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Advances of section drying in citrus fruit: The metabolic changes, mechanisms and prevention methods

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ABSTRACT

Citrus fruit are consumed worldwide due to their excellent features, such as delicious taste and health-promoting compounds. However, section drying, a physiological disorder of citrus fruit, often occurs both in the preharvest and postharvest storage, causing a significant reduction in fruit quality and consumer acceptance. In this review, section drying of citrus fruit was divided into three types: granulation, vesicle collapse and both above. The main causes, metabolic changes and mechanisms of section drying were discussed, respectively. Furthermore, the prevention methods of section drying in citrus fruit, including preharvest and postharvest methods, were also summarized. Given the significant influence of section drying in citrus fruit production, the mechanisms and prevention methods of section drying are worth further exploration. A better understanding of section drying may provide guidance for the prevention of this disorder and future breeding of citrus fruit.

1. Introduction

Citrus fruit are one of the most important fruit crops worldwide, which belong to the family *Rutaceae*. With an annual production of more than 124.3 million tons, citrus fruit has been widely grown in 140 countries all over the world (Mahato et al., 2020). They are composed of 150 genera and 1600 species, including mandarin, pummelo, orange, lemon and grapefruit (Denaro et al., 2020). However, citrus fruit suffered from many preharvest and postharvest diseases, including Huanglongbing, fungal infections and section drying, causing a huge loss for the citrus industry.

Section drying, also known as segment drying, crystallization, scorification and dryness, is a particular physiological disorder of citrus that happens both in the preharvest and postharvest periods. After being infected with this disorder, the juice sacs become enlarged, hardened, shrunken, and have little marketable value (Wu, Pan, Guo, & Pan, 2014). Although the pulp of section drying citrus fruit usually tastes off, the peel of the fruit seems normal. Thus, it is difficult to distinguish the section drying fruit from normal fruit without peeling off.

So far, numerous studies have demonstrated that a series of metabolic changes occur in juice sacs during the section drying process. With the increasing respiration rate in granulated fruit, the depletion of energy increased, causing the decline in soluble sugars and organic acids contents (Yao, Cao, Xie, Deng, & Zeng, 2018). In contrast, the contents of cell wall component, including pectin, cellulose and lignin, were significantly increased in section drying fruit (Hwang, Huber, & Albrigo, 1990). The aroma of citrus fruit was partially lost during section drying, as several volatile compounds were significantly decreased (Cao et al., 2020; Yao et al., 2020). In addition, section drying can also damage the integrity of cellular membranes, which was reflected by the increased relative electric conductivity (Hu, Shao, Wang, Zhu, & Qin, 1997; Chen, Nie, Wan, Gan, & Chen, 2021).

As for the mechanisms of section drying, many different perspectives have been proposed in the last two decades. Some researchers held the view that section drying in citrus fruit was actually a senescence process attributed to the imbalance of ROS metabolism (Nie, Huang, Chen, Wan, & Chen, 2020; She, Pan, & Lin, 2009). Others postulated that the changes in cell wall metabolism were substantial for the formation of section drying (Wu et al., 2020; Chen, Nie et al., 2021). The imbalance in the ratio and proportion of phytohormone can also trigger section drying, as reported by Wang (2005) and Xiong et al. (2017). Recent studies found that juice sac lignification was a critical process in section drying, which was modulated by structural genes, transcriptional factors and microRNAs (Shi et al., 2020; Zhang et al., 2016).

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To date, there have been many reports of section drying in citrus, mainly focused on pummelo, mandarin and orange (Chen, Nie et al., 2021; Cao et al., 2020; Wu et al., 2020). However, the information about section drying is currently dispersed, and a comprehensive review of section drying is urgently needed. Here, we summarize the main causes and metabolic changes during the section drying process, focusing on mechanisms and prevention methods of section drying. This review provides systematic profiles of section drying in citrus fruit, including practical guidance about preventing section drying for the growers and sellers and valuable insights for future research, aiming to promote the healthy development of the citrus industry.

2. Classification of section drying in citrus fruit

The symptoms of section drying vary among different citrus cultivars or even under different situations, and the mechanisms also vary among different symptoms of section drying. Thus, the classification of section drying is certainly warranted. Based on the previous studies and different symptom characteristics, we classified section drying into three types (Fig. 1).

2.1. Granulation

Granulation, the most intensively studied section-drying type, is commonly seen in pomelo fruit such as 'Guanximiyou' pomelo (X.Y. Wang et al., 2014), 'Huyou' pomelo (Chen, Xu, Wang, Zheng, & Chen, 2005) and 'Majiayou' pomelo (Nie et al., 2020). The disordered juice sacs become hardened, enlarged, dry, colorless and opaque (Chen et al., 2005; Nie et al., 2020; X.Y. Wang et al., 2014). As reported by Lacerna, Bayogan, and Secretaria (2018), granulation happened initially in the middle and stylar-end sections of 'Magallanes' pomelo, then developed gradually to other sections. According to Goto and Araki (1983), granulated juice sacs from the stem-end of Sanbokan fruit were swelled markedly, while juice sacs from middle sections were scarcely swelled. Goto (1989) also found that healthy juice sacs undergo a process called gelation before granulation, in which juice sacs became hardened but have no inner cavities.

2.2. Vesicle collapse

Vesicle collapse is another dominant section-drying type of citrus fruit, which often occurs in mandarin fruit such as 'Shatangju' (Cao et al., 2020) and 'Satsuma' mandarin (Burdon et al., 2007). In 'Shatangju' fruit, vesicle collapse developed initially in the peel-side of segments, which is quite different from pomelo fruit (Cao et al., 2020). With the development of vesicle collapse, the transparency of the juice sacs decreased, and then the juice sacs became soft and shrunken gradually. Similar to 'Shatangju' fruit, the characteristic of vesicle collapse juice sacs in 'Satsuma' mandarin was shrunken, hollow and have little extractable juice (Burdon et al., 2007).

In loose-skinned mandarin, vesicle collapse is usually accompanied by skin puffiness. In the study by Burdon et al. (2007), magnetic resonance (MR) imaging was used to quantify the space between skin and segments of Satsuma mandarin. The results showed that the skin-segments gap of puffy fruit was approximately 5% of the total fruit cross-sectional area, which was significantly larger than normal fruit.

2.3. Both granulation and vesicle collapse

Some citrus cultivars develop both granulation and vesicle collapse during postharvest storage, such as grapefruit (Hwang, Albrigo, & Huber, 1988) and Ponkan fruit (Wang, 2005). Hwang et al. (1988) reported that granulation in grapefruit happened more commonly than vesicle collapse. Furthermore, granulation in grapefruit began with the hardening of juice sacs and then forming a crystalline-like cavity, while vesicle collapse exhibited shrunken juice sacs without cell wall thickening.

Similar to grapefruit, the majority of disordered juice sacs in Ponkan fruit developed granulation and became hard, dry and cloudy white in color. In contrast, the other juice sacs developed vesicle collapse and became shriveled and grayish in color (Yao et al., 2018). Furthermore, granulation in Ponkan fruit developed from the stem-end to stylar-end of the fruit segment, which was quite different from that in pomelo fruit.

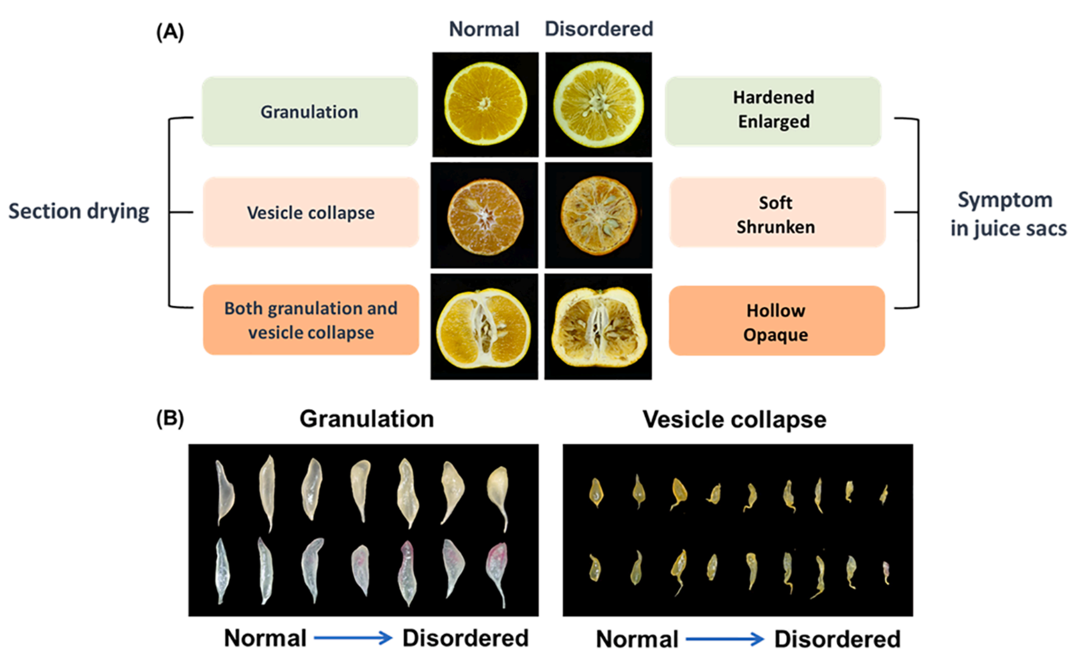

Fig. 1. (A) The classification of section drying types in citrus fruit and their specifical symptoms in juice sacs. Huyou, 'Shangtangju' mandarin and grapefruit were used as the representive cultivars for granulation, vesicle collapse and both granulation and vesicle collapse, respectively. (B) The appearance of disordered juice sacs from granulation and vesicle collapse. The juice sacs were ranked by their section drying level. Upper row, unstained juice sacs; bottom row, juice sacs stained by phloroglucinol-HCl for the marking of lignin.

3. Metabolic changes in citrus fruit during section drying

3.1. Morphological changes of juice sacs

In citrus fruit, the morphology of juice sacs was changed gradually during the process of section drying (Fig. 2). According to Zhang, Xie, and Xu (1999), the granulation process of 'Guanximiyou' pomelo was divided into four stages, including the healthy juice sac, gelatination, granulation and late granulation. The healthy juice sacs were juicy and apparent, while the juice sacs in the late granulation stage were yellowish-white in color, hardened and had no extractable juice. Shomer, Chalutz, Vasiliver, Lomaniec, and Berman (1989) observed that the cell walls of elongated cells and juice cells were both thickened during granulation in pomelo, together with the occurrence of opaque white regions in transparent tissue. Similarly, it was reported that the cell wall of juice sacs thickened, and intracellular content decreased with the development of granulation in Lanelate navel orange (Wu et al., 2020). Moreover, by using SEM and TEM, Pan et al. (1999) found that the number of golgiosomes and the volume of the nucleus were both increased in granulation juice sacs, accompanied by the thickening of cell wall.

3.2. Juice content and water content

Juice content is an important internal trait of citrus fruit, which affects consumers' general acceptance. As demonstrated by Sharma, Singh, and Saxena (2006), among 20 different citrus cultivars, granulated fruit had lower juice content compared to normal fruit, indicating a worse edible quality. A similar result was obtained in Ponkan fruit, in that the juice yield was 39.5% in granulated juice sacs, which was significantly lower than 60.1% in normal juice sacs (Yao et al., 2018). Wu et al. (2020) also found that water content in the juice sacs of late-ripening navel orange also decreased with the development of granulation. Interestingly, researchers demonstrated that, contrary to juice content, the water content of granulated juice sacs was even higher than normal juice sacs in Ponkan fruit (Tan et al., 1985). Similarly, our results on 'Shatangju' fruit also showed that big size fruit, with the highest vesicle collapse index and vesicle collapse rate, had even slightly higher water content than other groups (Kang, Cao, et al., 2022).

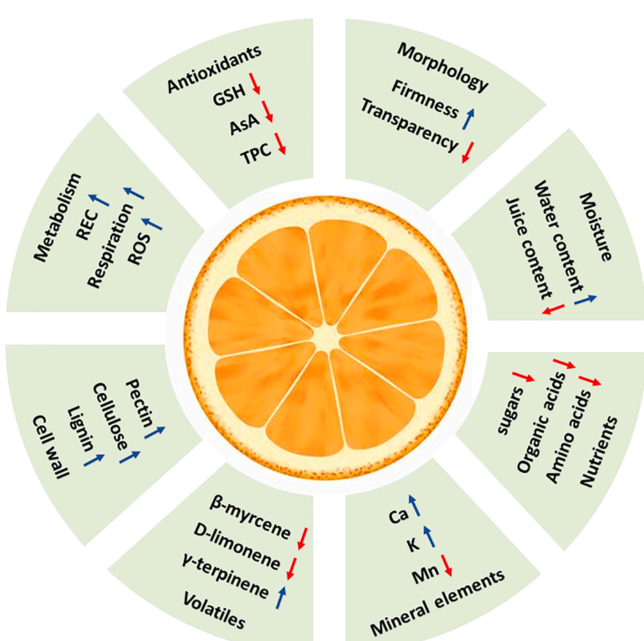

Fig. 2. The metabolic changes in citrus fruit during section drying. Red downward arrows represent negatively correlated to section drying, whereas blue upward arrows represent positively correlated to section drying.

We can see that juice and water content showed quite different patterns in citrus fruit. Fruits possess both free water and bound water. Perhaps during the process of section drying in citrus fruit, free water content decreased while bound water content increased. Although water content in granulation fruit increased, the juice yield still decreased, for most of them are unextractable. Goto and Araki (1983) reported that in Sanbokan fruit, granulated sacs had less expressible juice content than healthy sacs, despite no significant difference in water content. In order to find the underlying reasons, Goto (1989) studied the relationship between pectic substances and calcium in juice sacs of Sanbokan. The results showed that with the participation of Ca^{2+}, free water was bounded in the pectin and formed into gel, causing the extractable juice content decreased significantly.

3.3. Nutrients content

Nutrients in citrus fruit include primary metabolites, such as soluble sugars, organic acids and amino acids as well as secondary metabolites, notably carotenoids and flavonoids, which are also contributors to fruit flavor (Adeyemi et al., 2020). Numerous studies have reported that nutrients in the pulp of citrus fruit declined with the increasing level of section drying (Sharma et al., 2006; Shomer et al., 1989; Singh & Singh, 1980a; X.Y. Wang et al., 2014). In the study by Singh and Singh (1980a,1980b), physical and chemical changes in 'Kaula' mandarin fruit were observed during granulation. The results showed that total soluble solids, total sugars, reducing sugars, non-reducing sugars and total acidity decreased during the process of granulation. Similarly, Shomer et al. (1989) also found that the content of insoluble neutral sugars, soluble sugars, and organic acids were lower in granulated juice sacs than in normal ones, as did that of insoluble proteins. Sharma et al. (2006) found that granulated fruit had significantly lower content of TSS and acidity than normal fruit, irrespective of cultivar. In 'Guanximiyou' pummelo, X.Y. Wang et al. (2014) demonstrated that granulated juice sacs had lower TA concentrations, mainly due to the decreased concentration of citrate and isocitrate. The primary metabolites tended to be down-regulated during the section drying process, which might partly be due to the elevated respiratory pathway and conversion into other metabolites (Yao et al., 2018). In order to investigate the transportation of primary metabolites in *Batangas* mandarin, ^{14}C-labelled glucose was injected into the fruit segment, and radioactivity in the rind was measured later (Wang, Xi, Wang, & Chen, 1996). The results showed that granulated fruit had higher radioactivity in the rind than normal fruit, which indicated the translocation of sugars from juice sacs to the rind existed during section drying process.

However, changing patterns were quite different in the secondary metabolites. Cao et al. (2020) reported that carotenoids content was decreased after being affected by this disorder, which accounted for the light grey color of section drying segments. Flavonoids are also very important secondary metabolites in citrus fruit, which were associated with the defence of adverse environmental factors (Khan et al., 2020; Zhong, Farag, Chen, He, & Xiao, 2022). As reported by Cao et al. (2020), the flavonoids were up-regulated in the vesicle collapsed segment, especially naringin and narirutin, two dominant flavonoids in 'Shatangju' fruit. Unfortunately, the metabolic pathways of carotenoids and flavonoids during the section drying process have not been clarified so far.

3.4. Mineral elements content

Mineral elements, including macro elements, trace elements and ultra-trace elements, play important roles in the growth and development of citrus (Demir, Kipcak, Ozdemir, & Derun, 2020). Both macro- and trace elements contents changed in varying degrees during section drying of citrus fruit, Kumar, Kumar, and Daulta (1993) found that the concentration of Zn, Fe, Cu, Mn, N and P were significantly lower in granulated fruits compared to healthy fruits. On the contrary, the concentration of K and Ca was higher in granulated fruit than in healthy fruit. In another study, X.Y. Wang et al. (2014) investigated the effects of granulation on mineral elements concentration in 'Guanximiyou' pummelo and drew an opposite conclusion: granulation resulted in a higher concentration of mineral elements, especially P, Mg, S, Zn and Cu. As reported by Munshi, Jawanda, Singh, and Vij (1980), the changes of mineral elements showed partly different patterns in the peel and pulp of Dancy tangerine. Compared to normal fruit, a significant increase of N, P, K and Ca was observed in the pulp of granulated fruit, while the content of K and Mg in the peel of granulated fruit was significantly higher.

3.5. Volatile compounds content

Citrus fruit from different cultivars have their characteristic aroma, which is consisted of several volatile compounds, including esters, aldehydes, hydrocarbons, alcohols, and ketones (Ren et al., 2015). However, during the process of section drying, both species and contents of volatile compounds are changed. Cao et al. (2020) found that D-limonene and β-myrcene, the main volatile compounds in the pulp of 'Shatangju' fruit, decreased dramatically in the section drying segments. However, γ-terpinene can be detected only in the section drying segments. It is worth noting that ethanol and ethyl-acetate, two off-flavor compounds, were significantly lower in the section drying segments. Similar results were also reported for navel orange fruit, in which researchers found that the total amount of volatile compounds decreased by 46 % during granulation (Yao et al., 2020). Compared to normal juice vesicles, 12 volatile compounds significantly decreased in granulated juice vesicles, of which D-limonene was the most significant one. Further study is still needed to explore the relationship between volatile compounds content and section drying of citrus. Maybe evaluating the degree of section drying in citrus fruit can be achieved by determining several characteristic volatile compounds content in the future.

3.6. Cell wall components content

Cell wall components are important contributors to the texture quality of citrus fruit, which are mainly consisted of alcohol insoluble solids. Previous studies suggested that the dynamic change of cell wall components, including pectin, cellulose and lignin, was strongly correlated to section drying in citrus fruit (Cao et al., 2020; Hwang et al., 1990; Sinclair & Jolliffe, 1961; Yao et al., 2018). Sinclair and Jolliffe (1961) investigated the chemical changes in the juice vesicle of granulated Valencia orange, and findings indicated that the alcohol-insoluble fraction increased with the degree of section drying, which exhibited a strong correlation with the hardness of the juice vesicles. A similar result was obtained by Cao et al. (2020), who found that the content of alcohol insoluble solids in the vesicle collapsed segment was significantly higher than the healthy tissue. In the study by Hwang et al. (1990), a comparison of cell wall components in grapefruit was conducted in normal and granulated juice vesicles. The results showed that the contents of structural polysaccharides in granulated vesicles, including pectin, hemicellulose, and cellulose, were more than two folds of normal vesicles. Similarly, Yao et al. (2018) reported that the content of cell wall components such as protopectin, cellulose and lignin increased during the granulation of Ponkan mandarin.

Taking these results together, we conclude that the content of cell wall components, mainly cellulose and lignin, are higher in section-drying fruit compared to normal fruit. However, the relationship between the accumulation of cell wall components and section drying still remains to be clarified.

3.7. Respiration rate

Respiration rate, measured by O_2 uptake or CO_2 output, is an indicator of overall metabolic activity during postharvest storage, and greatly influences the senescence of citrus fruit. Previous studies found that high respiration rate accelerated the loss of nutrients and the senescence process in fresh fruit such as apple (Ge et al., 2019), Longan (Lin et al., 2018) and raspberry (Giovanelli, Limbo, & Buratti, 2014), thus leading to poor edible quality. As reported by Nakajima (1976), vesicle-drying fruit had a higher respiration rate than healthy ones. At the same time, total soluble solids, total sugars and citric acid contents in vesicle-drying fruit became much lower than that of healthy fruit, which could be due to the consumption of respiratory metabolism. Similar findings were obtained in Ponkan fruit, in which respiration rate increased gradually with the granulation level (Tan et al., 1985). In the study by Burns (1990), oxygen uptake in granulated and normal juice sacs was measured in 'Lee' tangelos, 'Dancy' tangerine and 'Marsh' grapefruit, respectively. The results showed that O_2 uptake was 2- to 3-fold higher in granulated juice sacs compared to normal ones, which suggested that metabolic activities were increased in granulated juice sacs. Based on the results, the author concluded that increased metabolic activities mean more energy production in granulated juice sacs, which might be used to support cell wall synthesis and modification.

3.8. Relative electric conductivity

Relative electric conductivity (REC) is often used to reflect the membrane permeability of fresh fruit and vegetables. Numerous studies have shown that the higher REC is, the severer the damage in the cellular membranes of fresh fruit will be (Castro, Teixeira, Salengke, Sastry, & Vicente, 2004; Du, Li, Zhou, Liu, & Li, 2017). Based on the report of Chen, Nie et al. (2021), as storage time prolonged, REC in juice sacs of 'Majiayou' pomelo increased with the increment of granulation index, which indicated that the destruction of cellular membranes was aggravating with the development of granulation. The same pattern was found in the peel of Ponkan and Satsuma mandarin, in which the REC of granulated fruit was significantly higher than that of normal fruit (Hu et al., 1997). We can draw the conclusion that the increased level of REC in both peel and pulp indicate a higher membrane permeability, which accelerates the senescence of citrus fruit, thereby leading to the section drying in juice sacs.

3.9. Endogenous antioxidants

Endogenous antioxidants act as health-promoting compounds for human health and play important roles in the plants themselves for coping with biological and abiotic stresses, which can be applied to reflect the antioxidant capacity of fresh products (Tomás-Barberán et al., 2001). In citrus fruit, endogenous antioxidants are mainly ascorbate (AsA), glutathione (GSH) and phenolic compounds (Kazeem, Bankole, Oladokun, Bello, & Maliki, 2020). As reported by She et al. (2009), the content of AsA and GSH in non-granulated juice sacs from optimum-aged trees was significantly higher than in granulated juice sacs from old trees. In another study, Sharma et al. (2006) found that granulated fruit exhibited a lower level of total phenolic compounds and antioxidant activity compared with normal fruit in 'Kinnow' mandarin.

3.10. ROS scavenging enzymes

During the postharvest storage of fruit crops, ROS are continuously produced with the undergoing of various life activities. However, excessive accumulation of ROS can accelerate lipid peroxidation and damage membrane permeability, causing senescence and quality deterioration (Gill & Tuteja, 2010). Antioxidant enzymes, including superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX) and other enzymes, play vital roles in scavenging ROS and thus decelerates the rate of postharvest senescence (Tian, Qin, & Li, 2013). Previous studies demonstrated that the activities of antioxidant enzymes were changed greatly during storage and closely associated with the occurrence of section drying. Nie et al. (2020) found that the non-enzymatic antioxidants (i.e., AsA, GSH) contents and ROS-scavenging enzymes (i.e., SOD, APX, GR) activities decreased continuously with storage time, accounting for the excessive ROS accumulation and postharvest granulation. Further studies showed that the expression level of ROS-scavenging genes such as *MnSOD*, *APX* and *GR* was decreased during postharvest storage, leading to the decrement of relevant enzymes activity and oxidative stress. Zheng, Pan, Qiu, and Pan (1999) also reported that the activities of SOD, POD and CAT changed continuously during storage, both in the pulp and peel of pomelo fruit. During the section drying process, the senescence of pulp was accompanied by the increased physiological activity of peel, which was reflected by the different patterns of SOD activity. Taken together, researchers held the view that the disequilibrium of ROS metabolism was responsible for section drying, possibly due to the unsynchronized senescence between peel and pulp.

4. Influencing factors for section drying and probable underlying mechanisms

Given that section drying posed an enormous threat to the citrus industry, researchers had done a lot of observations to find out the factors causing section drying. According to the existing reports, the section drying of citrus might be determined by the combined effects of genetics, environmental factors, growth condition, pollination and pruning, harvest maturity and postharvest storage (Fig. 3).

4.1. Genetics

Some researchers had reported that the incidence and degree of section drying varied greatly among different citrus cultivars. Sharma et al. (2006) compared the incidence and degree of granulation in seven citrus cultivars, including mandarin, sweet orange, lemon, lime, grapefruit, pummelo and tangelo. The results showed that the highest incidence of granulation was recorded in a sweet orange group (33.3%), while the lime group had the lowest (12.2%). As for the degree of granulation, the grapefruit group was significantly higher than other groups. In another study, researchers even found that granulation incidence varied among the same citrus cultivars (El-Zeftawi, Thornton, & Lloyd, 1985). They noted that Newton had the most granulated fruit among eight Valencia orange selections, which cannot be recommended for planting. In a study by Daulta and Arora (1990), granulation incidence and physiochemical indexes were investigated among 7 citrus cultivars, indicating that cultivars with thin rind were more susceptible to granulation than cultivars with thicker rind.

The genetic background exerts a significant impact on the development of citrus fruit, which is the basic factor determining the occurrence and severity of section drying. Researchers found that loose-skin citrus fruit, such as 'Shatangju' and Satsuma mandarin, were more prone to section drying than citrus with tight-skin. Due to the anatomic structural differences among loose-skin and tight-skin citrus fruit, the transportation of nutrients and water between flesh and rind showed different patterns. According to Ding et al. (2015), loose-skin citrus fruit had a powerful vascular bundle system for the transportation of nutrients and water between flesh and rind, leading to dehydrated flesh and fresh rind. In contrast, the flesh-rind communications in tight-skin citrus fruit mainly through an intracellular diffusion pathway, which was less developed than the vascular bundle system, causing delayed senescence of flesh. By a radioactive isotope labelling experiment, Chen et al. (1996) exemplified that glucose was transported from juice sacs to peel during postharvest storage of huyou fruit, which was caused by the senescence of pulp and regrowth of peel. The material transportation between peel and pulp may be one of the triggers for section drying. However, the concrete mechanisms of peel-pulp transportation and the regulatory pathways still need further exploration.

4.2. Environmental factors

Environmental factors include temperature, soil water content and fertilization, which are fundamental external causes for the section drying of citrus fruit. As one of the most important climatic conditions, temperature affects the growth of citrus fruit in many aspects, including sprouting, flowering and fruit setting. Previous studies demonstrated that section drying might be caused by extreme low or high temperatures. As reported by Bartholomew, Sinclair, and Turrell (1947), freezing temperatures increased the number of granulation fruit in the production of Valencia oranges. Similarly, Wu et al. (2020) found that the late-ripening navel orange were vulnerable to the injury of low temperature in winter and tended to develop granulated fruit in the following year, which was due to the cell wall modification. After being exposed to low temperature, the activities of PG and Cx in juice sacs decreased, while that of PME increased with the aggravation of

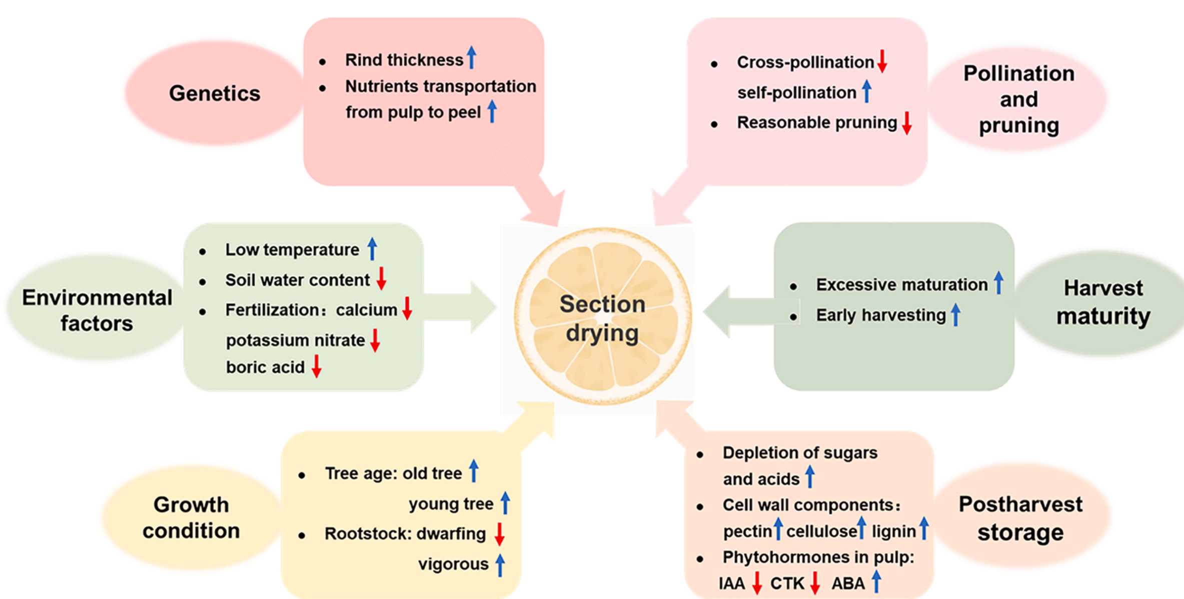

Fig. 3. The influencing factors for section drying in citrus fruit. Red downward arrows represent negatively correlated to section drying, whereas blue upward arrows represent positively correlated to section drying.

granulation. They postulated that the increased activity of PME caused the demethylation and esterification of a significant portion of pectin. However, the decreased activity of PG was insufficient for the dissociation of side chains and the decomposition of pectin, leading to the overaccumulation of high molecular weight pectin. At the same time, the lignin biosynthesis enzymes, including phenylalanine ammonia lyase (PAL), cinnamol dehydrogenase (CAD), and POD were up-regulated, resulting in the overaccumulation of lignin. During the navel orange season in 2003, the relatively high temperature in the blooming period accounted for the excessive development of granulation in the fruit (Ritenour, Albrigo, Burns, & Miller, 2004), but the reasons have not been defined.

Soil water content is determined by the frequency of rainfall and artificial irrigation. A study by Singh and Singh (1980b) demonstrated that the frequency of irrigation was positively correlated with granulation rate in Valencia Late sweet orange, in which granulation degree in trees treated by irrigation every ten days was up to 35% compared to only 20% in irrigation every 30 days. Pérez-Pérez, Robles, and Botía (2009) found that deficit irrigation can increase total soluble solids (TSS) and titratable acidity (TA) of 'Lanelate' sweet orange when applied in phase III. The increment of sugars and acids in fruit was probably due to the osmotic adjustment under mild water-deficit stress. This was further confirmed by Navarro, Pérez-Pérez, Romero, and Botía (2010) in 'Clemenules' mandarin. After reducing the frequency of irrigation, the elevated content of soluble sugars and organic acids may partially explain the decreased section drying rate by reducing irrigation, for that sugar and acid content was claimed to be associated with section drying. However, the definitive mechanisms for the soil moisture content and section drying are as yet unclarified and worth further investigation.

Fertilization is another important factor that affects growth condition of crops. The demand of fertilizer often differs among different crops and life stages, so reasonable fertilization is crucial for the quality of products. Singh and Singh (1981a) reported that the foliar spray of 1% potassium nitrate on 'Dancy tangerine' mandarin effectively reduced granulation rate by 24%. Meanwhile, the content of juice, sugars and ascorbic acid were increased, exhibiting a better quality than control. It was consistent with the study by Wu et al. (2021), in that potassium improved the accumulations of soluble sugar and citrate in Cara Cara navel orange due to the higher activities of sucrose-synthesizing and citrate-synthesizing enzymes. Singh and Singh (1981a) also found that low concentrations of boric acid (25 and 50 $mg{\cdot}l^{-1}$) markedly alleviated section drying. This was further validated by Zhou, Sun, Zhang, Zeng, Liu, and Sheng (2022) and Wu et al. (2017) that lignin accumulation occurred in the vascular bundles of citrus leaves and root cell walls under boron deficiency stress, which was due to the increased enzyme activities and gene expression involved in lignin biosynthesis. That may be the probable underlying mechanism for the alleviation of section drying. According to Shiraishi, Mohammad, and Makita (1999), pre-harvest application of calcium compound significantly reduced section drying and peel puffing fruit of satsuma mandarin, which was due to the inhibition in the separation and disorganization of cell walls. As mentioned in section 3.4, mineral elements content changed greatly during the section drying process, which varied among different citrus cultivars. That may be due to the difference in the absorption, transportation and utilization of mineral elements among different citrus cultivars. Previous studies implicated that the foliar spray of fertilization was feasible for retarding section drying in citrus fruit. However, whether the mineral elements being transported into juice sacs or just function on the peel are largely unknown.

4.3. Growth condition

Growth condition of citrus trees is affected by tree age and rootstocks. She et al. (2009) demonstrated that tree age exerted a great influence on the granulation rate of 'Guanximiyou' pomelo. They found that fruit from old trees had a higher juice sac granulation rate than that of optimum-aged trees, which attributed to the different patterns in reactive oxygen species (ROS) metabolism and lignin accumulation. ROS are primary mediators of oxidative damage in plants, including superoxide anion ($O^{2\bullet-}$), hydrogen peroxide (H_2O_2), hydroxyl radicals (·OH), and singlet oxygen ($^1O_2$) (Tian et al., 2013). Overaccumulation of ROS can induce irreversibly damage to plant cell. According to She et al. (2009), the H_2O_2, MDA and lignin contents were higher while GSH and AsA contents were lower in fruit from old trees. They postulated that the abnormal ROS metabolism resulted in the accumulation of H_2O_2 and MDA, and the increase of POD activity, which promoted the biosynthesis of lignin and finally triggered juice sac granulation.

As a source of nutrients and water for trees, rootstock had significant impacts on the agronomic performance of grafted scions, such as yield, fruit quality and resistance to diseases (Filho, Espinoza-Núñez, Stuchi, & Ortega, 2007). El-Zeftawi (1978) demonstrated that rootstock is one of the factors affecting granulation incidence of late-picked Valencia oranges. Kotsias (2004) investigated the influence of rootstocks on granulation of Valencia sweet orange and found that using Poncirus trifoliata rootstock can markedly reduce granulation to 31%, compared to 73% on C. aurantium rootstock. According to Sharma and Saxena (2004), Kinnow mandarin had different growth conditions and performances on three rootstocks. The results showed that the recommended rootstock for Kinnow mandarin was Troyer citrange, a kind of dwarfing rootstock, because fruit on Troyer citrange had the lowest granulation incidence and best quality characteristics. In a recent study, Hong et al. (2022) demonstrated that rootstocks affected soluble sugar contents in 'Mini-hyang' mandarin by regulating sugar metabolism enzymes activities. The life cycle of citrus includes vegetative and reproductive growth. Abnormal vigorous vegetative growth often happened in young citrus trees or vigorous rootstocks. This resulted in uneven distribution of nutrition in different fruit, which may be one of the triggers for section drying (Sharma & Saxena, 2004). As reported by Qureshi, Jaskani, Khan, and Ahmad (2021), the endogenous phytohormones level of Kinnow mandarin varied among nine rootstocks. They found that the leaf gas exchange, vegetative performance, and yield of Kinnow mandarin were manipulated by different levels of indole acetic acid (IAA), gibberellin acid (GA_3), and zeatin (ZT), abscisic acid (ABA). However, the exact mechanisms of phytohormones level in both scion and rootstock on section drying incidence are still exclusive.

4.4. Pollination and pruning

Self-pollination and cross-pollination are two forms of pollination in plant. After cross-pollination, citrus fruit produce several fertile seeds, which are the resource of endogenous phytohormones in fruit. As reported by Pan et al. (1999), the contents of endogenous phytohormones, such as GA_3, IAA, ABA and ZT, were changed significantly after artificial pollination. They found that the granulation rate was significantly lower in the cross-pollinated fruit, which might be due to the counterbalance of endogenous phytohormone provided by fertile seeds. Chen et al. (2005) demonstrated that artificial pollination was effective for retarding granulation and improving fruit quality, owing to the lower content of ABA in the pulp after pollination. As for navel orange, cross-pollination could significantly improve the internal quality, including TSS, total amount of sugars and phenolics (Wang et al., 2019). However, Cao et al. (2020) reported an opposite observation in 'Shatangju' fruit, in which the vesicle collapse incidence of seedless segments was significantly lower than in segments containing seeds. It may be the cultivar differences that induced the completely opposite results. Taken together, the dynamic changes of phytohormones after pollination and the exact function of changed phytohormones requires further exploration in the future study.

Reasonable pruning keeps the balance between vegetative and reproductive growth, which is important for fruit development of economic crops. Compared to no pruning, using a suitable pruning method significantly improved the yield and overall quality of Hamlin sweet orange (Jiang, Peng, Cao, Chun, & Ling, 2012). After pruning, the photosynthetic efficiency of the leaves can be enhanced by the improved ventilation and light transmission capacity of the tree. Pruning strategies were particularly important for young citrus trees, as reported by Cronje, Human, and Ratlapane (2021). Reasonable pruning based on different citrus cultivars can avoid alternate bearing patterns and produce medium-size fruit. Based on the report by El-Zeftawi (1972), the alternate bearing cycle had an influence on the granulation rate of Valencia oranges. The results showed that granulation was severer in the off-year (light-bearing) than in the on-year (heavy-bearing), partly due to the bigger fruit size in off-year. Previous studies exemplified that the fruit size was correlated to section drying incidence. In Valencia orange, findings indicated that the larger fruit had higher granulation incidence, partly due to the faster senescent speed in large fruit compared to small fruit of the same bloom (Sinclair & Jolliffe, 1961). A similar observation was obtained by Burns and Albrigo (1998) in grapefruit. Thus, pruning may indirectly affect section drying incidence by modulating fruit size. Unfortunately, there have been few reports concerning pruning and section drying. Thus, further studies should focus more on the precise function of pruning on section drying and the underlying mechanisms.

4.5. Harvest maturity

Harvest maturity is determined by the time of harvest, which also exerts a great impact on the granulation rate of citrus fruit. Burns and Albrigo (1998) found that compared to be harvested late in March and May, 'Ruby Red' grapefruit had the lowest granulation scores when harvested in January. Interestingly, Burns also reported that versus off-tree storage, on-tree storage could retard the granulation process of 'Ruby Red' grapefruit to some extent. A study by Dai et al. (2021) also demonstrated that the juice sac granulation was aggravated with the increased maturation of Guanxi pomelo. Correlation analysis showed that juice sacs granulation was closely related to the increased cellulose content and thickened secondary wall, which was modulated by the cellulose genes including *CrCESA4*, *CrCESA7-1* and *CrCESA8*. However, harvesting too early also triggered section drying, owing to the poor storability during postharvest storage. Early harvesting in 'Guanximiyou' pummelo could diminish production and even exacerbate the juice sac granulation after storage (Zhu, Wang, Shen, & Li, 2019). In the future study, the molecular basis for the relationship between maturity and section drying in citrus fruit is urgently needed to be explored.

4.6. Postharvest storage

As reported by many researchers, postharvest storage, especially long-term storage, is one of the most important factors accounting for section drying. After being harvested from trees, citrus fruit undergo a series of metabolic changes, which mainly include ROS metabolism, sugar and acid metabolism, cell wall modification, and phytohormone metabolism.

4.6.1. Sugar and acid metabolism

Sugar and acid metabolism plays a crucial role in the postharvest storage of fruit. After harvesting from trees, fruit still need to consume energy to maintain respiratory metabolism, which is provided by sugars and acids in the pulp. However, over-consumption of sugars and acids may cause quality deterioration and finally loss of commercial values. According to previous studies, the depletion of sugars and acids is one of the typical symptoms of section drying. A study by Tan et al. (1985) demonstrated that the consumption of nutrients such as sugars and organic acids was the primary cause for section drying. Wang (2005) also reported that both granulated and vesicle collapsed fruit had a higher respiratory rate than normal fruit, partially explained the lower dry weight and nutrients content in section drying fruit. For the mechanisms underlying the depletion of sugars and acids during section drying, there were two possible hypotheses. One is that the consumed sugars and acids were utilized for the biosynthesis of cell wall components. By using transcriptome analysis, Yao et al. (2018) systematically studied the sugar and acid metabolism during section drying of 'Ponkan' fruit. It was demonstrated that the genes involved in sugar and citric acid degradation and secondary cell wall synthesis were up-regulated. Meanwhile, a down-regulated pattern was observed in the genes involved in the synthesis of sucrose and citric acid, and the degradation of cell wall components. Thus, they deduced that the consumed sugars and acids during section drying were largely utilized for the modifications of cell wall components. This was consistent with their later research on navel orange (Yao et al., 2020). The other is the nutrients translocation from pulp to peel during the section drying process. After injecting glucose-^{14}C into the juice sacs of huyou, Chen et al. (1996) found that the radioactivity of glucose-^{14}C decreased in the juice sacs but increased in the peel. This proved that sugars were transported from juice sacs to peel during storage, which accounted for the senescence of pulp and regrowth of peel, a probable mechanism for the section drying of huyou. However, both of the hypotheses remain to be further verified.

4.6.2. Cell wall modifications

Cell wall modifications, including polysaccharides degradation and lignin biosynthesis, are undesirable for the fresh products but inevitably occur during postharvest storage. The degradation of cell wall polysaccharides (i.e., cellulose, hemicelluloses, pectins and xyloglucan) is catalyzed by cell wall degrading enzymes, including polygalacturonase (PG), pectin methylesterase (PME), cellulase (Cx) and xyloglucan endotransglycosylase/hydrolase (XTH). PME and PG are pectinases that act in the depolymerization of pectins during postharvest storage, while Cx is responsible for the hydrolysis of cellulose (Xiao et al., 2020). XTH can cleave xyloglucan and then religate xyloglucan molecules (Anderson & Kieber, 2020). During the section drying process, the activities of cell wall degrading enzymes changed considerably, which accounted for juice sac hardening and tissue fibrosis of citrus fruit (Chen, Peng, Chen, Gan, & Wan, 2021). Sharma, Awasthi, and Kumar (2016) also found that PME activity was higher in granulated juice sacs of 'Kinnow' mandarin. However, a downtrend of PME activity during granulation was reported by Chen et al. (2021). They also found that chitosan treatment on 'Majiayou' fruit effectively maintained higher cell wall degrading enzymes (i.e., PME, PG, Cx, XTH) activities and then suppressed juice sac granulation. Cell wall metabolism genes also changed dramatically with the development of section drying. During the section drying process, the pectin metabolism genes showed different expression patterns, in which *PME* was up-regulated but *PG* down-regulated (Chen, Nie et al., 2021). The expression level of *Cx* was significantly reduced, which might be responsible for the overaccumulation of cellulose in juice sac. Taken together, we can hypothesize that the changes of cell wall degrading enzymes activities may be one of the triggers for section drying.

Lignin is a crucial phenolic component of plant cell walls, which provides mechanical support and compression strength for the cells. However, overaccumulation of lignin is undesirable for fresh fruit, which is accompanied by section drying in citrus fruit, stone cell development in pear fruit and flesh lignification in loquat fruit (Zhang, Wang, Li, Dong, & Wang, 2019; Xu et al., 2014). In plants, the lignin biosynthetic pathway involves a series of enzymes, which mainly includes PAL, cinnamate 4-hydroxylase (C4H), 4-coumarate CoA ligase (4CL), p-coumarate 3-hydroxylase (C3H), cinnamoyl CoA reductase (CCR), dehydrogenase (CAD), laccases (LACs) and POD. Among them, PAL, CAD and POD have been reported to be associated with section drying in citrus fruit. PAL is the first rate-limiting enzyme in the phenylpropanoid pathway, which catalyzes the conversion of phenylalanine to cinnamic acid. CAD plays an essential role in reducing three types of cinnamaldehyde into p-coumaryl alcohol, sinapyl alcohol and coniferyl alcohol, which are the precursors of lignin monomers (Kumar, Campbell, & Turner, 2015). After the biosynthesis of three lignin monomers, including p-hydroxyphenyl (H), guaiacyl (G) and syringyl (S) units, POD acts as a critical enzyme for polymerizing them into lignin (Zhang et al., 2019). Previous studies have been reported that lignin content can be reduced by inhibiting the activities of PAL, CAD and POD (Vanholme, Morreel, Ralph, & Boerjan, 2008). A study by Pan, Zhu, Pan, and Zheng (2013) demonstrated that the activities of PAL, CAD and POD with SA treatments were significantly lower than that of control, accounting for the decrement in lignin content and granulation level. Similar findings were obtained by Chen, Nie et al. (2021). As storage time went by, the PAL, CAD and POD activities of 'Majiayou' fruit increased with the increment of granulation level. In contrast, chitosan-coated MP fruit exhibited a relatively lower level of these lignin biosynthesis enzymes. Collectively, we can conclude that the activities of PAL, CAD and POD were positively correlated with section drying in citrus fruit.

Lignin biosynthesis was modulated by a series of structural genes, which exhibited an up-regulated pattern during the postharvest storage, as reported by Chen, Nie et al. (2021). They found that increased *PAL*, *CAD* and *POD* expression significantly promoted the lignin biosynthesis pathway, causing juice sacs hardening and section drying. As important structural genes for lignin biosynthesis, the expression level of *CgPAL1*, *CgPAL2*, *Cg4CL1*, and *CgC3H* were all increased with the increment of granulation level, which was confirmed by FPKM results and qRT-PCR results (Shi et al., 2020).

Transcriptional factors (TFs) act as pre-transcriptional regulators, playing prominent roles in modulating gene expression (Taylor-Teeples et al., 2015). They can directly bind to target genes' promoters or interact with other TFs and hence function as activators or repressors. Previous studies indicated that NAC and MYB were two important families involved in the lignification of the juice sacs, a critical process in section drying (Jia et al., 2018). As reported by Jia et al. (2018), CsMYB330 and CsMYB308 played crucial roles in the lignification of sweet orange by regulating the expression of *Cs4CL1*, an important lignin biosynthesis-related gene. Interestingly, they played nearly opposite functions, in which CsMYB330 was acting as an activator while CsMYB308 appeared to be a repressor of *Cs4CL1*. Furthermore, Jia et al. (2019) identified another MYB transcriptional factor in citrus, MYB85, which was also participated in juice sac lignification. They found that MYB85 bound to the promoter of *CsMYB330* and interacted with CsMYB308, thereby indirectly regulating the expression of *Cs4CL1*. Nevertheless, a different conclusion was obtained by Shi et al. (2020) via an in vitro cultivation of pummelo juice sacs. They found that CgMYB58 up-regulated lignin content via directly binding to the promoters of *CgPAL1*, *CgPAL2*, *Cg4CL1* and *CgC3H*, which were critical genes involved in lignin biosynthesis. NAC family was also reported to function in cell wall metabolism during section drying. A recent study by Yao et al. (2020) showed that 17 differentially expressed NAC TFs were identified during granulation in orange fruit, among which Cs9g14460 and Cs3g26000 were both significantly downregulated, indicating a potential role in citrus granulation. Furthermore, their homologs in *Arabidopsis*, *VND7* and *E2Fc*, were reported to be key TFs involved in secondary cell wall synthesis (Kumar et al., 2015; Taylor-Teeples et al., 2015). However, the exact function of Cs9g14460 and Cs3g26000 in the section drying process of citrus still needs to be verified.

MicroRNAs (miRNAs) are approximately 21-nt-long noncoding RNAs, which act as post-transcriptional regulators to suppress target gene expression either by degrading or repressing the translation of cognate mRNA, thus affecting a variety of biological and physiological processes in plants (Sunkar, Li, & Jagadeeswaran, 2012; Zhao et al., 2020). Since the plant miRNAs were first identified in *Arabidopsis* by Llave, Kasschau, Rector, and Carrington (2002), numerous studies have demonstrated that miRNAs played crucial roles in phytohormone response, abiotic stress and cell wall modifications, which were correlated with the process of section drying in citrus. Lu et al. (2013) found that *trmiR397a* was a negative regulator of laccases, a key enzyme involved in lignin biosynthesis. The result showed that overexpression of *Ptr-MIR397a* in transgenic *Populus trichocarpa* decreased the activity of laccases and thereby reduced lignin content. This was further confirmed by C.Y. Wang et al. (2014) that *MiR397b* regulated both lignin content and seed number in *Arabidopsis* via modulating a laccase gene (*LAC4*). In sweet orange, Zhang et al. (2016) found that *csi-miR397* and *N-miR828* were negatively correlated to the granulation process. With the aggravation of granulation, the expression levels of *csi-miR397* and *N-miR828* decreased, while the expression level of their target genes (laccase gene and *MYB114,* respectively) increased significantly. Similarly, in other fruit such as pear, *PbrmiR397a* was also found to be involved in lignification during stone cell development (Xue et al., 2019). Collectively, it can be concluded that the juice sac lignification was regulated by lignin biosynthesis genes from the *NAC* or *MYB* family, which was subjected to the modulation by miRNAs and TFs. However, the mutual cause-effect relationship between juice sac lignification and section drying are required further investigation.

4.6.3. Phytohormone metabolism

During the postharvest storage, phytohormones level changes greatly both in the peel and pulp of citrus fruit. Phytohormones are physiologically important regulators that can modulate a series of metabolic processes in plants with very low concentrations (Wani, Kumar, Shriram, & Sah, 2016). They have been classified into ten families, which include cytokinins (CTKs), GAs, IAA, ABA, brassinosteroids (BRs), jasmonates (JAs), salicylic acid (SA), ethylene (ETH), strigolactone (SL) and polyamines (PAs) (Xiang, Wang, & Sun, 2021). Recently, numerous studies have shown that phytohormones participated in almost all stages of the plant life circle, including sprouting, blooming, fruit set and ripening. Among all phytohormone species, ABA, ETH, GAs, CTKs, IAA, and PAs have been reported to be involved in the section drying process.

ABA and ETH are both important regulators involved in ripening and senescence. Wang (2005) found that the ABA content of section drying fruit was significantly higher than normal fruit both in peel and pulp, which indicated that the increase of ABA content may be one of the instigators of section drying. However, in 'Bendizao' citrus fruit, the dynamic changes of ABA content in peel were not synchronous with pulp, resulting in delayed senescence of pulp (Chen, Chen, & Zhang, 1997). In line with ABA, the content of ETH was also reported to be higher in section drying fruit (Wang, Xi, & Wang, 1997). It seems that section drying in citrus fruit is actually a senescence process. IAA, GAs and CTKs are growth-promoting phytohormones that can delay ripening and senescence. Based on the study of Wang et al. (1997), the content of IAA and CTK was shown to be lower in section drying fruit compared to normal fruit. The authors assumed that section drying was partially due to the decrease of CTK content, which was further confirmed by the exogenous BA treatment. Notably, the GA_3 content was even slightly higher in section drying fruit. In addition, the effect of exogenous GA_3 treatment was quite distinct in different cultivars and application period, and the mechanisms of which deserves further exploration. PAs are organic polycation compounds that contain two or more amine groups. The major plant PAs are spermidine (Spd), spermine (Spm), and putrescine (Put). Previous studies elucidated that the ratio of (Spd + Spm) / Put in plants reflected the resistance to abiotic stress. During the section drying process of Wakiyame-Wase Satsuma mandarin, the content of Spd and Spm reduced. At the same time, Put increased rapidly, causing the decrement in (Spd + Spm) / Put ratio (Wei, Zhang, & Zheng, 2001). This was further confirmed by Xiong et al. (2017) in *Huangguogan*. They found that exogenous Spd treatment increased the ratio of (Spd + Spm) / Put and the total content of free PAs, thereby reducing the granulation index of *Huangguogan*.

Combining all the recent findings, section drying in citrus fruit may be modulated by the relative equilibrium of phytohormones, which was essential for source/sink transitions and nutrient redistribution between peel and pulp. Based on the previous studies, one of the possible inferences for section drying was that the nutrients transported from pulp to peel, causing the senescence of pulp and regrowth of peel. This was largely related to the contents and relative proportion of phytohormones in pulp and peel. Our research team also found that the content of IAA and ABA in pulp and peel was closely associated to the section drying rate (Kang, Jiang, et al., 2022). However, in the past, due to the limitation in the detection of phytohormones, the dynamic change of phytohormones levels during section drying has not been fully understood, especially the crosstalk between different kinds of phytohormones. Nowadays, liquid chromatography-tandem mass spectrometry (LC-MS), a fast and accurate quantification method, has been extensively used in the detection of phytohormones, which may contribute to our knowns of the roles of phytohormones involved in section drying. The modulating effect of other phytohormones on section drying, especially the stress response related phytohormones such as BRs and SL, are worth exploring in the future.

Researchers implicated that postharvest storage was a leading cause of section drying, and they clarified the mechanisms from three aspects, including sugar and acid metabolism, cell wall modification and phytohormone metabolism, respectively. However, the three metabolic pathways are not independent. For example, Yao et al. (2018) demonstrated that the depletion of sugars and acids during the section drying process was partly due to the transformation of cell wall component. Furthermore, the cell wall modification was also positively regulated by like JA and SA, which are defence-related phytohormones (Bethke et al., 2015). Thus, the crosstalk between the three metabolic pathways happened in section drying still needs further clarification.

5. Prevention methods of section drying in citrus fruit

5.1. Preharvest methods

5.1.1. Choosing proper cultivars and rootstocks

Cultivars firstly determine the section drying rate of citrus fruit. Researchers found that the incidence of section drying varied among different citrus cultivars (Sharma et al., 2006) and even among the same cultivar (El-Zeftawi et al., 1985). He noted that Newton had the most granulated fruit among eight Valencia orange selections, which was not recommended for planting.

Rootstocks also affected the incidence of section drying, as reported by previous studies (Table 1). Sharma and Saxena (2004) found that the granulation rate of Kinnow mandarin was relatively low when grafted on dwarfing rootstock (Troyer citrange). In another study by El-Zeftawi (1978), rootstocks from sweet orange strains were found to be effective for reducing granulation and improving fruit quality. Thus, the choice of cultivars and rootstocks should be based on the growing locations, which is particularly important for diminishing the disorder of section drying. Future studies on breeding citrus cultivars insusceptible to section drying are urgently needed.

Table 1
Prevention methods for section drying applied in different citrus cultivars.

Methods		Types	Cultivars	Specific implementation	References
Preharvest	Choose proper cultivar	Granulation	Valencia orange	Casey and Smith selections	(El-Zeftawi et al., 1985)
	Utilize suitable rootstock	Vesicle collapse	Kinnow mandarin	Dwarfing rootstock	(Sharma & Saxena, 2004)
		Granulation	Valencia orange	Rootstocks from sweet orange strains	(El-Zeftawi, 1978)
	Artificial pollination	Granulation	'Guanximiyou' pummelo	Increase the proportion of cross-pollinated fruit	(Pan et al., 1999) (She et al., 2008)
	Diminish irrigation frequency	Granulation	Valencia orange	Irrigate every 30 days at harvest	(Singh and Singh, 1980b)
	Foliar spray of nutrients	Vesicle collapse	Satsuma mandarin	Calcium compounds	(Shiraishi et al., 1999)
			'Dancy tangerine' mandarin	KNO_3, $CuSO_4$, and boric acid	(Singh & Singh, 1981a)
	Plant growth regulator	Granulation	'Guanximiyou' pummelo	Treatment of 6-BA, GA_3 and 2,4-D at young fruit stage	(Xie et al., 1999)
		Vesicle collapse	'Kaula' mandarin	NAA or GA_3 treatment	(Singh & Singh, 1981b)
	Harvest at due time	Both granulation and vesicle collapse	'Ruby Red' grapefruit	Harvest earlier in January	(Burns and Albrigo, 1998)
		Granulation	'Guanximiyou' pummelo	Harvest at maturity stage	(Zhu et al., 2019)
Postharvest	Fruit selecting	Granulation	'Guanximiyou' pummelo	Hyperspectral imaging	(Jie et al., 2021)
			'Sai Num Pung' tangerine	Near infrared (NIR) spectroscopy	(Theanjumpol et al., 2019)
			Navel orange	X-ray radiographs	(Dael et al., 2016)
		Vesicle collapse	Satsuma mandarin	Selecting small- and middle-size fruit	(Wen et al., 2013)
			'Shatangju' mandarin	Choose small-size fruit for long-term storage	(Kang, Cao, et al., 2022)
	Pre-storage management	Granulation	'Shatianyou' pummelo	Pre-storage for 10–15 d	(Diao et al., 1998)
		Vesicle collapse	Satsuma mandarin	Short high temperature treatment of 3–5 days at 30 °C	(Burdon et al., 2007)
	Low temperature storage	Granulation	'Dianjiang' pummelo	Short-duration exposure of cold stress	(Hu et al., 2015)
			'Guanximiyou' pummelo	4 °C and 7 °C storage	(Pan et al., 2013)
			'Shatianyou' pummelo	10 °C storage	(Cao et al., 2020)
		Vesicle collapse	'Shatangju' mandarin	6 °C and 8 °C storage	(Zeng et al., 2000)
	Chemical treatment	Granulation	'Huyou' fruit	$CaCl_2$ treatment	(Chen et al., 2005)
			'Huyou' fruit	GA_3 treatment	(Chen et al., 1995)
			Huangguogan	1.0 mM spermidine treatment	(Xiong et al., 2017)
			'Guanximiyou' pummelo	1.0 $g \cdot L^{-1}$ SA treatment	(Pan et al., 2013)
	Edible coating	Granulation	'Majiayou' Pummelo	1.5% chitosan coating	(Nie et al., 2020), (Chen, Nie et al., 2021), (Chen, Peng et al., 2021)

5.1.2. Artificial pollination

Artificial pollination can increase the number of fertile seeds in fruit, which was reported to be effective for alleviating section drying, especially in pummelo fruit. A study by Pan et al. (1999) showed that artificial pollination could reduce granulation rate, which may be due to the several fertile seeds provided by cross-pollination. She, Zhao, and Pan (2008) also found that cross-pollinated fruit had a higher content of AsA and GSH, and lower content of MDA, leading to a lower granulation incidence. A study by Chen et al. (2005) showed that the granulation rate was reduced while overall fruit quality improved after artificial pollination. Though artificial pollination can reduce the section drying incidence, it also has the adverse effect of increasing seed number in the fruit, which is an undesirable trait for edible quality. As reported by Schneider, Goldway, Rotman, Adato, and Stern (2009), cross-pollination resulted in yield improvement of 'Orri' mandarin and increased seed set at the same time. Thus, artificial pollination or adding pollination trees can be used for alleviating section drying in pummelo fruit, but at the price of increasing seed number.

5.1.3. Improving cultivation management

Well-established cultivation management can alleviate section drying in citrus fruit, including reasonable irrigation and fertilization during the whole growth cycle. Tree water status and irrigation frequency have been reported to affect granulation to some extent (Ritenour et al., 2004). According to the study by Singh and Singh (1980b), granulation incidence of Valencia late orange could be reduced by 35% when irrigation was applied every 30 days compared to every ten days. The appropriate application of fertilizers, such as calcium compounds, could prevent fruit puffing of Satsuma mandarin to some extent, as reported by Shiraishi et al. (1999). Furthermore, foliar spray of other macro-and micro-nutrients (e.g., KNO_3, $CuSO_4$, and boric acid) also markedly reduced the disorder in 'Dancy tangerine' mandarin (Singh & Singh, 1981a).

5.1.4. Plant growth regulators

As one of the biotechnological treatments, plant growth regulators are non-toxic and harmless for human health and the environment. Preharvest treatment of plant growth regulators, such as GA_3, NAA and 2,4-D, was proven effective for the retardance of section drying if treated at the appropriate growth stage. A study by Singh and Singh (1981b) showed that Planofix (NAA) or GA_3 treatment significantly reduced the incidence of granulation. The overall fruit quality also improved after treatment, making the exploitation of these treatments practical in the industry. Similarly, Xie, Xu, Huang, Wang, and Zhuang (1999) found that the combined treatment of 6-BA, GA_3 and 2,4-D at the young fruit stage significantly alleviated the granulation symptom of 'Guanximiyou' pummelo. However, the result was strikingly different when GA_3 was applied to 'Guanximiyou' pummelo at fruit enlargement or postharvest stage, which instead aggravated the granulation symptom (Pan, Chen, Zheng, Lin, & She, 1998). It was speculated that the opposite effect might be due to the different application sites and periods, causing differences in the sensitivity and absorption rate of phytohormone.

5.1.5. Harvesting at due time

Time of harvest is a critical factor affecting both fruit quality and storage results, varies among different citrus cultivars and latitudes. Burns and Albrigo (1998) found that the granulation rate of 'Ruby Red' grapefruit was substantially reduced when harvested earlier in January. This was consistent with the study conducted by El-Zeftawi (1972), in which granulation increases the longer the fruit is held on the tree. However, early harvesting is not suitable for all citrus cultivars. Early harvesting in 'Guanximiyou' pummelo could diminish production and even exacerbate the juice sac granulation after storage (Zhu et al., 2019). Taken together, to reduce section drying and increase commercial quality, scheduling harvest at due time based on selling period and cultivar characteristics is recommended in the production of citrus fruit.

5.2. Postharvest methods

5.2.1. Fruit selecting

As one of the deep-learning approaches put forward in recent years, non-destructive detecting technologies have been intensively used in the horticulture industry. By using new computer technologies and collecting big data during production, non-destructive detecting technologies can detect the internal state of horticultural products without destroying it, which is feasible and convenient for fruit selection before storage (Yang & Xu, 2021). Previous studies demonstrated that non-destructive detecting technologies, including hyperspectral imaging, near-infrared spectroscopy, and X-ray radiographs, could be used to differentiate the granulation fruit from normal fruit in some citrus species. In the study by Jie et al. (2021), detection models for *Citrus grandis* granulation were established using hyperspectral imaging, with an accuracy of 100.0% and 97.92% in the training set and validation set, respectively. Theanjumpol et al. (2019) developed a non-destructive method for detecting and estimating the occurrence of granulation in 'Sai Num Pung' tangerine, which was based on the use of near-infrared (NIR) spectroscopy and physiochemical parameters such as moisture content, TA and SSC. In another study, a high-speed and robust algorithm for detecting granulation and endoxerosis was proposed by Dael et al. (2016), which was assisted with X-ray radiographs, a non-destructive inner inspection system. This algorithm was applied to inspect oranges and lemons, with the accuracy of 95.7% and 93.6%, respectively.

Previous studies demonstrated that fruit size has a substantial impact on the occurrence of section drying. Wen, Shi, Wang, and Wu (2013) found that small- and middle-size Satsuma mandarin maintained a higher activity of SOD and CAT both in pulp and peel, accounting for the lower vesicle collapse index. Similar results were obtained in our study on 'Shatangju' fruit, in that small-size fruit had a significantly lower vesicle collapse rate and better overall quality after storage (Kang, Cao, et al., 2022). Thus, fruit selecting is an efficient strategy for preventing section drying in citrus fruit, especially in long-term storage.

5.2.2. Pre-storage management

Pre-storage management, also called 'air drying and sweating', was applied to the postharvest storage of citrus fruit in order to reduce metabolism rate. Diao, Peng, and Zhang (1998) found that pre-storage for 10–15 d decreased stomatal contraction and respiration rate of 'Shatianyou', resulting in a significant decrease in weight loss and granulation rate. They speculated that pre-storage could inhibit the transportation of nutrients from pulp to peel and the regrowth of peel. Burdon et al. (2007) also found that pre-storage of 3–5 days at 30 ℃ can minimize the risk of weight loss and skin puffiness, which was reflected by a reduced space between the skin and segments, a decreased cross-sectional area and fruit diameter.

5.2.3. Low-temperature storage

As one of the most effective physical managements for postharvest storage of fruit, low-temperature storage can also retard the process of section drying. Cao et al. (2020) compared the vesicle collapse rate of 'Shatangju' fruit stored at different temperatures. They found that low temperature (6 ℃ and 8 ℃) storage could effectively reduce vesicle collapse rate by more than 50%, compared with high-temperature storage (10 ℃ and 20 ℃). Similar findings were observed in 'Guanximiyou' and 'Shatianyou' pummelo (Hu, Kong, Pang, Liu, & Zhang, 2015; Pan et al., 2013). The underlying mechanisms by which low temperature reduced section drying might be due to the reduction of metabolic intensity, alleviation of ROS injuries and inhibition of lignin biosynthesis enzymes (Hu et al., 2015; Pan et al., 2013). Apart from low-temperature storage, short-duration exposure of cold stress was reported to be effective for retarding the occurrence of granulation in 'Dianjiang' pummelo, mainly by reducing respiration rate and the content of MDA (Zeng, We, Xie, & Qi, 2000).

5.2.4. Chemical treatment

Chemical treatment has been widely used to preserve fresh fruit and vegetables, with the function of reducing postharvest diseases and retarding senescence. Based on the study of Chen et al. (2005), $CaCl_2$ exhibited a strong effect of retarding postharvest granulation in 'Huyou' fruit, which might act as a repressor of fruit senescence. In addition, the treatment of plant growth regulators on citrus fruit is also effective for reducing section drying during the postharvest period. For instance, Chen, Zhang, Li, Chen, and Liu (1995) found that GA_3 treatment reduced the granulation incidence of 'Huyou' fruit by delaying the senescence of pulp and the regrowth process of peel, respectively. Spermidine, one of the major polyamines in plants, has been reported to have inhibitory efficacy of granulation in *Huangguogan* through the antioxidant pathway (Xiong et al., 2017). As reported by Pan et al. (2013), the juice sac granulation in 'Guanximiyou' pummelo could be prevented by 1.0 $g \cdot L^{-1}$ SA treatments through inhibiting the activities of lignin biosynthesis enzymes.

5.2.5. Edible coating

Edible coating, a healthy and environment-friendly postharvest application, is widely used to maintain the quality of the fresh products by modifying the internal gas composition and decreasing water losses (Maringgala, Hashima, Tawakkalb, & Mohamed, 2020). The main components of edible coating used in food preservation are polysaccharides, lipids and resins, among which the polysaccharides are the most commonly used components (Palou, Valencia-Chamorro, & Pérez-Gago, 2015). Chitosan, one of the most functional polysaccharides, has been employed in the postharvest storage of citrus fruit recently. The research team from Jiangxi Agricultural University found that chitosan coating effectively reduced granulation rate and delayed postharvest senescence of 'Majiayou' pummelo. After 1.5% chitosan treatment, the development of postharvest granulation in 'Majiayou' was alleviated, which was due to the mitigation of ROS accumulation (Nie et al., 2020), suppression of cell wall modification (Chen, Nie et al., 2021) and reduction of energy depletion (Chen, Peng, Chen, Gan, & Wan, 2021) in juice sacs.

6. Outlook

Section drying is a particularly physiological disorder happened in citrus fruit, posing an enormous threat to the sustainable development of the citrus industry. The current review systematically summarized the classification, main causes, metabolic changes, mechanisms and prevention methods of section drying in citrus fruit. During the section drying process, juice sacs undergo a series of metabolic changes, regulated by enzymes, endogenous phytohormones and related structural genes, TFs and miRNAs. Numerous studies have focused on the phytochemical changes during the section drying process, while the exploration of the molecular mechanisms is comparatively lacking. Previous researches investigated ROS metabolism, cell wall metabolism and hormone signaling during the section drying process, respectively, while the interactions between these metabolic pathways still need further clarification. Ultimately, studies on section drying should focus more on cultivation management and postharvest handling in order to establish an integrated control strategy for effectively preventing section drying. It is expected that gene-editing technologies (i.e., CRISPR/Cas) may be used for the manipulation of this disorder during breeding and genetic improvement of citrus.

CRediT authorship contribution statement

Chen Kang: Writing – original draft. **Jinping Cao:** Conceptualization, Writing – review & editing. **Yue Wang:** Conceptualization, Investigation. **Chongde Sun:** Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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