Advances in Mechanisms and Omics Pertaining to Fruit Cracking in Horticultural Plants

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Abstract: Fruit cracking is a physiological disease that occurs during fruit development, which limits the quality and marketability of the fruit and causes great economic losses. Fruit cracking is affected by physiological, genetic and environmental factors. In this paper, the mechanism of fruit cracking was elaborated from cutin and cell wall, especially the gene families related to cell wall metabolism, including the polygalacturonase (PG) gene family, xylologlucan endotransglucosylase/hydrolase (XTH) gene family and expansin gene family. In addition, due to the advancement of high-throughput sequencing technology, an increasing number of horticultural plants have completed genome sequencing. This paper expounds the application of omics, including transcriptome, proteome, metabolomics and integrative omics in fruit cracking. The measures to reduce fruit cracking include using plastic rain covers and bagging, and spraying mineral and plant growth regulators. In this paper, the mechanisms of fruit cracking are reviewed at the molecular level, and the problems needing to be solved in fruit cracking research are put forward.

Keywords: fruit cracking; cuticular membrane; cell wall; polygalacturonase; xylolcurcan endotransglucosylase; expansin; omics

1. Introduction

Peel plays a vital role in crack resistance, transportability, storability and shelf-life quality. Fruit cracking is a common physiological disease, in which the fruit surface cracks in response to uncoordinated internal growth and the external environment. Generally speaking, when the fruit is in the mature stage and encounters rainfall, the probability of fruit cracking is higher [1–5]. The fruit cracking rate of litchi cultivar ‘Nuomici’ is 10–30% in average years, but it is 90% in some particular years [6]. The fruit cracking rate of the pomegranate cultivar ‘daqingpitian’ is more than 30% (unpublished data).

Russetting is usually considered as a hard epidermal tissue formed after the cuticle of the epidermis is damaged, which leads to micro-cracks in the cuticle, with some forming macro-cracks [7–9]. Fruit cracking seriously affects the appearance and quality of the fruit. In addition, the cracked fruit is prone to different degrees of fungal and bacterial storage diseases, which shorten the storage period and shelf life of the fruit, resulting in significant economic losses [3,10,11]. The measures to reduce fruit cracking include using plastic rain covers and bagging, and spraying mineral and plant growth regulators.

With the innovation of high-throughput sequencing technology, omics sequencing has been widely used in many plants because of its low cost, rich and comprehensive information, and high practicability [9,10,12]. It has become an effective tool to reveal
the mechanism of fruit cracking. Understanding the reasons for cracking is the premise of preventing and reducing cracking, which is of great significance to improve the yield and quality of various fruits. This paper reviews the research status and progress of the mechanism of fruit cracking in horticultural and agricultural production plants and the corresponding control methods, in order to provide references for future fruit cracking control and related research work.

2. Fruit Cracking Types and Occurrence Period

Fruit cracking often occurs in sweet cherry [13], apple [14], grape [15], jujube [16,17], pomegranate [18,19], litchi [20], citrus [21], pear [22], tomato [23,24], watermelon [25] and melon [26]. Generally speaking, cracks include micro-cracks and macro-cracks. Figure 1 shows a micro-crack and macro-crack in pomegranate peel under scanning electron microscope.

![Ultra-microstructure of pomegranate peel by scanning electron microscope (SEM; magnification 300×). (A) A micro-crack in pomegranate peel; (B) A macro-crack in pomegranate peel.](image)

The common types of fruit cracking include apical end cracking, deep side cracking, stem end cracking, longitudinal cracking, transversal cracking, longitudinal and transversal cracking, cuticular cracking, and irregular cracking. The period of fruit cracking is generally in the phase of rapid fruit growth or when it rains near harvest. Different horticultural plants have different types of fruit cracking and occurrence period, as shown in Table 1. Fruit cracking is affected by the physiological, genetic, and environmental factors of the fruit [27], such as the cuticle and wax [28], the properties, components and endogenous hormones of the cell wall [23], the characteristics of the fruit itself (fruit size and hardness [29], the anatomical structure of the peel [30] and the biomechanics [29]), the genotype of the fruit [31], moisture [32], and nutrients [33].

<table>
<thead>
<tr>
<th>Species</th>
<th>Fruit Cracking Types</th>
<th>Occurrence Period</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cherry</td>
<td>Apical end cracking, deep side cracking, stem end cracking</td>
<td>Early stage of fruit development or when rain happens near harvest</td>
<td>[2,34]</td>
</tr>
<tr>
<td>Grape</td>
<td>Longitudinal cracking, ring cracking, Cuticular cracking, ring and longitudinal cracking</td>
<td>Growth and development</td>
<td>[15]</td>
</tr>
<tr>
<td>Citrus</td>
<td>Flavedo-splitting, inner-cracking and albedo-splitting (fruit creasing or pitting)</td>
<td>Cell enlargement or fruit maturity</td>
<td>[35]</td>
</tr>
</tbody>
</table>
Table 1. Cont.

<table>
<thead>
<tr>
<th>Species</th>
<th>Fruit Cracking Types</th>
<th>Occurrence Period</th>
<th>Reference</th>
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<tbody>
<tr>
<td>Tomato</td>
<td>Radial and concentric cracking, circular cracking</td>
<td>Last phase of fruit growth</td>
<td>[36]</td>
</tr>
<tr>
<td>Apple</td>
<td>Calyx-end cracking, internal ring cracking and stem-end splitting</td>
<td>Pre-harvest period, the phase of rapid fruit growth</td>
<td>[37,38]</td>
</tr>
<tr>
<td>Jujube</td>
<td>Longitudinal cracking, transversal cracking, longitudinal + transversal cracking, irregular cracking</td>
<td>Fruit maturity</td>
<td>[39]</td>
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3. Factors Involved in Cracking

3.1. Physiological Factors

Fruit characteristics such as fruit shape, size and hardness can affect the occurrence of fruit cracking. The physiological metabolism inside the fruit is closely related to the growth and development of the fruit, and studies have shown that fruit soluble sugar, soluble solids, pectin, enzymes and endogenous hormones have a close relationship with fruit cracking [12,27]. Sugar is an important component of fruit and the material basis of its growth and development. Li et al. [40] found that the crack resistance of varieties was related to the content of reducing sugar, soluble total sugar and cellulose, but not to the starch content. The reducing sugar content and cellulose content of the crack-resistant varieties (‘Muzao’ and ‘Xiangzao’) were higher than those of the crack-susceptible varieties (‘Goutouzao’, ‘Junzao’ and ‘Tuanzao’). Total soluble sugars of crack-resistant varieties were lower than those of crack-susceptible varieties [40].

3.2. Genetic Factors

In 1981, Cuartero et al. [41] found that fruit cracking was determined by genetic characteristics. The sensitivity of fruit cracking was different in different cultivars [42]. Fruit cracking was not controlled by a single gene, but controlled by multiple genes [43]. The fruit cracking traits can act on offspring through inheritance, and the degree of cracking varies greatly between different varieties [13]. Polat et al. [44] observed that the pomegranate fruit cracking rate in an early seedless variety is lower than two late varieties Hicaz and Katurbaş. This result is consistent with that of Keziban Yazici and Sezai Erciși [31]. Yamaguchi et al. [45] investigated 37 sweet cherry varieties for fruit cracking and found that fruit cracking varied significantly among varieties and was positively correlated with fruit quality and flesh hardness, and Simon et al. [46] identified that sweet cherries with different fruit quality had different rates of fruit cracking. Greco et al. [47] analyzed crack susceptibility of 30 sweet cherry varieties in Italy and confirmed that crack susceptibility was genotype dependent.

3.3. Environmental Factors

Water is the main environmental factor causing fruit cracking, and both soil water and water on the fruit surfaces are important factors inducing fruit cracking [48]. Exposing the fruit surface to liquid water or high-water vapor will lead to the formation of cutin membrane microcracks. Studies have shown that pomegranate fruits are sensitive to water deficit at the end of the fruit growth and ripening period. When rainfall affects previously water-stressed pomegranates, an asymmetric increase in pericarp swelling pressure occurs because aril swelling increases much more than pericarp swelling. The increase in aril pressure stresses the peel and makes it susceptible to rupture [32,49]. In addition, improper irrigation during fruit ripening, the occurrence of sunburn, and mineral deficiencies can also cause fruit cracking, and Yazici and Özgüven [50] showed that sunburned fruits have a higher probability of fruit cracking. Excessive temperature differences can lead to the
accumulation of carbohydrates, reducing the plants osmotic potential and allowing them to absorb more water, grow faster, and crack more easily [51].

3.4. Postharvest Storage Factors

During postharvest storage, the structure of lenticels, microcracks, wax patterns and pericarp tissue components changed in fruits, which affected fruit quality [52]. Therefore, it is particularly important to carry out postharvest treatments on fruits. In the U.S. Pacific Northwest (PNW), sweet cherries are hydrocooled as soon as possible after harvest and shipped in cold flume water during packing to reduce respiration rates and extend storage/shipping life [53]. Wang et al. [53] revealed that hydrocooling cherry fruit in appropriate CaCl$_2$ solutions (i.e., 0.2–0.5%) for 5 min and then passing the fruit in cold flume water for 15 min increased fruit firmness, peel color, and reduced cracking and decay following 4 weeks of cold storage.

4. Mechanisms of Fruit Cracking

Fruit cracking is affected by the arrangement of epidermal cells, sub-epidermal cells and the thickness of the cell layer. Zhang et al. [15] found that grapes with tightly arranged epidermal cells had the highest rate of fruit cracking, reaching 57.00%. In terms of epidermis cell arrangement, the fruit cracking rate was 50% higher in loosely arranged varieties than that in compactly arranged varieties. Kertesz and Nebel [1] found no correlation between cell size and cracking in cherry epidermis, but the thickness of the inner wall of the epidermis seemed to be positively correlated with the degree of cracking. However, Correi et al. [54] found that the larger the cell size of the cherry epidermis, subepidermis and parenchyma, the lower the cracking rate.

4.1. Cuticular Membrane

The cuticular membrane (CM) is composed of cutin and wax. CM covers the stems, leaves, flowers and fruits of plants. The main components of cutin are mainly carbon-rich, 16 or 18 (C16 or C18) oxidized fatty acids and glycerol polyesters [55,56]. The waxy components are mainly very-long-chain fatty acids (VLCFAs) and derivatives (alkanes, aldehydes, alcohols, esters, etc.), flavonoids and triterpenoids [57,58]. A natural waterproof barrier protects plant tissues from stress damage, invading pathogens and insect herbivores [59–61]. The CM has a major effect on fruit cracking, rots and russet [61,62]. Studies have found that wax and cutin are deposited in the CM during the growth process, “fixing” the strain in the CM [63]. At present, numerous genes related to cuticle formation and regulation have been found in Arabidopsis, tomato, apple, cherry and other plants [57,64–67]. Related studies have found that some proteins (BODYGUARD (BDG), structural) and enzymes (Glycerol-3-Phosphate Acyltransferase GPAT6, catalytic) play an important role in the process of cutin biosynthesis [68,69]. In addition, fruit cutin is regulated by its composition and polysaccharide ratio during the development process [70]. Alkio et al. sequenced and annotated the exocarp of cherries, and annotated the synthesis of cutin and wax in the biological process [71]. Konarska et al. [30] found that apples with less crystalline wax are easy to crack.

SHINE branch transcription factors act on epidermal pattern formation and fruit cuticle formation [72], and its direct regulation targets are LCS2, GPAT4, CYP86A4 and other cutin synthesis-related genes, but it only indirectly regulates the formation of cuticle wax [73]. The SHN transcription factor family includes SHN1, SHN2, and SHN3, which regulate genes involved in the formation of cell wall polysaccharides and the extracellular protein structure of Arabidopsis flowers [72,74]. Lashbrooke et al. [66] performed QTL mapping on the full sibling population of apples, showing that MdSHN3 may regulate apple fruit cuticle biosynthesis.
4.2. Cell Wall

The cell wall is composed of a network of interactions between polysaccharides (cellulose, hemicellulose, pectin, etc.), proteins and polyphenol compounds, which provide mechanical support and hardness for plant cells [75,76]. Fruit ripening, softening and cracking are closely related to metabolism and biochemical modification of cell wall components, which are the result of a number of enzymes, such as polygalacturonase (PG), pectinesterase (PE), xyloglucan endoglucanase/hydrolase xyloglucan endotransglucosylase/hydrolase (XTH) and expansin [77,78]. Gine-Bordonaba et al. [79] found that cherry cracking sensitivity is related to cell wall modifying enzymes, and Chen et al. [12] found that cell wall polysaccharide metabolism is closely related to mature cracking of African Pride (AP) atemoya through KEGG pathway enrichment analysis of DEGs of transcriptomic data.

4.2.1. Polygalacturonase Gene Family

Polygalacturonase (PG) is an enzyme that catalyzes the hydrolysis and decomposition of pectin (the main component of plant cell walls) [80,81]. Generally, the pectin network in the cell wall will decompose as the shape of plant cells changes. PG is encoded by a large gene family that is involved in fruit development of tomato, apple, peach and pear [82–85]. Dautt-Castro et al. [80] found that MiPG21-1, MiPG14, MiPG69-1, MiPG17, MiPG49, MiPG23-3, MiPG22-7, and MiPG16 were highly upregulated during fruit ripening. Chen et al. found that pectinesterase (PE) and PG were involved in the degradation of pectin of atemoya pericarp, thus affecting fruit ripening and cracking [12].

4.2.2. Xylologlucan Endotransglucosylase/Hydrolase Gene Family

Xylologlucan endotransglucosylase/hydrolase (XTH) is an enzyme with xyloglucan molecular transferase activity or xyloglucan β-1,4 glycosidic bond hydrolysis activity, which has xyloglucan endotransglycosidase (XET) activity and xyloglucan endohydrolase (XEH) activity [86], which play an important role in regulating cell wall elongation and skin softening [87–90]. The genes related to fruit ripening found in tomato and apple are SIXTH5, SIXTH8, MdXTH2, MdXTH10, MdXTH11 [91,92]. As for the relationship between XET genes and fruit cracking, Lu et al. [93] found that the different accumulation of LcXET1 in the peel and flesh tissues of the cracking-susceptible variety ‘Nuomici’ and the cracking-resistant variety ‘Huaizhi’ was closely related to fruit cracking, and found that NAA treatment of ‘Nuomici’ litchi fruit could increase the accumulation of LcXET1 mRNA in its peel, thus reducing fruit cracking. A schematic diagram of the fruit cracking associated with the cuticle membrane and cell wall is shown in Figure 2.

4.2.3. Expansin Gene Family

In the process of plant growth, cells secrete a plant cell wall protein called expansin. Expansins are a large gene family, and the main factors regulating cell wall stress relaxation. They cause fruit softening and cracking by breaking the hydrogen bond between cell wall polymers (such as hemicellulose and cellulose microfibrils) [94,95]. The transcription level of the expansin coding gene is related to fruit cracking. Brummell et al. extended the shelf life of tomato from 17 d to 21 d by inhibiting the expression of LeExp1 in tomato, suggesting that the expressed protein gene was related to fruit softening [96]. Six expansin genes (MdExp1, MdExp2, MdExp3, MdExp4, MdExp5, MdExp6) have been identified in apples [97] and MdEXP A3 affects fruit cracking [38]. In addition, the expression of LcExp1 and LcExp2 genes in lichi peel was closely related to fruit growth and cracking [98]. The identified genes related to fruit cracking are shown in Table 2.
Gene Family | Species | Gene | Gene Function | Reference
--- | --- | --- | --- | ---
AP2/ERF | Watermelon | ERF4 | Rind hardness | [99]
 | Peppers | SHN1 | Contributing to the high cutin content | [100]
 | Apple | SHN3 | Cuticle formation | [66]
PG | Atemoya | PG | Pectin degradation | [12]
 | Mango | PG21-1, PG14, PG17 | Fruit ripening | [80]
XTH | Tomato | XTH5, XTH8 | Fruit mature | [91]
 | Apple | XTH2, XTH10, XTH11 | Fruit mature | [91]
 | Lichi | XET1 | Fruit cracking | [93]
 | Watermelon | XET1, XET2 | Fruit cracking | [25]
Expansins | Tomato | EXP1 | Cell wall disassembly | [24]
 | Lichi | EXP2 | Cracking-resistant | [98]
 | Apple | EXP3 | Fruit cracking | [38]
 | Apple | EXP4 | Cell-wall modification/loosening | [101]

5. Studies on the Omics Regarding Fruit Cracking

Different omics studies play a vital role in the study of fruit cracking [12,24,102]. Transcriptomics is a discipline that studies gene transcription and transcriptional regulation in cells. It is the sum of all RNA transcribed by a species or a specific cell in a certain functional state, including mRNA and non-coding RNA. Non-coding RNA refers to RNA that does not encode protein, including ribosome RNA (rRNA), transfer RNA (tRNA), microRNA (miRNA), long non-coding RNA (lncRNA), and circular RNA (circRNA). The transcriptome can be used to study gene structure, function and prediction of new transcripts. The transcriptome sequencing showed that the cracking of African Pride (AP) atemoya fruit was closely related to the starch metabolism pathway, in which seven
Agronomy 2021, 11, 1045

Proteomics is a discipline that describes all protein interaction mechanisms and functions in the genome, cells or tissues of organisms under various environmental conditions [103]. Proteomics can identify a large number of proteins in vivo and study the changes of post-translational modifications and protein expression differences [104]. Shi et al. [9] identified 309 differentially expressed proteins in ‘Cuiguan’ pear by an iTRAQ-based proteomic approach, among which eight down-regulated proteins related to lignin synthesis were identified: PAL, CCR1, CAD, two peroxidases (K9URQ0 and M5W3Y0 respectively), 2 COMT (S5TPC3 and Q09K02 respectively) and HHT1. In sorghum, the down-regulation of CCR can lead to a change of cell wall structure, a decrease in lignin content and the accumulation of unusual phenols in cell wall lignin. Biochemical synthesis of lignin affects the deposition of russetting and further affects fruit cracking.

Metabolomics is an important part of system biology after genomics, transcriptomics and proteomics, and it is also one of the research hotspots in the field of omics. These metabolites detected by metabolomics are generated by the reaction of endogenous substances in the organism, and therefore, changes in metabolites reveal changes in endogenous substances or at the genetic level [43]. Metabolomics is the closest to phenotyping and is the ultimate expression of the overall function or state of a biological system. Rios [105] used gas chromatography-mass spectrometry (GC-MS) to find that varieties (‘Kordia’, ‘Regina’ and ‘Lapins’) with higher concentrations of nonacosane are not prone to cracking, and the higher proportion of C29 alkane in cherry epidermal wax plays an important role in the cracking resistance of fruits.

Association analysis of omics has become an effective method to break through the bottleneck of single omics research. Different omics reflect the transcription, translation and metabolism of horticultural plant genes from different levels, so as to achieve data complementation and better understand the regulation process behind various physiological phenomena of horticultural plants. Natarajan et al. [100] found that Habanero pepper genotype PI 257145 has much higher cutin content than PI 224448 through integrated metabolomic and transcriptomic methods. Wang et al. [20] analyzed the peels of three litchi varieties (cracking-resistant ‘Feizixiao’, non-cracking ‘Baitangying’, and cracking ‘Baitangying’) through the transcriptome and quantitative proteome. It showed that three of the KEGG pathways are related to cuticle biosynthesis: cutin, suberin, and wax biosynthesis (ko00073); phenylpropanoid biosynthesis (ko00940); and linolenic acid metabolism (ko00592). The expression of genes related to cuticle biosynthesis in litchi peel is closely related to fruit cracking. In addition, Niu et al. [10] elucidated the fruit cracking mechanism by comprehensive transcriptome and proteome analysis of Akebia trifoliata, and KEGG

Synthetase genes (one glgA, three glgB, one glgC, and two GBSS) were all down-regulated during fruit cracking, while 17 starch degradation enzyme genes (such as AMY1, AMY3, AMYG, BAM1, BAM3, BAM9, PUL, glgX, glgP, etc.) were up-regulated [12]. At the transcription level, the transformation from starch to soluble sugar may be one of the important processes of fruit softening and cracking. Jiang et al. [25] identified 14 differential genes (e.g., POD1, GST, GPAT, SMT, XET1, XET2, DHCR24, and SULTR3) involved in fruit cracking by RNA-Seq of four watermelon cultivars (two cracking-resistant cultivars, W11 and W96; two cracking-susceptible cultivars, W13 and W85), which were enriched in metabolic pathways such as phenylpropanoid biosynthesis, phenylalanine metabolism and starch and sucrose metabolism. Zhu et al. [102] conducted pericarp transcriptome sequencing analysis of the cracking-susceptible grape variety ‘Xiangfei’ and found that genes related to cell wall metabolism and cutin biosynthesis play an important role in fruit cracking. With the development of transcriptome sequencing technology, Xue et al. [24] constructed a LncRNA-mRNAs network for tomato fruit cracking in the crack-resistant tomato genotype ‘LA1698’ and the easy-to-crack tomato genotype ‘LA2683’ for the first time, and screened out genes related to fruit cracking, such as EXP, PG2, XTH7, XTH9 and ERF4. In addition, some LncRNAs (XLOC_033910, XLOC_007053, XLOC_008464) involved in fruit cracking through dioxygenase activity, redox process, oxidoreductase activity and cell wall metabolism were identified.

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analysis showed that cell wall-related pathways, including the interconversion of pentose and glucuronide, galactose metabolic pathway and benzyl propane biosynthetic pathway, were common to DEGS and DAPs, and 13 DEGS (such as NAC-like, EXP1, CAD, β-GAL1, 4CL, ENDOB, PE, PG3, CEL) involved in cell wall metabolism and 14 DAPs involved in cell wall metabolism were strongly correlated with RNA-seq data and protein expression levels. These omics data provide a new perspective for understanding fruit cracking.

6. Breeding and Conventional/Cultural Approaches to Reduce Fruit Cracking

6.1. Finding a Quantitative Trait Loci Marker

Quantitative trait loci (QTL) play a significant role in elucidating the genetic basis of fruit cracking. Capel et al. [106] established a genetic linkage map of the tomato recombinant inbred line (RIL) *Solanum lycopersicum* × *S. pimpinellifolium* population and determined the QTL that controls fruit cracking. Zhang et al. [107] used a new genetic linkage map based on cleaved amplified polymorphic sequence to locate 40 QTLs for fruit quality traits in melon. The QTLs for fruit quality traits were mainly concentrated in the vicinity of LG6 and LG9, and they were found to be related to exocarp thickness (ET7.1, ET11.1), peel hardness (EPFI3.1), and cracking (FCR4.1, FCR6.1, FCR9.1). By finding QTLs related to fruit cracking, reducing fruit cracking becomes a reality at the genetic level.

6.2. Plastic Rain Cover and Bagging

Measures to reduce fruit cracking include rain-proof cultivation and bagging. Plastic rain covers can be used in rain-proof cultivation to prevent the influence of rain on fruits and reduce fruit cracking [2,9]. At present, fruit bagging plays a vital role in preventing diseases and insects, reducing rust spots and pesticide residues [8,108]. In addition, bagging makes the fruit peel clean and smooth, reduces the rust index and sunburn, and is one of the effective ways to produce pollution-free and high-grade fruits [109]. In fact, bagging is widely used in the cultivation of apples, pears and pomegranates in Japan, China, America and India [109–112]. Bagging can reduce surface irritation such as mechanical damage and the expression of related genes, and enhance fruit cracking resistance [38]. Asrey et al. [113] found that when pomegranate was bagged in red, the fruit peel cracking rate decreased by 1/3, and the content of ascorbic acid and total anthocyanin was the highest in the fruit. Grñán et al. [111] discovered that pre-harvest bagging may have a negative effect on pomegranate fruit growth and ripening, reducing fruit size and ripeness index. While bagging significantly reduced the incidence of sunburn on pomegranate peels, Kasai et al. [38] found that bagging induced *MdEXPA3* expression in ‘Fuji’ apples pericarp at an early stage, resulting in reduced incidence of internal ring cracking and stem-end splitting. Nevertheless, different researchers have come up with contradictory results regarding the effect of fruit bagging on fruit quality, where bagging significantly improved the appearance of fruit quality, but bagging negatively affected the intrinsic quality of the fruit, such as reduced sugar content and sugar-acid ratio. Chen et al. [109] found that bagging significantly reduced the content of phenolic compounds in peel and pulp of apples (‘Golden delicious’, ‘Red delicious’ and ‘Royal gala’), and had a greater impact on peel.

6.3. Mineral and Plant Growth Regulators Spray

Mineral and plant growth regulators are closely related to the growth and development of plants [88,89]. Hepler P.K. [114] elaborated that Ca$^{2+}$ is a crucial regulator of growth and development in plants. During cell wall formation, the acidic pectin residues are secreted as methylesters, and only later deesterified by pectin methylesterase, liberating carboxyl groups, which bind Ca$^{2+}$. Studies have shown that calcium spraying increases the calcium content of the peel, which in turn strengthens the peel and reduces cracking [115]. Correia et al. [54] found that 5 g kg$^{-1}$ CaCl$_2$ plus 10 µmol $^{-1}$ abscisic acid (ABA)/1 mL$^{-1}$ glycine betaine (GB) was the most effective treatment for reducing cherry cracking, the rate of fruit cracking was less than 2%. The surface of cherries had higher wax, cutin content
and skin thickness. Spraying calcium (CaCl$_2$, CaHCO$_3$) on cherry leaves was found to reduce fruit cracking [116]. The treatment of CaCl$_2$ plus GB increased the expression of EXP1. Metabolomics analysis showed that the primary metabolites of cherry fruits treated with Ca$^{2+}$ had obvious changes, such as sugar, soluble alcohol, organic acid and amino acid. Jiang et al. [23] demonstrated that the cracking incidence was significantly correlated with cell wall and wax thickness, and the content of cell wall protopectin and cellulose, but not with Ca$^{2+}$ content.

A large number of studies have shown that foliar application of hormones can improve the physical properties of fruits (for example, GA$_3$ treatment increases the size and weight of pomegranates, loquats and blueberries) [10,87,88], and reduce the rate of fruit cracking [30,92,93]. The application of gibberellin (GA$_4+7$) can reduce the surface tension of epidermal cells in the apple cultivar ‘Golden Delicious’, resulting in the decrease of cuticle microcracks [26]. It was found that the peel of pomegranate with cracked fruit had higher ABA content [94], which was the same as litchi [20]. A further study showed that the peel of lichi of the cracking-susceptible cultivar ‘Baitangying’ had higher ABA, ethylene and jasmonic acid content, but lower auxin and brassinosteroid content than the cracking-resistant cultivar ‘Feizixia’ [96]. Ethylene plays a pivotal role in fruit softening and ripening, and the cracking susceptible cherry cultivar ‘prime giant’ has higher ethylene content than that in the tolerant cultivar ‘Kristalina’ [62].

7. Conclusions and Future Perspectives

In summary, there are various factors affecting fruit cracking, such as physiology, genetics, environment and postharvest storage. The cuticle membranes and gene families associated with cell walls have been used to further elucidate the mechanism of fruit cracking, and the use of omics in fruit cracking is becoming more widespread. Fruit cracking can be effectively reduced by bagging, foliar spraying of calcium chloride, gibberellin and 6-BA. At present, there are still plenty of horticultural plants that have not completed whole genome sequencing, and lack reference genomes and genetic information. In the future, we should focus on DEGs related to the fruit cracking, clone those genes, verify the transgenic function and construct the transformation system. We can have a better understanding of their functions and lay a solid theoretical foundation for elucidating the mechanism of fruit cracking in horticultural plants, so as to prevent and control fruit cracking more efficiently.

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Agronomy 2021, 11, 1045
12 of 14

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Agronomy 2021, 11, 1045


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