradiation led to the reduction of production of linalyl- β -D-glucoside and of expression of *PpUGT85A2* in peach fruit.

In the same year, several peach varieties were considered in order to discover the volatile acetate esters that contribute to defence against biotic stresses, to which these fruits are exposed post-harvest [131]. Here, VOC analysis (through GC-MS technology) and gene expression analysis (through RNA-Seq and Real-time quantitative PCR) were carried out with the aim of exploring the functions of carboxylesterase (CXE) enzymes with regard to VOC ester content. Interestingly, results showed that acetate ester levels were negatively correlated with *PpCXE1* gene expression. Furthermore, peach fruits treated with MJA maintained higher content of esters, with a significant reduction of *PpCXE1* but not of *PpCXE2* or *PpCXE3* transcript content. Conversely, UV-B treatment increased *PpCXE1* expression levels. Consequently, *PpCXE1* seems to have a more major role compared to the other two genes in mediating catabolism of volatile acetate esters in this fruit [131].

Recently, multi-omics approaches were also applied to investigations focused on peach treatment with 1-MCP. In particular, it was demonstrated that 1-MCP exposure strongly influences peach VOC metabolism, as highlighted by transcriptomic (RNA-Seq) and metabolomic analyses (GC-MS based on SPME) [145]. Results indicated that 1-MCP significantly reduced ethylene formation, resulting in lower expression levels of genes involved in signal transduction such as *PpaSAMS1/2* (S-adenosylmethionine synthetase), *PpaACS1/2* (1-aminocyclopropane-1-carboxylic acid synthase), *PpaACO1* (1-aminocyclopropane-1-carboxylic acid oxidase 1), *PpaETR1/2* (ethylene receptor), *PpaERS1* (ethylene response sensor 1), *PpaEIN4* (ethylene insensitive 4) and *PpaCTR1* (constitutive triple response 1). They also showed that the content of peach aroma volatiles, such as aldehydes and alcohols, was different after 1-MCP treatment and the esters were found to be inhibited.

Finally, recent reviews analyzed molecular and genetic aspects of *Prunus* species fruit maturation processes, including both pre-harvest and postharvest ripening, focusing on the relevance of adopting a combined genomic, transcriptomic and metabolomic approach. The aim was to improve our knowledge about their impact on breeding, and to underline how it is necessary today to shift from conventional to molecular breeding. This involves the development of DNA markers for selection, and RNA markers for monitoring ripening traits [33]. Similarly, Scossa et al. [146] highlighted how the importance of conducting multi-omics studies consists not only in identifying relationships between different layers of biological complexity, but also, due to the descriptive nature of the related datasets, in developing predictive models for key agricultural traits.

6. Conclusions

NGS technologies and the advances in new biotechnologies have made it possible to design specific breeding programmes aimed at improving peach quality and aroma, especially taking into account that peach intake is not as high as other popular fruits.

Among these are programmes based on the development of specific markers by adopting marker-assisted selection procedures (MAS). In fact, the increasing number of available genomic resources has enabled QTL analysis to be rapidly converted into readily usable markers for MAS, greatly facilitating peach breeding for superior quality [147].

Table 2, showing studies in which only one omics technology was applied, highlights how many significant omics studies have focussed on QTLs. Moreover, metabolomics studies appear to be among the most prevalent methods used to investigate post-harvest peach conditions and treatments. Recently, transcriptomics studies based on an RNA-Seq approach took the place of the initially popular microarray methods, and they were applied not only to analyse post-harvest peach ripening, but also specific related treatments. Remarkably, very recently, CS treatment studies were coupled with UV and 1-MCP treatment investigations. Mutagenesis techniques were finally applied to identify genome loci responsible for aroma biosynthesis.

Table 2. Table summarizing many of the most significant single omics studies examined in this review. * indicates the post-harvest treatment applied and ** indicates that the study also focused on other species.

Omic Sciences and Techniques	Post-Harvest Study *	Description	References
transcriptomics/microarray		μPEACH1.0 definition	[107]
transcriptomics/microarray		Analysis of auxin and ethylene in ripening	[34]
transcriptomics/microarray	CS	Identification of woolliness response	[108]
transcriptomics/microarray	CS	Identification of cold-responsive genes	[110]
metabolomics	CS	Analysis of post-harvest temperature influence on lactone production via acyl-CoA oxidases	[122]
metabolomics		CNA to study the effect of pre- and post-harvest treatments	[2]

Table 2. Cont.

Omic Sciences and Techniques	Post-Harvest Study *	Description	References
transcriptomics/microarray		Transcriptomic changes at different ripening stages	[111]
genomics		Peach v2.0.a1 definition	[99]
transcriptomics/RNA-SEQ		RNA-Seq and the peach transcriptome landscape	[95,96]
genomics/QTL		Analysis of genes responsible for fruit quality traits **	[100]
genomics/QTL/SNP	CS	High resolution SNP mapping and QTL analysis for fruit quality traits	[103]
metabolomics	CS	Metabolic pathways involved in heat and cold responses in post-harvest conditions	[126]
genomics/QTL	CS	Identification of putative genes associated with mealiness and ripeness in peach	[102]
genomics/QTL		QTL mapping of peach traits	[142]
transcriptomics/RNA-SEQ	CA, CS	Study of gene expression in post-harvest conditions	[113]
metabolomics		Analysis of compounds important for organoleptic properties during post-harvest ripening	[123]
transcriptomics/RNA-SEQ		Transcriptome analysis during the late stage of ripening	[112]
metabolomics		Correlation among FADs and VOCs	[127]
metabolomics	CS	Metabolic responses to low temperature of different cultivars	[76]
metabolomics	CS	Study of effect of CS on intact peach VOCs	[124]
metabolomics	CS	Fruit volatilome profiling and gene expression analyses amongst peach cultivars	[7]
metabolomics		Identification of key metabolites involved in organoleptic and health-benefit traits **	[125]
genomics/SVs		Genes associated with fruit traits and VOCs	[106]
transcriptomics/RNA-SEQ		Analysis at high temperature conditions during fruit ripening and post-harvest	[114]
transcriptomics/RNA-SEQ	CS, 1-MCP	Analysis of gene expression changes in pre-storage treatments during CS	[115]
transcriptomics/RNA-SEQ	UV-C	UV-C treatment in post-harvest	[28]
genomics/mutagenesis		Identification of the key gene regions of PpAAT1 responsible for peach aroma	[130]

NGS also allowed the design and development of multi-omics applications, whose results made it possible to gain a further understanding of the mechanisms regulating many agricultural traits and of fruit gene expression changes in pre- and post-harvest ripening stages.

A considerable number of multi-omics studies in peach are now available (Table 3), showing again that many studies focus on QTL analyses, with some of them based on innovative genomics technologies and CRISPR/Cas9 approaches [129].

Table 3. Table summarizing many of the most significant multi-omics studies examined in this review. * indicates the post-harvest treatment applied and ** indicates that the study also focused on other species.

Omic Science and Techniques	Post-Harvest Study *	Description	References
metabolomics, transcriptomics/microarray		Integrated omics analysis to study tomato development and ripening **	[133]
metabolomics, transcriptomics/microarray		Genetic and Metabolic Regulatory Network Analysis in Tomato development **	[134]
genomics, EST resources, metabolomics, qRT-PCR	Post-harvest ripening at 20 °C	Study about aroma and fatty acids pathway	[5]

Table 3. Cont.

Omic Science and Techniques	Post-Harvest Study *	Description	References	
metabolomics, transcriptomics genomics, transcriptomics, metabolomics genomics/QTL/SNP, metabolomics metabolomics, transcriptomics/microarray genomics/QTL, metabolomics genomics/QTL, metabolomics metabolomics, transcriptomics/qRT-PCR metabolomics, transcriptomics/RNA-SEQ metabolomics, transcriptomics/qRT-PCR metabolomics, transcriptomics/RNA-SEQ metabolomics, transcriptomics/RNA-SEQ genomics/QTL, transcriptomics/RNA-SEQ metabolomics, transcriptomics/RNA-SEQ metabolomics, transcriptomics/RNA-SEQ genomics/CRISPR/Cas9, metabolomics, transcriptomics/RNA-SEQ genomics, metabolomics, transcriptomics genomic, transcriptomic metabolomics, transcriptomics/RNA-SEQ genomics/GWAS/SNPs, transcriptomics/RNA-SEQ genomics, metabolomics, transcriptomics		Survey of molecular regulation in fruit ripening **	[135]	
		Survey on 'omics' methods to investigate fresh fruit quality **	[92]	
		Identification of candidate genes and QTL analysis through SNP maps	[139]	
		Identification of new candidate genes to impact aroma volatiles	[70]	
		QTL analysis in Prunus: a breeding perspective	[140]	
		QTL analysis and individuation of new loci	[141]	
		GWAS to study 12 peach agronomic traits	[104]	
		Relationships among metabolites, genes, and transcription factors/regulators in developing grape berries **	[137,138]	
		CS	Exploring priming responses to cold stress	[19]
		UV-B	Regulation of genes encoding terpene synthases and terpene levels	[132]
		1-MCP UV-B	PpUGT85A2 regulates volatile glycosylation in peach	[144]
			Expression QTL analyses and individuation of genes associated with fruit softening rate	[143]
		MJA, UV-B	Correlation between PpCXE1 and catabolism of volatile esters	[131]
		1-MCP	1-MCP treatment affects peach fruit aroma	[145]
		Correlation between PpAAT1 activity and Aroma peach varieties	[129]	
		Review on multi-omics applications with a breeding perspective-Prunus species	[33]	
	CS and CI	Review about genomic and transcriptomic studies to find QTLs and genes responsible for CI symptoms	[97]	
		Organic acid accumulation and related genes	[116]	
		Study of genes associated with aroma profile	[117]	
		Survey on multi-omics studies for crop improvement **	[146]	

In peach, the involvement of major genes localized in QTLs confirmed through gene expression analysis (RNA-Seq) is an approach used recently for studying many agronomic traits, including those characterizing peach post-harvest processes [143].

On the other hand, combined transcriptomic and metabolomic analyses (Table 3) have allowed the discovery of genes related to the biosynthesis of the main peach aromatic VOCs, including lactones, esters and phenolics at different maturation stages and during post-harvest ripening. This has enabled the detection of a core of genes that are closely related with peach fruit VOCs and could be useful for future biotechnological aims. Moreover, in depth analysis based on this approach has allowed the identification of changes occurring in peach fruit during post-harvest treatments, investigating the most common degradative processes impacting on their quality, and trying to clarify their molecular basis.

Similarly, to single omics applications, for multi-omics peach post-harvest ripening studies an increasing application of UV, MJA and 1-MCP techniques coupled to CS treatments has been observed recently (as highlighted in Table 3).

However, despite the fact that the multi-omics post-harvest ripening studies have already produced significant results, due the complexity of this process, these investigations have not yet covered all underlying molecular mechanisms and elucidated completely the role of key genes involved in the biological post-harvest ripening pathway, making further studies still necessary.

Furthermore, many technological aspects must be taken into account. In fact, the combination of different omics approaches requires integration of heterogenous data, and better tools to manage data coming from the pangenomes and generally from different omics layers are still being developed. Even today, we are aware that with multi-layer datasets integration is a challenging issue and that careful planning of a multi-omics

applications is thus required. The role of publicly available databases, grouping genomics, genetics, transcriptomics, metabolomics data and advanced bioinformatic tools will become even more crucial. However, the benefits of applying these approaches will ensure that research will overcome current technological limitations, and this will be possible thanks to the rapid progress in bioinformatics.

Overall, it is suggested that future multi-omics studies, based on extensive data integration, could contribute to provide further knowledge about the complexity of peach post-harvest physiology. For instance, investigations based on a classification of genes involved in peach quality or senescence based on a timeline, deriving information from data integration of multi-omics approaches, could help to identify genes that can be used for gene editing technologies. Furthermore, gene manipulation through gene editing tools, such as CRISPR-Cas9, could support the characterization of genes whose function in the post-harvest process is still unclear.

In addition, future research could investigate variation of gene expression during post-harvest ripening by understanding and manipulating gene DNA methylation status. A promising approach could be the use of gene editing techniques for the demethylation or hypermethylation of targeted genes to improve peach post-harvest quality traits and control fruit shelf-life. An understanding of the role of histone modification may also contribute to defining the different layers of control.

On this basis, the use of omics and gene editing methods, could be proposed as novel precision tools for plant breeding programs, being more targeted than existing approaches, which often negatively impact fruit quality.

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