chemistry proceedings

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Proceeding Paper

Molecular Investigations of Peach Post-Harvest Ripening Processes and VOC Biosynthesis Pathways: A Review Focused on Integrated Genomic, Transcriptomic, and Metabolomic Approaches †

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† Presented at the 1st International Online Conference on Agriculture—Advances in Agricultural Science and Technology, 10–25 February 2022; Available online: https://iocag2022.sciforum.net/.

Abstract: Peach (*Prunus persica* L.) represents a very important model plant given its small and publicly accessible genome, the availability of homozygous doubled haploids, and its taxonomic similarity to other popular stone fruits. Albeit it is an economically important crop with a great production potential, the consumption of peach is still considered low in comparison with that of other fresh fruits, such as apple and banana. A way to increase it could be to improve its quality and aroma, which tend to be affected during the often-prolonged storage and transport periods. Recently, substantial research efforts have been directed towards the characterisation of the regulatory mechanisms underlying the hormonal, transcriptomic, and metabolomic changes happening during peach fruit post-harvest ripening. Biosynthesis pathways of volatile organic compounds related to changes in aroma have also been investigated. Due to advances in next-generation sequencing, new insights into the molecular functions of peach genes have been gained. Studies have mapped out the molecular bases of peach fruit post-harvest ripening using a multi-omics approach, combining genomic, transcriptomic, and metabolomic methods. This review aims to discuss the most relevant recent research results in this area in order to provide a useful starting point for researchers in the field and future perspectives for improving peach quality.

Keywords: peach post-harvest ripening; volatiles; genomics; transcriptomics; metabolomics

Citation: Sirangelo, T.M.; Rogers, H.J.; Spadafora, N.D. Molecular Investigations of Peach Post-Harvest Ripening Processes and VOC Biosynthesis Pathways: A Review Focused on Integrated Genomic, Transcriptomic, and Metabolomic Approaches. *Chem. Proc.* **2022**, *10*, 8. https://doi.org/10.3390/IOCAG2022-12179

Academic Editor: Massimo Cecchini

Published: 10 February 2022

1. Introduction

Peach (*Prunus persica* (L.) Batsch) belongs to the Rosaceae family, particularly to species that produce drupe fruits, which are important crops worldwide. It is considered a model plant, and its small genome is relevant to the agricultural research field [1]. Since the consumption of peach is lower than that of other fresh fruits [2], most investigations have focused on the improvement of its quality and aroma, which may decrease over long storage periods after harvest.

Peach ripening is a very complex process, in which the related underlying mechanisms cause structural modifications, and the fruit acquires new organoleptic characteristics [3]. During this process, changes in the expression levels of thousands of genes occur, and they profoundly affect carbohydrate and organic acid metabolism, chlorophyll breakdown,

anthocyanin accumulation, ethylene production, and the biosynthesis of volatile organic compounds (VOCs).

Once peaches are collected from the plant, during the post-harvest ripening period, changes dependent on the specific fruit metabolism occur. These modifications involve protein and lipid degradation, resulting in an alteration in different fruit quality features, including texture, taste, and aroma [4]. In order to limit these effects, several post-harvest strategies have been investigated and developed.

Peaches are characterised by a rapid deterioration at a temperature of about 20 °C [5]. Therefore, cold storage (CS) treatments are often used to enhance fruit shelf-life. However, if applied incorrectly, they can result in chilling injury (CI), characterised by specific changes in texture and a reduction in aroma quality [6,7]. Some post-harvest treatments designed to prevent CI include the use of a controlled atmosphere (CA; with low O_2 and high CO_2 concentrations) under cold conditions. 1-methylcyclopropene (1-MCP) treatments also prevent CI development [8]. Moreover, there is also a genetic influence on the development of CI: notably, nectarines show a better resilience to storage conditions than peaches [9].

However, to date, in spite of the large number of studies available, many aspects of the ripening process under post-harvest conditions remain obscure. Therefore, the aim of the present work is to discuss the most relevant recent evidence and studies in the field, focusing on omics and especially multi-omics approaches. In particular, we intend to provide a concise overview of the latest advances in plant metabolomics, genomics, and transcriptomics to act as a useful starting point for researchers in the area.

2. Growth Regulator Control of Peach Ripening and Phytochemical Changes

In species belonging to the genus Prunus, as shown by a large number of studies, the complex and integrated action of auxins, cytokinins (CKs), and gibberellins (GAs) underlies the regulation of several key fruit traits. Moreover, abscisic acid (ABA) and ethylene also contribute to some key effects observed during fruit ripening in all these species [10].

Ethylene signalling is often considered the main growth regulator involved in fruit ripening; in climacteric fruit, such as peaches, it underlies a complex transduction pathway affecting genes involved in traits such as aroma, colour, firmness, and post-harvest shelf-life [10]. However, ABA interacts with ethylene in a complex cross-talk, and it regulates cell wall modulation, as well as genes involved in auxin signalling [11]. ABA is accumulated before ethylene synthesis starts, and its levels reach the highest values in the fully ripe stage. Lower ABA levels are correlated with an increase in ethylene, and, conversely, a decrease in ABA is associated with a higher acid and sugar content during fruit maturation.

Auxin also interacts with the ethylene regulation of fruit ripening by upregulating its synthesis, but a genomic-level approach has shown that many auxin biosynthesis genes, as well as those involved in auxin transport and signalling, increase in expression during fruit maturation [12]. This provides evidence for the direct involvement of auxin in the ripening process [12]. CK levels are finely regulated and seem to be crucial to plant growth, stimulating mitosis, but they may also partially act as auxin inhibitors, causing an increase in fruit size [13]. GAs also appear to be involved in fruit development, promoting mitosis and cell growth, and post-harvest treatment with GA_3 has been found to delay ripening by inhibiting ethylene biosynthesis [14]. From this perspective, ABA and ethylene can be seen as GA antagonists.

Downstream of growth regulators, fatty acid composition is modulated during the different stages of peach ripening and has a major influence on the aromatic profile. Several well-studied families of enzymes, including alcohol acyltransferases (AATs), alcohol dehydrogenases (ADHs), fatty acid desaturases (FADs), hydroperoxide lyases (HPLs), and lipoxygenases (LOX), are involved in the production of fatty-acid-derived VOCs [15]. Polyunsaturated fatty acids (PUFAs), such as linoleic and linolenic acids, accumulate significantly during fruit maturation. However, it was found that palmitic acid decreased, while the amounts of oleic, stearic, and other fatty acids did not change significantly [15].

Fatty acid metabolism is also involved in the production of another growth regulator: jasmonic acid. LOX enzymes catalyse the peroxidation of PUFAs, the first process in the biosynthesis of oxylipins, which include the family of jasmonates (JAs) [16]. In peach fruit, JAs have been shown to impair ethylene and auxin biosynthesis, as well as signalling, and to slow down the ripening process [16]. The treatment of fruit with methyl jasmonate (MeJA) downregulated the expression of genes related to ripening while upregulating defence-related genes [17]. In apples, endogenous JA was higher in fruit stored under chilled conditions than in that stored at ambient temperature, suggesting a role for JA in post-harvest storage, and, indeed, JAs are used as a treatment to extend shelf-life and prevent CI damage [18].

Among antioxidants, flavonoids and carotenoid levels also vary during peach ripening, resulting in a more favourable nutritional profile. Carotenoids are not just accessory pigments involved in photosynthesis, but they are also norisoprenoid precursors, a family majorly influencing the final peach aroma and whose levels increase during ripening. In peach, the most important carotenoid pigment is xanthophyll, which is found in high amounts in both the peel and flesh of the fruit [19]. The specific amounts of carotenoid species are profoundly affected by post-harvest conditions and factors such as CA composition and temperature [20].

Phenolics are also important nutritionally in peaches, with major groups being flavonols, anthocyanins, and hydrocinnamic acids, and a higher polyphenol content was found to be associated with higher density nectarines [21]. During ripening, phenolics increase and then fall again, and there seems to be a complex interaction with ethylene signalling [22].

3. Volatile Organic Compounds

The volatilome is a crucial part of the plant metabolome due to its contribution to fruit aroma and flavour. About 110 different volatiles, including alcohols, aldehydes, carboxylic acids, esters, ketones, lactones, phenols, and terpenoids, have been described for peach fruit. Among them, around 40 compounds directly involved in aroma perception in peach have been detected [23]. Lactones, particularly γ- and δ-decalactones, are considered the major contributors of the typical 'peach aroma', with the former being the most relevant and widely employed in the food industry as added aroma [2,24].

Several detection methods have been applied to detect VOCs in peach, including solid-phase microextraction (SPME), which, however, can suffer from saturation [25]. Moreover, many reports are based on analyses of homogenised tissue [25]. The use of thermal desorption tubes and minimally processed or whole fruit has more recently provided a better overview of the volatilome of relevance to the fruit supply chain in peach and other species [26–28].

VOCs are produced during fruit ripening through metabolic pathways involving fatty acids, proteins, and carbohydrates. These pathways can be influenced by pre-harvest factors, including genotype, cultivation conditions, and ripening stages [15,28]. VOC levels undergo dramatic changes during fruit maturation, with specific patterns among different species but also at the cultivar level [28]. Post-harvest aroma is critical for the consumer and is influenced by CA composition, ethylene exposure, and temperature [28,29]. Aldehyde levels have been found to decrease and esters have been found to increase during peach shelf-life [30]: in particular, cold storage enhances the synthesis of both alcohols and aldehydes, while esters increase with storage at 20 °C after a cold treatment period. However, the pattern of change in response to post-harvest treatments also varies with cultivar [28].

4. Metabolomic Peach Profile

The volatilome is a part of the wider metabolome, and the complex relationships between VOC levels and metabolites have been investigated using powerful statistical methods, such as those based on Correlation Network Analysis (CNA). In particular, an integrated approach, based on a hierarchical cluster analysis and a metabolomic CNA, has

been used in peach to investigate the effect of pre- and post-harvest treatments on VOC levels [2]. Volatile compounds were found to be clustered according to their chemical nature or previously known biosynthetic pathways. VOC groups showing a similar organisation were isolated, as well as those included in specific metabolic pathways.

Lactone biosynthesis during post-harvest maturation appears to be regulated by Acyl-CoA oxidase, the first enzyme of the b-oxidation metabolic pathway [31]. Furthermore, important differences in VOC profiles amongst several cold-stored peach cultivars and varieties have been confirmed [29,32].

A recent review considering the relationship between the metabolome and quality traits [33] concluded that the integration of different approaches, such as transcriptomic and proteomic analyses with metabolomic approaches, can be a powerful tool for exploring how changes in metabolism during fruit post-harvest storage result in changes in quality. In particular, more research is needed to understand the genome-wide reconfiguration of gene expression and the consequent changes in metabolism in response to abiotic stresses experienced by the fruit post-harvest.

5. Genomic and Transcriptomic Peach Profiles

The first peach genome used as a reference was assembled in 2008 by the International Peach Genome Initiative. The first release was only published in 2010, followed by a second one based on reads sequenced from the double haploid variety 'Lovell', making it possible to obtain a new genome sequence that was more consistent and accurate than the previous one [34].

The initial peach transcriptome and large-scale differentially expressed gene analyses among the different maturation stages were carried out using microarrays. The first release, referred to as μPEACH1.0, was developed by the Italian Consortium for Genomics studies in Rosacea species, aiming to investigate the effects of ethylene and propylene on peach maturation and post-harvest processes [12]. A few years later, another highly specific microarray was created, with the aim to investigate differentially expressed transcripts between two peach genotypes, showing a different aromatic profile. The study revealed over one thousand five hundred significant transcripts [35].

Subsequently, next-generation sequencing (NGS) methods, such as those based on Roche 454 pyrosequencing and Illumina technologies, became gold-standard practices, making it possible to generate large amounts of both genomic and transcriptomic data at an unprecedented speed. As a consequence, bioinformatics and biostatistics packages, as well as a constantly growing number of tools and databases, are now crucial to correctly analyse and integrate the wide variety of datasets available, ranging from completely annotated whole-genome sequences and metabolomic data to transcriptomes and expression data. At first, the short size of NGS reads was often considered one of the main limits of these new methods, because they made it quite demanding to assemble genomes correctly, resulting in a large number of unassembled sequences. Repetitive regions, particularly common in many species, and structural variants were also often hard to map [36]. To address this issue, recently, third-generation high-throughput technologies were developed, making it possible to obtain higher quality assemblies [37].

cDNA is also often obtained and sequenced using NGS technologies, making it possible not just to investigate the expression levels of previously chosen genes but also to analyse the transcriptome as a whole, including genes expressed at low levels, as well as splicing variants [38]. This kind of evidence, correctly integrated with other omics data, can be used to obtain more accurate gene models, as previously carried out for Arabidopsis in the TAIR database [39].

Structural variants (SVs) have also been investigated, being often associated with economically relevant characteristics in crops [40]. More specifically, in peach, whole-genome sequencing data from over one hundred accessions made it possible to carry out a Genome-Wide Association (GWA) study to analyse crucial agronomical traits, including some affecting flavour, fruit texture, shape, and size.

A pangenomic approach was also recently used, obtaining correctly integrated SVs and a limited number of putative casual variants, opening new perspectives for future studies aiming to investigate the relationships between SVs and VOCs [41].

6. Peach Post-Harvest Ripening and Multi-Omics Approach

Over the last decade, due to advances in NGS, combined omics approaches have been applied in several fields, including fruit post-harvest ripening. Multi-omics analyses have been targeted at identifying key genes controlling metabolites and transcript levels and at investigating their regulation, revealing significant metabolic changes behind the fruit ripening process [42]. This approach has also been valuable in linking regulatory genes and metabolic changes associated with pre-harvest stress and its effect on ripening.

Integrated metabolomic and genomic methods have also been used to investigate pre- and post-harvest maturation. This approach has confirmed the involvement of a limited number of gene regions controlling the peach aromatic profile [43]. Quantitative Trait Loci (QTL) positions within chromosomes have been identified using the peach genome as a reference, and they proved to be different from those forecasted in previous work, also providing superior QTL mapping for several peach species.

The accessibility of gene expression and metabolomic analyses has made it possible to investigate the effects of post-harvest treatments on peach CI development [5]. In particular, this approach has explained the mechanisms underlying pre-conditioning, which inhibits CI and results in an enhanced ethylene production. These approaches open new perspectives for understanding peach fruit adaptation and response to cold temperature storage.

Different peach development stages, as well as differences amongst cultivars, have also been investigated using a combination of omics and other approaches, aiming to identify the gene responsible for the modulation of the VOC linalool between glycosylated and volatile states [44]. GC-MS allowed to perform metabolomic analysis, and RNA-Seq libraries were used to investigate transcriptomic data, together with quantitative Polymerase Chain Reaction (qPCR) to confirm fold-change expression changes in a few selected genes and to identify the UDP-glucosyltransferase responsible [44].

In a previous study, a combination of volatilomics and RNA-Seq together with expression studies also demonstrated that specific carboxylesterases are important in modulating ester levels, as well as previously identified alcohol acyltransferases [45]. At the same time, it was highlighted that the highest amounts of esters were detected after MeJA exposure.

Recently, multi-omics methods were also used to investigate the effects of 1-MCP on peach post-harvest quality. It is widely recognised that 1-MCP has profound effects on the peach aromatic profile, as it affects the gene expression of the enzymes responsible for the production of key VOCs. In particular, it was found that esters decreased after 1-MCP exposure, and the levels of some alcohols and aldehydes were also significantly affected. Transcriptomic data were obtained through RNA-Seq and metabolomic analysis based on SPME and GC-MS [46], showing that the inhibition of peach VOCs was concomitant with an increase in green leaf volatiles, and both were associated with a transcriptional downregulation of ethylene biosynthesis and signalling, and the modulation of fatty acid levels.

Furthermore, an overview of key genetic and molecular approaches presented to better understand the mechanisms involved in fruit maturation in Prunus species [10] underlined the importance of a wise integration of genomic, metabolic, and transcriptomic approaches. The authors emphasise the need for the development of new marker-assisted selection strategies and the identification of more markers and genes responsible for key traits to provide a better understanding of ripening mechanisms and to successfully apply the gained knowledge in breeding new varieties.

7. Conclusions

Multi-omics-based studies integrating relationships between physiological changes in peach post-harvest maturation and volatilomic, transcriptomic, and metabolic changes are

gaining pace. However, for these studies to be translated into new more resilient varieties and for real change in the organoleptic quality of stored peaches, further work is needed. This will need to be aimed at translating gene discoveries into breeding markers and at providing a full understanding of the effects of different pre- and post-harvest treatments on key traits important to consumers.

Author Contributions: Conceptualization, T.M.S., N.D.S. and H.J.R.; writing preparation, T.M.S., N.D.S. and H.J.R.; supervision, N.D.S., H.J.R. and T.M.S. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: Work was supported by Fondazione con il Sud Fondazione con il Sud, call Brain2South, as part of the FRUITY collaborative project (2015-0245).

Conflicts of Interest: The authors declare no conflict of interest.

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