



Review

Internal Flesh Browning in Apple and Its Predisposing Factors—A Review

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Abstract: This review article is focused on internal flesh browning (IFB)-related physiological disorders affecting apple (*Malus domestica* Borkh.) fruit. The expression of different physiological and metabolic IFB-related disorders during post-harvest storage are investigated along with the pre-harvest factors contributing to development. The effectiveness of commercially available pre-harvest technologies for preventing IFB-related disorders are also examined. Internal flesh browning-related disorders are erratic and devastating disorders that result in post-harvest deterioration of fruit quality in apples. Internal flesh browning-related disorders can result in severe economic losses to the apple industry through reduced consumer trust and market acceptability of susceptible cultivars. There are several IFB-related disorders and incidence can range from 0 to 100% of a crop, with severity ranging from no brown flesh to browning of the entire fruit flesh. While IFB-related disorders are found in several apple cultivars, some cultivars are more prone than others. The development of IFB-related disorders involve complex mechanisms depending upon the different types and causes, or factors involved in loss of structural integrity and functional stability of the cell membranes and cell components. Membrane disruption followed by enzymatic oxidation of fruit phenolic compounds by polyphenol oxidases and the production of brown polymers is considered to be the general underlying mechanism causing the browning of flesh tissue. It can be observed in different patterns based on the injured portion of the fruit flesh and the cause of membrane disruption. Three broad categories of IFB-related disorders, including chilling injury, internal CO₂ injury, and senescent-related browning disorders, are discussed along with their sub-types. The development of IFB-related disorders can be influenced by both pre-harvest factors and post-harvest conditions and their interactions. Although commonly associated with storage, IFB can also be found immediately after harvest and sometimes in unharvested fruit prior to full maturity. As pre-harvest conditions are a strong contributor to IFB-related disorders, the influence of several pre-harvest orchard conditions, including fruit size, crop load, maturity at harvest, cultivar, climatic conditions, seasonal temperatures, growing degree days, and major mineral nutrients, such as nitrogen (N), phosphorus (P), potassium (K), and calcium (Ca) are reported. Although there are contradictory findings in the studies reported, in general, factors such as larger fruit size, light crop load and delayed harvesting, along with cool temperatures after bloom and warmer temperatures before harvest, increase the risk of IFB-related disorders. In relation to fruit mineral concentrations, high N and low Ca have been associated with increasing IFB, while there is conflicting evidence in relation to the impact of both P and K. This review also examines the effectiveness of commercial pre-harvest technologies such as 1-methylcyclopropene, aminoethoxyvinylglycine and diphenylamine in the prevention of IFB-related disorders, but none of these technologies were found promising due to varied and contradictory results.

Keywords: fruit quality; physiological disorders; chilling injury; CO₂ injury; pre-harvest; crop load; maturity; mineral nutrients; 1-MCP; AVG



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1. Introduction

Apple (*Malus domestica* Borkh.) is one of the most economically and culturally important fruit crops in temperate regions of the world [1]. The apple originated in the Tian

Shan Mountain region of Kazakhstan and was later dispersed to western Europe and other parts of the world [2]. The modern cultivated apple is domesticated from *Malus sieversii* (primary progenitor), with *Malus sylvestris* (wild European crabapple) being a major secondary progenitor [3]. Apples are cultivated in diverse climatic environments of the world, including temperate and subtropical regions [4], confined to latitudes between 25° to 52° [5]. Worldwide apple production ranks fourth in the list of most important fruit crops after citrus, grapes, and bananas [6]. In 2020, world apple production was 86.44 million tonnes, covering an area of 4.62 million ha with overall productivity of 18.70 tonnes ha⁻¹ [7]. In Australia, apples are grown in multiple regions across six states, and in 2021, total Australian apple production was 280,273 tonnes, valued at \$619.9 million [8]. The apple industry in Australia is globally known for its outstanding quality and has great potential in the international export market [9].

Apart from increasing sustainable productivity and profitability, improving fruit quality and storability remains a prime focus of the apple industry. Apple research and breeding programs globally are continually focused on improving overall fruit quality [4] with new cultivars that have desirable eating attributes [10]. Fruit quality includes external appearance, internal physicochemical properties, and nutritional value. Yet, there are several disorders/diseases that reduce fruit quality and contribute to post-harvest deterioration in apples. Physiological disorders remain one of the most prominent causes of post-harvest deterioration [11]. According to Watkins and Mattheis [11], “physiological disorders are abnormal non-pathological changes in plant tissues expressed in response to the interaction between genotype and environment.” While some of these disorders are reversible in nature [12], the majority are non-reversible [13]. Physiological disorders such as bitter pit, pudding spot, core flush, water core, senescent breakdown, fruit softening, and internal flesh browning (IFB) lead to a significant decline in fruit quality and storability. Although many physiological disorders develop whilst in post-harvest storage, they are often directly influenced by different pre-harvest factors [14–16] such as rootstock, growing climate and environmental conditions, orchard management practices, and fruit maturity and handling at harvest [11,17–20].

Internal flesh browning affects several popular and widely grown apple cultivars such as ‘Cripps Pink’, ‘Fuji’, ‘Braeburn’, ‘Honeycrisp’, and ‘Empire’, and is a result of membrane disruption followed by enzymatic oxidation of fruit phenolic compounds by polyphenol oxidases (PPOs) producing brown-coloured polymers that turn fruit flesh brown [21–23]. This brown flesh, accompanied by off-flavours, results in a severe decline in market acceptability [24], cultivar/brand reputation and trust, leading to significant economic losses to the industry [1,25,26]. In the year 2000, a consignment of Tasmanian-grown ‘Pink Lady’ apples was rejected after facing criticism in Europe due to the incidence of IFB-related disorders; this resulted in severe losses to apple growers and marketers and adversely affected marketing relationships [25,26].

Internal flesh browning is a complex problem influenced by several pre-harvest factors, post-harvest storage conditions, and interactions between these factors [27–30]. Internal flesh browning can occur when the fruit is still on the tree and immediately after harvest, indicating that pre-harvest factors are strong contributors to the development of IFB [31–34]. Multiple studies have described the direct relationship of pre-harvest factors and conditions with the development of IFB-related disorders, including fruit size [35], crop load [29,34,36–38], mineral nutrition [35,37,39–41], fruit maturity at harvest [26,32,42–47], spatial and seasonal climatic variations in temperature and growing degree days (GDD) [29,33,34,42,48], and orchard management practices such as time of pruning (e.g. winter pruning increases the incidence of IFB-related disorders) [30]. This review investigates the expression of physiological and metabolic IFB-related disorders during post-harvest storage and examines the pre-harvest factors contributing to its development and effectiveness of commercially available pre-harvest technologies for preventing IFB-related disorders.

2. Physiological Disorders

Apple is a climacteric fruit and is stored for long durations (up to 12 months) using different types of storage facilities to regulate the year-round availability of fruit. However, physiological disorders remain the major economically important fruit quality deteriorator in the apple industry. The development of various physiological disorders, such as bitter pit, pudding spot, core flush, water core, lenticel breakdown, superficial scald, fruit softening, senescent breakdown, and IFB-related disorders, limits the long-term storability of several apple cultivars as fruit quality is reduced over time.

Some physiological disorders, such as bitter pit, pudding spot, core flush, water core and lenticel breakdown, are considered to be calcium (Ca)-related disorders [16,17,49], and their incidence and severity are influenced by factors that limit Ca uptake from the soil, translocation of Ca to, as well as within, the fruit and irregularity in the partitioning of Ca at cellular levels [50,51]. These factors can include the tree training system, cultivar and root-stock combination, nutrient management in the orchard, seasonal and climatic variations, Ca availability in the soil, fruit position in the tree, and the time of harvest [16,52,53].

3. Internal Flesh Browning

Deterioration in the components of apple fruit cells, including the cell wall, cell membrane, mitochondria and vacuole, is directly associated with the development of IFB-related disorders caused by three types of injuries—chilling injury, internal CO₂ injury (referred to as ‘CO₂ injury’ in the text here onwards), and senescent breakdown—resulting in deterioration of fruit quality during storage [54–57].

Internal flesh browning is the formation of brown-coloured polymers in apple flesh that occur when cell membranes are disrupted or disintegrate, leading to the action of polyphenol oxidases on phenolic compounds [21–23,58]. The cellular decompartmentalisation leads to the spilling of phenolic compounds from the vacuole and polyphenol oxidases from the plastids and vacuole into the cytosol. This interaction results in enzymatic oxidation of phenols to o-quinones by polyphenol oxidases and the formation of melanin which is responsible for the brown discoloration of the fruit flesh tissue [10,27,59]. Cell viability studies of affected fruit found that cells were dead in the brown tissue, while healthy cells were found in unaffected tissue [27].

3.1. Types of Internal Flesh Browning

Different patterns of IFB-related disorders are observed based on the injured portion/area of the fruit flesh and the cause of membrane disruption/disintegration [35]. Broadly, IFB-related disorders can be categorised into chilling injury, CO₂ injury (metabolic breakdown), and senescent breakdown. However, each of these can be subdivided further into different types, as discussed below:

3.1.1. Chilling Injury

A chilling injury occurs during storage when sensitive tissue is exposed to very low temperatures. This causes a reduction in plasma membrane fluidity caused by alterations in the lipid phase [55–57,60,61]. When the plasma membrane lipid bilayer undergoes lateral phase separations, these transitions become irreversible and result in impairment of the function of the plasma membrane, leading to deterioration and browning of the apple flesh [61,62].

This metabolic disorder is also known as low-temperature breakdown, core browning, or core flush, diffuse flesh browning (DFB), firm flesh browning and soggy breakdown, depending on the expressed symptoms and cultivar (Table 1). James and Jobling [28], Bergman et al. [36], Moggia et al. [42], Crouch et al. [44], Watkins and Liu [63], and Tong et al. [64] suggest that the DFB disorder found in ‘Cripps Pink’, ‘Empire’, and ‘Honeycrisp’ apples is a chilling injury induced disorder that is more predominant in apples produced in cooler regions. In DFB, the entire cortex tissue turns brown while the vascular tissue stays unchanged (Figure 1a). Symptoms are observed more frequently towards the stem as

well as calyx ends of the fruit but less so in the central portion. Diffuse flesh browning is commonly seen in larger fruit with thinner cortex cell walls, which are more susceptible to chilling damage. In contrast, vascular cells are smaller with thicker walls that aid in resisting cell collapse when the membrane is damaged. Core browning involves the browning of the core region (Figure 1b) [63,65]. Firm flesh browning is extensively reported in ‘Empire’ apples, occurring when flesh tissue browns yet remains firm and juicy (Figure 1c), hence differentiating it from senescent breakdown [63,66]. Firm flesh browning commonly develops in low temperature-controlled atmosphere (CA) conditions, particularly when fruit is stored at 0 to 0.5 °C [47,67]. In order to reduce the risk of firm flesh browning in ‘Empire’, a storage temperature of 2 °C was recommended. Storage at higher temperatures (≥ 3 °C) was shown to accelerate fruit softening and quality deterioration, and symptoms of firm flesh browning were further exacerbated when accompanied by 1-MCP treatment [68,69]. Symptoms of firm flesh browning usually appear first with higher incidence on the stem end and then progress through the calyx end tissue of the fruit [70–72]. Incidence of firm flesh browning was also found to be associated with metabolic changes [71,73], high polyphenol oxidase and peroxidase activity [67,69,70] and low antioxidant levels, especially ascorbic acid and glutathione [66,72]. Soggy breakdown, another chilling injury-related flesh browning disorder, displays as sharply demarcated irregular dark brownish portions developing in the flesh, distinguishing it from DFB (Figure 1d) [64,74,75]. Although the mechanism of development of soggy breakdown is still unclear, Leisso et al. [75] reported comparatively higher gamma-aminobutyric acid and lower antioxidant concentration along with polymerisation of phenolic monomers in the affected tissue compared to healthy tissue. This suggests that oxidative stress, fermentative respiration and consequent membrane disruption are the major contributors to soggy breakdown.

Table 1. Types of internal flesh browning (IFB)-related disorders, their subcategories and symptoms found in different apple cultivars.

Type of IFB Disorder	Sub-Category	Characteristic Feature/Symptoms	Cultivar	Reference
Chilling injury	Low temperature breakdown	Browning of vascular bundles and some portion of fruit flesh while other portions of flesh remain unaffected	‘Cox’s Orange Pippin’ ‘McIntosh’	Johnson and Yagaratnam [76] Webster and Lidster [77] Bramlage [39] Meheriuk et al. [78] Watkins et al. [79]
	Core browning/Core flush	Browning of core region	‘Empire’	Meheriuk et al. [78] Little and Holmes [65] Watkins and Liu [63]
	Internal browning	Discolouration of fruit flesh	–	Meheriuk et al. [78] Little and Holmes [65] Watkins et al. [79]
	Diffuse flesh browning	Browning of entire cortex tissue browning, while vascular bundles remain unaffected	‘Cripps Pink’ ‘Empire’	James and Jobling [28] Watkins and Liu [63] Bergman et al. [36] Butler [35] Crouch et al. [44] Moggia et al. [42]
	Firm flesh browning	Browning of flesh tissue, while the affected tissue remains firm and juicy, hence differentiating it from senescent breakdown	‘Empire’	Watkins and Liu [63] Lee et al. [66]

Table 1. *Cont.*

Type of IFB Disorder	Sub-Category	Characteristic Feature/Symptoms	Cultivar	Reference
	Soggy breakdown	Typically develops irregular dark brownish portions in flesh, with sharp demarcation from healthy tissue, which distinguish it from DFB	‘Honeycrisp’	Watkins et al. [74] Leisso et al. [75] Tong et al. [64]
CO ₂ injury	Brown heart	Browning of vascular tissue extending to mid-cortex along with irregular, sunken dry patches on fruit skin	‘Fuji’	Smock [80] Moon and Koo [81] Meheriuk et al. [78] Johnson et al. [82] Volz et al. [83] Argenta et al. [84] James et al. [85]
	Braeburn browning disorder	Brown portions in fruit flesh followed by formation of lens-shaped pits or cavities	‘Cripps Pink’ ‘Fuji’ ‘Bramley’s Seedling’ ‘Braeburn’ ‘Elstar’	Blanpied et al. [86] Elgar et al. [31] Lau [32] Streif and Saquet [30] James et al. [48]
Senescent related IFB disorders	Radial flesh browning	Browning of vascular tissue, while cortex tissue remains unaffected	‘Cripps Pink’	James and Jobling [28] Bergman et al. [36] Butler [35] Crouch et al. [44] Moggia et al. [42]

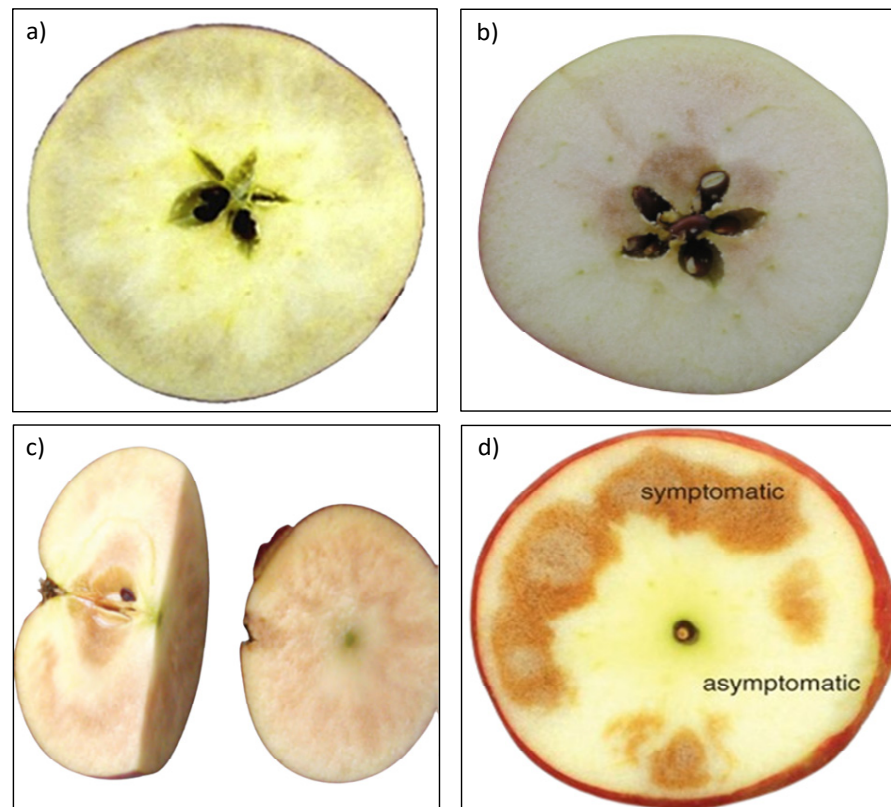


Figure 1. Symptomatic fruit with chilling injury-related internal flesh browning disorders: (a) diffuse flesh browning in ‘Cripps Pink’ [adapted from Moggia et al. [42]], (b) core browning in ‘Luiza’ [adapted from Argenta et al. [87]], (c) firm flesh browning in ‘Empire’ [adapted from James et al. [47]] and (d) soggy breakdown in ‘Honeycrisp’ apples [adapted from Leisso et al. [75]].

3.1.2. CO₂ Injury

Internal flesh browning-related disorders arising from CO₂ injury are considered physiological and metabolic disorders because they are directly associated with the respiration rate and metabolism of the fruit. CO₂ injury is a response to high CO₂ and/or low O₂ concentrations in flesh tissue [57], influenced by rates of gas diffusion whilst in storage [32,88]. The fruit respiration process continuously consumes O₂ and produces CO₂; however, as apples are relatively bulky, restricted diffusion of CO₂ can lead to a concentration gradient [89] with a consistent decline from the cortex tissue towards the core [90–92]. Gas diffusivity mainly depends on fruit tissue microstructures which includes cell shape, cell packing, intercellular spaces or tissue porosity that can act as barriers to diffusion and, thus, rates of fruit respiration [89–92]. The region under the fruit skin and the core line or the inner cortex region where most of the vascular bundles are located are identified as the main diffusion barriers [90,91]. Restrictions to gas diffusion through these barriers and a limited external supply of O₂ under CA conditions create localised hypoxic or anoxic conditions within the fruit flesh. Consequently, respiration shifts to a fermentation pathway with reduced adenosine triphosphate (ATP) production and enhanced CO₂ production [89,91,93,94]. The increased CO₂ accumulation in flesh tissue and insufficient energy availability for sustaining essential cellular defences, such as membrane repair, leads to membrane failure and cell death. The collapse and collision of cellular contents result in the subsequent browning of flesh tissue [93,94].

CO₂ injury is mainly characterized by the development of pits and cavities in the flesh, which are surrounded by brown tissue (Figure 2a,b) [78,79] and commonly develop in CO₂-sensitive apple cultivars such as ‘Braeburn’, ‘Cripps Pink’, ‘Fuji’, ‘Honeycrisp’, and ‘Santana’ during CA storage. CO₂ injury is also known as brown heart and ‘Braeburn’ browning disorder (BBD). Brown heart is associated with browning of the vascular tissue of the fruit following storage which further extends to the mid-cortex (Figure 2c) [78,80,95,96]. In addition, the brown heart can also express irregular, sunken, dry, and brownish patches that generally appear over the greener portion of the fruit skin [80]. Braeburn browning disorder occurs in the flesh of ‘Braeburn’ and other apple cultivars when the apples are stored under CA conditions with CO₂ concentration higher than 1%, but symptoms have also been observed in fruit under regular air storage [31,32]. Braeburn browning disorder is associated with cultivar-specific fruit characteristics, such as higher flesh density and skin resistance, which contribute to elevated levels of internal CO₂ [32,97]. The typical characteristic of BBD is the formation of brown portions throughout the fruit flesh tissue and, with increasing severity, the appearance of brownish lens-shaped pits or cavities in the cortex tissue [48,86]. In general, cell collapse, followed by the mixing of cell contents and enzymatic oxidation of phenolic compounds, leads to the browning of flesh tissue. Herremans et al. [94] suggested that the formation of the cavities results from the loss of cellular fluids to the surrounding tissues, and the pattern of browning depends upon the variation in tissue microstructures resulting in localised ‘hotspots’ of brown flesh while surrounding tissue with better diffusivity remains unaffected. Sub-optimal CA conditions (1% O₂, 5% CO₂) can lead to a drastic decline in O₂ in the flesh of healthy ‘Braeburn’ fruit and can induce the fermentation process; even optimal CA conditions (3% O₂; 0.7% CO₂) can induce browning in dense flesh with poor diffusivity [94].

In a study focused on investigating the changes in the transcriptomic events of fruit flesh of ‘Braeburn’ apples, Mellidou et al. [59] revealed that alterations in lipid metabolism-related genes in the inner cortex tissue (associated with oxidation of fatty acids and membrane modifications) and energy and stress metabolism genes (which are associated with electron transport chain and tricarboxylic acid cycle) could be responsible for the development of BBD.

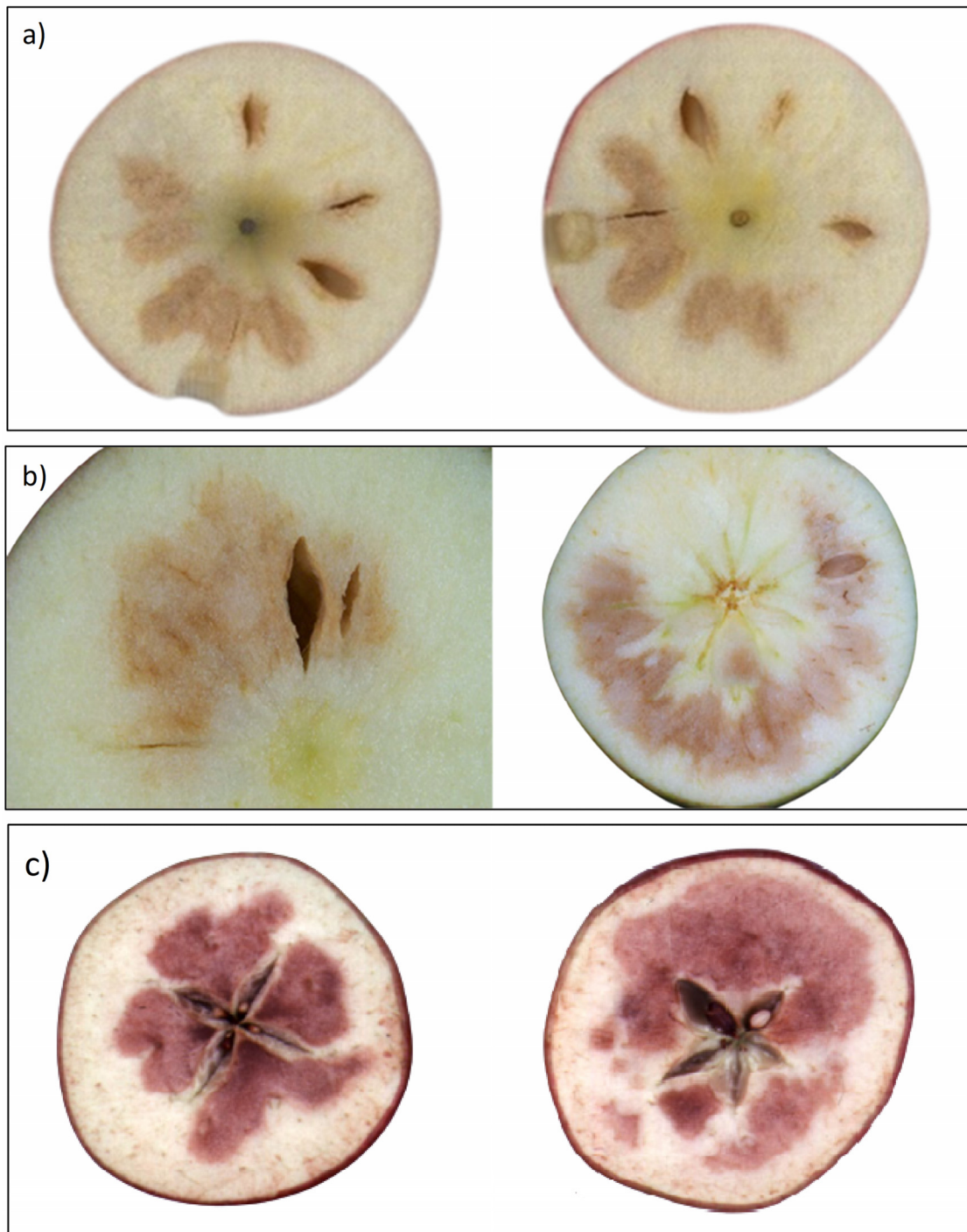


Figure 2. Symptomatic fruit with CO₂ injury-related internal flesh browning disorders: (a) CO₂ injury in ‘Scilate’, and (b) ‘Honeycrisp’ [adapted from—Contreras et al. [98]] and (c) brown heart in apples [adapted from—Cross et al. [99]].

3.1.3. Senescent Related IFB Disorders

The process of senescence involves physiological changes in fruit tissue, including changes in cell shape as the even or round-shaped cells become irregular in shape with alterations in the intercellular spaces [88]. Senescent breakdown, also known as ‘mealy breakdown’ (Figure 3a) [80], involves the loss of membrane integrity, which leads to alterations in fluidity and consequent decompartmentalisation and fracturing of the cell wall [48,55,57,62]. These alterations at the cellular level and leakage of cell contents lead

to compromised intercellular spaces and poor diffusion of O₂ and CO₂ [88]. Thus, while senescent-related disorders can aggravate the incidence of other disorders, such as chilling and CO₂ injury [37,57,88], they are different [100]. Depending upon the cultivar, senescent disorders produce a range of symptoms, including textural changes in fruit flesh and browning extending outwards from the vascular bundles [37]. In ‘Cripps Pink’ (Pink LadyTM), senescent disorder is categorised as radial flesh browning (RFB) [28,35,36,42,44]. It is mainly associated with the browning of vascular tissue within the fruit, while the cortex tissue remains unaffected (Figure 3b). Its occurrence is higher towards the stem end portion of the fruit as opposed to the calyx end, and is more prevalent in fruit from warmer regions. The incidence of RFB is exacerbated by factors such as delayed harvesting, low temperature during storage and higher levels of CO₂ in storage. This type of IFB disorder occurs in cultivars with smaller vascular cells that limit the emission of CO₂ from the fruit, resulting in cell death due to toxic levels of CO₂ accumulation. The incidence of senescent disorders is associated with fruit maturity at harvest, where in general, the risk of RFB incidence increases with over-maturity or delayed harvesting [37]. Other risk factors include lower fruit Ca content [60,101], length of time in storage with longer duration increasing the incidence, mineral composition (explained in detail in Section 3.2), and mechanical injury [55]. According to Sánchez-Contreras et al. [102], RFB had a positive relationship with the metabolism of sphingolipids in ‘Cripps Pink’, hence increased levels of sphingolipids in the flesh tissue could be associated with lipid catabolism in the membrane, cell apoptosis, and senescence process and subsequent development of RFB.

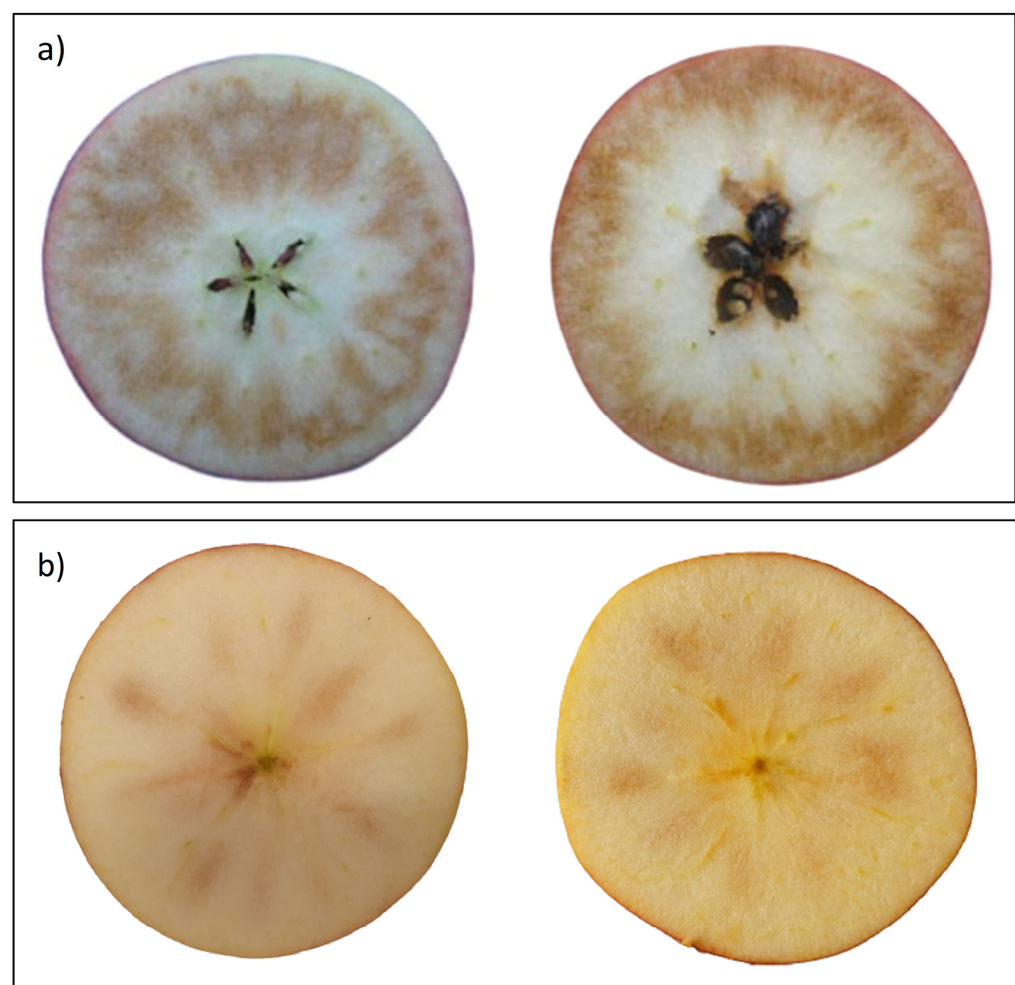


Figure 3. Symptomatic fruit with senescent related internal flesh browning disorders: (a) senescent breakdown in ‘Luiza’ [adapted from Argenta et al. [87]] and (b) radial flesh browning in ‘Scilate’ apples.

3.2. Factors Contributing to Internal Flesh Browning and Fruit Quality Deterioration

Depending upon the final cause of alterations in structural integrity and functional stability of the cell membranes and cell components resulting in IFB-related disorders, different factors influencing its development have been reported. Because of the large number of factors involved and their complex interactions, the incidence of IFB-related disorders in apples is highly erratic and unpredictable. Only a percentage of fruit develop IFB-related disorders, and of these, not all the fruit flesh is affected; there is also a large variation between seasons, regions or orchards or even between trees within the same orchard block [26,32,36,38,40,42,103,104]. However, as reported in studies undertaken around the world, the incidence of different IFB-related disorders can range from 0 to 100% and severity can also range from browning of a minute portion to the entire flesh of the fruit. Hence more research is required to determine the actual causal pre- and post-harvest factors and their interactions [40].

3.2.1. Pre-Harvest Orchard Factors

The fact that internal flesh browning can be found when the fruit is on the tree and immediately after harvest indicates that pre-harvest factors are involved in its development [31,32]. Various pre-harvest factors influencing the development of IFB-related disorders are discussed below.

Fruit Size

There is a general perception that larger fruit, which often has low Ca concentrations, are more susceptible to physiological disorders compared to smaller-sized fruit [105]. Butler [35] found that the incidence of “combination” browning (i.e., the combined incidence of RFB and DFB) in ‘Cripps Pink’ apples was positively correlated with fruit size. Similarly, larger fruit size has been associated with increased susceptibility towards the senescent breakdown of cold-stored ‘Spartan’ apples [106] and rapid fruit softening and flesh breakdown of ‘Royal Gala’ apples [100,107,108]. This increased susceptibility of large fruit towards various physiological disorders, including IFB-related disorders, may be due to the earlier onset of maturation and faster ripening in large fruit [109], resulting in faster softening and ripening or senescence [108]. Watkins et al. [110] associated advanced fruit maturity at harvest with the development of various physiological disorders during storage. As cell size can be greater in large fruit [111], this means fewer cells per unit area [112], consequently leading to a reduction in cell wall matrix components and total surface area for intercellular attachments [109]. Both earlier ripening and larger cell size increase the risk of developing senescent-related IFB disorder, flesh breakdown and fruit softening or senescent-related cracking during storage [108]. In contradiction to these studies, De Castro et al. [40] reported that the incidence of CO₂ injury in ‘Pink Lady’ apples was higher in average-sized (173–176 g) fruit compared to larger (183–200 g) fruit.

Crop Load

An inverse relationship has been demonstrated between fruit size and crop load in apples [113], with maximum fruit size being cultivar dependent [114]. Crop load is an important measure of productivity used in orchards and can be defined as “the amount (number or weight) of fruit produced per tree or branch unit” [115]. Crop load is measured in terms of the number of fruit per tree, the number of fruit per 100 blossom clusters or the number of fruit cm⁻² limb/trunk cross-sectional area (LCSA/TCSA) [116–118]. The most widely used method of expressing crop load is the number of fruit cm⁻² LCSA/TCSA.

As crop load is associated with fruit size, quality, maturity, and nutritional balance [119], it is assumed to influence the development of various post-harvest physiological disorders. However, contrasting findings have been observed in different studies. Ferguson and Watkins [120] suggested that fruit from trees with lighter crop loads are more susceptible to physiological disorders during storage compared with fruit from trees with medium-heavy crop loads. Fruit size tends to increase with lighter crop loads, and as larger

fruit are likely to have lower Ca concentrations due to dilution [121], they become more prone to Ca-related physiological disorders [105]. Lighter crop load trees are also more vigorous and consequently have a higher shoot:fruit ratio, which alters the movement of mineral nutrients to developing fruit [122]. Because shoots act as better sinks than fruit, they compete more strongly than fruit for mineral nutrients, leading to mineral deficiency in the fruit, especially Ca [50]. Jones et al. [49] also noted that vigorous tree growth could lead to a decline in Ca supply to the fruit. Thus, nutrient distribution to fruit from vigorous trees with a high shoot:fruit ratio, as found with lighter crop loads, is adversely affected [50], and fruit from these trees are more prone to the development of IFB-related disorders [35].

More specifically, the incidence of BBD in 'Braeburn' has been reported to be higher in lighter crop load conditions [34,38]. In 'Cripps Pink', RFB has been observed to be more prevalent under lighter crop loads than heavy, and this has been attributed to nutritional imbalance (especially lower Ca and higher K) in fruit from lighter crop load trees [29,36,37]. Several authors have reported that the increase in fruit size under lighter crop load conditions results in firmer and denser fruit [123–126], thus limiting gas diffusion and leading to anaerobic conditions in the fruit, which consequently increases the incidence of IFB-related disorders, specifically CO₂ injury [65,127].

In contrast, De Castro et al. [40] found that the incidence of CO₂ injury was higher during heavy crop load years and lower during light crop load years. These authors related the incidence of IFB to the higher ascorbic acid content of the fruit and supported this with the findings of Kondo [128], who reported that ascorbic acid content was decreased due to heavy crop loads. However, Brown et al. [25] concluded that there is no influence of crop load on the incidence of CO₂ injury in 'Pink Lady'.

The contrasting results reported in different studies as to the role of crop load and fruit size affecting the incidence of internal browning indicate a need for further investigation, especially on a cultivar basis.

Fruit Maturity at Harvest

The time of harvesting influences fruit quality in storage and the risk of IFB-related disorders [129]. Early harvest can result in under-ripe acidic tasting fruit and lack of typical flavour development because of impaired biogenesis of volatile compounds [129]. Late or delayed harvest can result in soft floury tasting fruit due to a rapid decline in firmness, increased respiration rate and ethylene production [130–132]. Generally, advancement in fruit maturity at harvest can influence the incidence of different types of IFB-related disorders [28,40,42,44,85], but some studies reported that early harvesting may also affect IFB-related disorders.

Brown et al. [26], Moggia et al. [42], and Jung and Choi [133] observed that advancement in fruit maturity increased the incidence of IFB-related disorders in 'Cripps Pink' and 'Empire'. In 'Empire' apples, early harvesting prevented firm flesh browning development, while delayed harvesting increased its incidence [47,68]. Hence early harvesting (one week before normal optimum harvest) can be used as an effective tool for firm flesh browning management [134]. Doe et al. [43] reported that delayed harvesting of 'Rosy Glow' apples increased the incidence of RFB and DFB in comparison to fruit harvested at optimal maturity. Similarly, Crouch et al. [44], while working on South African-grown 'Cripps Pink' apples, observed that delayed harvesting of fruit induced the earlier development of DFB compared to fruit harvested at optimum maturity. Both Crouch et al. [44] and Moggia et al. [42] observed that, unlike DFB, which progressively worsens with delayed harvest and duration of shelf-life (7–10 days at 20 °C), RFB was only affected by maturity at harvest and did not progressively worsen in shelf-life. In contrast, Doe et al. [43] found that RFB progressively worsened during shelf-life. Crouch et al. [44] explained the cause of the increased incidence of DFB in post-optimally harvested fruit as the presence of higher levels of lipid peroxidation and lower total ascorbate during the early stages of storage. Under normal circumstances, the level of active oxygen species in plant tissues is regulated by active oxygen and scavenging enzymes and the antioxidants present in fruit [135,136].

Purvis [136] found that the increased production of active oxygen species (particularly the hydroxyl radical) in stressed tissue can lead to lipid peroxidation in cell membranes and loss of function of cell organelles, ultimately causing cell death which leads to the appearance of flesh browning.

The incidence of CO₂ injury and internal cavities have been shown to be exacerbated with delayed harvesting in 'Braeburn' [32,45] and 'Fuji' [46]; Lau [32] associated this with higher respiration rates, increased skin resistance and sensitivity to lower O₂, and higher CO₂ levels in storage atmospheres. Elgar et al. [38] found that 'Braeburn' fruit harvested prior to optimal maturity demonstrated a greater incidence of CO₂ injury-related internal cavities than in fruit harvested after the optimal harvest window. Contradictory trends between years were observed by De Castro et al. [40], who reported that both early and late harvesting could increase the incidence of CO₂ injury, depending on the year; this suggests that factors other than harvest date influence IFB-related disorders.

Cultivar

The susceptibility to IFB-related disorders varies between apple cultivars [45] and is influenced by seasonal conditions and the growing region for the specific cultivar [29,32,40]. Even when grown under the same conditions, apple cultivars can vary largely in both fruit size [137] and fruit internal tissue micro-structures, such as cell number, cell size, and intercellular spacing and their organisation [138]—according to Harada et al. [137] this may be related to cultivar specific genetic traits. For instance, Rojas-Candelas et al. [139] reported that smaller and more regular cells with more abundant intercellular spaces were found in less firm apple cultivars, such as 'Golden Delicious' and 'Delicious', than in the firmer cultivars 'Granny Smith' and 'Gala'. Similarly, Ting et al. [138] demonstrated that apple cultivars vary greatly with respect to porosity or overall intercellular space, finding that 'Jazz' had the lowest porosity of 17%, 'Braeburn' had medium porosity of 25.3%, while 'Golden Delicious' and 'Fuji' had the highest porosity of between 29 to 30%.

Consequently, the storage duration before the loss of quality due to physiological disorders varies between cultivars. Apple cultivars, such as 'Jonagold', 'Cox's Orange Pippin', 'Jonathan', 'Elstar', and 'Delicious', have been reported to be susceptible to different types of IFB [78]. According to Little and Holmes [65] and Watkins [101], 'McIntosh', 'Boskoop' and 'Elstar' are highly susceptible to chilling injury when stored at 0 °C and require relatively higher (2–4 °C) storage temperatures to mitigate that risk but 'Delicious' and 'Granny Smith' are less susceptible and can be stored at 0 °C. Apple cultivars can vary in relation to their sensitivities to CA storage conditions. 'Empire' and 'Braeburn' have been reported to be less tolerant and readily develop physiological disorders under certain CA conditions [31,32,101,140], whereas 'Golden Delicious', 'Gala', and 'McIntosh' were more tolerant, with 'Golden Delicious' and 'Gala' able to tolerate higher CO₂ concentrations (up to 5%) in CA conditions [65,101]. However, the cultivars sensitive to CO₂ injury, i.e., 'Braeburn' and 'Fuji', need to be stored at lower CO₂ concentrations (below 0.5%) [31,32,65,83,101].

Both Saquet et al. [141] and Hatoum et al. [24] found that 'Jonagold' was resistant to the development of CO₂ injury during CA while 'Braeburn' apple was highly susceptible. Ho et al. [89] also reported that due to the presence of a diffusion barrier in the cortex tissue, 'Braeburn' apples are more likely to develop CO₂ injury (or BBD) than 'Jonagold' and 'Kanzi' when stored under the same CA conditions. Hence, 'Braeburn' should be stored under higher O₂ partial pressure, while both 'Jonagold' and 'Kanzi' can be stored under lower O₂ partial pressure [93]. Similarly, Köpcke [142] reported differences between cultivars 'Elstar', 'Gloster', and 'Jonagold' in relation to their sensitivities to CA, dynamic CA and 1-MCP treatments and consequently to the incidence of chilling and CO₂-related injuries.

The susceptibility towards IFB-related disorders can vary between closely related cultivars, clones or even strains of the same cultivar. Williamson et al. [143] recommended separate storage conditions for 'Cripps Pink' and its clone cultivar 'Rosy Glow' because the latter experienced more CO₂ injury, which may be associated with higher greasiness and

potentially the denser flesh found in ‘Rosy Glow’. Similarly, Argenta et al. [144] reported differences in ‘Fuji’ strains, with ‘Fuji Superma’ showing the lowest susceptibility towards CO₂ injury, indicating the need for separate CA conditions for different strains.

The susceptibility of these cultivars to CO₂ injury-related disorders may be attributed to the high flesh density of these cultivars, differences in internal tissue micro-structures, such as cell shape and size and intercellular spacing, porosity levels, and skin greasiness, which reduces gas diffusivity [32,89,101]. Further, in a recent study comparing transcriptome changes between CO₂ injury-sensitive (‘Han Fu’) and -tolerant (‘Golden Delicious’) cultivars in CA storage, Li et al. [145] revealed that the greater CO₂ injury tolerance of ‘Golden Delicious’ was associated with upregulation of the genes ‘related to apetala 2’ and pyruvate decarboxylase encoding, and they also associated CO₂ injury in ‘Han Fu’ with greater upregulation of genes involved in lipid catabolism (patatin-like protein), polyphenol biosynthesis (phenylalanine ammonia-lyase), lactate synthesis (lactate dehydrogenase), and higher activity of polyphenol oxidase.

3.2.2. Climatic Factors

Seasonal Temperatures

According to James [37], the development of physiological disorders, particularly IFB-related disorders, is greatly influenced by pre-harvest climatic conditions. Seasonal weather conditions influence fruit quality and size along with cell number and cell size within the fruit, which determines the flesh density [36]. Bergh [146] suggested that several aspects of fruit development and quality are affected by seasonal temperature, which can also influence the development of IFB-related disorders [32]. Temperature, particularly during the first 40 to 50 days after full bloom (DAFB) is critical in determining cell number per fruit [147]; cool temperatures can lead to the lengthening of the cell division phase, thus producing fruit with a higher number of cells but of smaller size, leading to denser fruit [32,64,65]. In addition, seasonal variability in growing temperature can alter tissue resistance towards gas diffusion [148], and cooler climates, in particular, influence cellular metabolism and lead to reduced skin and tissue diffusivity [32]. This combination of an increase in fruit density and reduction in gas diffusivity may result in an increase in fruit susceptibility towards CO₂ injury during storage [32,65].

Elgar et al. [31] reported a greater prevalence of BBD mainly in colder growing regions in the south of New Zealand, particularly in regions with high altitudes. Similarly, in a recent study, Argenta et al. [149] noted a higher incidence of DFB and CO₂ injury in ‘Fuji’ apples grown at the coldest site. Corrêa et al. [150] found warmer average daily temperatures from 90 to 210 DAFB reduced the risk of CO₂ injury in CA-stored ‘Fuji’ apples. McCormick et al. [34] also observed that warmer night temperatures (>10 °C) four weeks before harvest markedly reduced the incidence of BBD in ‘Braeburn’ apples. However, no influence of earlier seasonal temperatures (three weeks post petal fall) was observed on BBD incidence. The temperature during the four-to-six-week period prior to harvest also directly influences fruit quality, maturity and storability. Lower temperatures before harvest delay ripening, while higher daytime temperatures lead to advancement in fruit maturity at harvest, making the fruit susceptible to IFB-related disorders [26,39].

Growing Degree Days

Growing degree days are calculated by taking the mean of the average daily maximum and minimum temperatures and subtracting a base temperature (generally 10 °C) [35,36,103,147]. The seasonal GDD_{>10 °C} is calculated as a sum of daily GDD_{>10 °C} from full bloom through to harvest. Lau [32] noted that in CA-stored ‘Braeburn’ apples grown in different regions of British Columbia, Canada, the development of BBD was associated with cool growing seasons experiencing less than 1300 GDD_{>10 °C}. Similarly, in their four-season study with ‘Pink Lady’ De Castro et al. [40] reported a higher incidence of CO₂ injury in seasons of lowest GDD_{>10 °C} (calculated for the first 50 DAFB) and vice versa for three seasons, but in one season the incidence of CO₂ injury was lower even with low GDD_{>10 °C}. Variation

in $GDD_{>10^{\circ}C}$ has been shown to influence two different types of IFB (DFB and RFB) [103]. While working on ‘Cripps Pink’ apples under Australian conditions, James and Jobling [28] and James et al. [103] reported that the incidence of DFB increased in fruit from regions that experienced seasonal $GDD_{>10^{\circ}C}$ below 1100, and the development of RFB during storage was exacerbated in regions accumulating $GDD_{>10^{\circ}C}$ between 1100 to 1700. They also found that the incidence of radial browning substantially decreased in regions experiencing more than 1700 seasonal $GDD_{>10^{\circ}C}$. Likewise, Tong et al. [64] reported that the $GDD_{>10^{\circ}C}$ 50 to 60 DAFB could explain a 31% variation in the incidence of DFB in Quebec-grown ‘Honeycrisp’ and accumulated $GDD_{>10^{\circ}C}$ below 500 can increase the risk of DFB.

3.2.3. Mineral Nutrition

Fruit mineral content could have an influence on fruit quality outcomes because mineral nutrients can directly influence cell structure, function, and stability and hence can play a critical role in increasing or decreasing susceptibility toward physiological disorders [57]. The minerals N, K, P, Ca, and boron (B) are associated with post-harvest fruit quality and physiological disorders [35,151].

Nitrogen

Nitrogen is an important macronutrient and plays a crucial role in apple fruit quality and storability; it is reported to influence various fruit quality parameters such as firmness, dry matter content, and total soluble solids [35]. Excessive tree vigour resulting from high N application may lead to an increase in fruit cell size, which can negatively affect fruit firmness [152]. Fruit N content has been found to be positively correlated with respiration rate and ethylene production and negatively correlated with fruit firmness [153,154]. While working with ‘Cox’s Orange Pippin’ and ‘Golden Delicious’ apples, Marcelle [155] found that higher fruit N content led to a decline in soluble sugar content and acidity. Bramlage et al. [156], Sharples [157], Shear and Faust [158], and Bramlage [39] reported that an increased risk of various postharvest physiological disorders, such as internal breakdown, core browning, cork spot, superficial scald, bitter pit, and pathogen infection may be associated with excessively high fruit N concentrations of $>500 \text{ mg kg}^{-1}$ fresh weight. Similarly, high fruit N concentrations of 400 mg kg^{-1} fresh weight increased the incidence of senescent and internal breakdown in ‘Lobo’ and internal breakdown and core browning in ‘Raike’ and ‘Red Atlas’ apples grown under Finland conditions [159]. Vigorous tree growth resulting from an excessive supply of N can lead to imbalances of other nutrients; for example, the increased competition between shoots and fruit for Ca is attributed to a reduction in fruit Ca content [160], and fruit size enhancement due to high concentration of N in trees leads to a decline in fruit Ca content, mainly due to dilution [160].

Phosphorus

The role of P has received little attention compared to N and K [35], and there is limited information in the available literature reporting a positive response of P fertilisation in apples. However, Taylor and Goubran [161] found that newly planted apple trees respond well to P application when their root growth is limited. Further, P has been positively associated with fruit firmness and has been found to directly influence fruit quality and storability [162]. Lower fruit P concentration ($<0.011\%$) has been reported to increase the risk of low-temperature and senescent breakdown [39]. Johnson and Yogaratnam [76] found that foliar application of P compounds on ‘Cox’s Orange Pippin’ increased fruit P levels and reduced the susceptibility of fruit towards low-temperature breakdown. Webster and Lidster [77] also reported that six foliar spray applications (at weekly intervals starting four weeks after full bloom) with phosphate compounds increased leaf and fruit P concentrations in ‘McIntosh’ apples, which resulted in a reduction in low-temperature breakdown and increased fruit firmness, while lower fruit P ($<85 \text{ ppm}$ whole fruit, minus seeds and stem) increased low-temperature breakdown. For good storage quality, adequate fruit P concentration has been reported to be 90 ppm for ‘McIntosh’ [77,163] and 110 ppm for

‘Cox’s Orange Pippin’ [157]. Marcelle [155] has also shown that fruit P content is negatively correlated with susceptibility towards low-temperature and senescent breakdown. This may be attributed to the role of P in ATP synthesis, which is required for recovery from chilling injury [41,60,164]. However, Neuwald et al. [165] reported a positive correlation between fruit P content and the incidence of BBD in ‘Braeburn’ apples and linked this to the involvement of P in energy metabolism processes associated with the development of IFB-related disorders [166], which can influence the status of enzymatic phosphorylation along with modulating the action of Ca as a secondary messenger [167].

Potassium

Potassium is a vital mineral nutrient, and low-fruit K content has been shown to increase susceptibility to low-temperature breakdown [39,157], while high-fruit K can lead to increased susceptibility towards core browning or core flush [157]. According to Hakerlerler et al. [168], higher fruit K content induces resistance to chilling injury by increasing phospholipids and permeability of the cell membrane along with improving various biochemical and biophysical properties of cells. Singer and El-Tohamy [169] associated K with the prevention of low-temperature breakdown due to its role in the regulation of osmotic and water potential in cell sap which reduced electrolyte leakage.

Fruit K concentration and K:Ca ratio at harvest were found to be positively correlated with the incidence of BBD in ‘Braeburn’ apples [165,170]. High-fruit K is associated with higher titratable acidity; however, high levels of fruit K (>0.12–0.15%) can negatively affect fruit quality and storability of apple fruit and may induce Ca deficiency (due to an antagonistic relationship), making fruit susceptible to storage disorders [39,171]. In general, titratable acidity declines with time in storage [172], whereas organic acids sustain fruit respiration and are required for the longer storability of fruit [35]. Fruit organic acids are the intermediates in the citric acid cycle; thus, changes in titratable acidity are directly associated with the rate of fruit respiration and metabolism [173]. Optimum fruit K content is crucial so that it contributes positively towards enhancing the accumulation of titratable acidity and prevention against chilling injury and other IFB-related disorders during storage without adversely affecting the Ca supply to the fruit. Hence, it is important to maintain fruit K content to improve overall storability [35].

Calcium

Calcium is a vital mineral nutrient for improving and maintaining fruit quality and storability in a range of fruit crops, including apples. Calcium is involved in various intra- and extra-cellular processes, affecting both fruit quality and senescence [121,174]. Apple leaves have been reported to contain higher concentrations of Ca than fruit tissue [50,121], and this may be due to cultural practices that enhance vegetative growth, such as high N supply or excessive pruning, that in turn lead to the partitioning of Ca towards the leaf tissue rather than fruit tissue [151]. However, fruit Ca content has a strong relationship with post-harvest quality in apples [35], as discussed above in relation to nitrogen.

De Castro et al. [40] suggested that high fruit Ca levels can considerably reduce CO₂ injury incidence. Corrêa et al. [175] linked the incidence of CO₂ injury in CA-stored ‘Fuji’ apples with lower fruit Ca content and found that the risk of CO₂ injury increased in fruit with <80 mg·kg^{−1} flesh Ca content. Similarly, in ‘Cripps Pink’ apples, James and Jobling [57] observed a negative correlation between fruit Ca:K ratio and incidence of DFB, but no such relationship was found for RFB. Calcium in fruit is primarily concerned with sustaining and strengthening the cell wall and plasma membrane along with facilitating the transmission of various extracellular signals into intracellular biochemical reactions [50,174,176]. Higher fruit Ca levels are known to reduce the activity of lipoxygenase along with decreasing 1-aminocyclopropane-1-carboxylic-acid concentration and ethylene emission and consequently help to delay senescence [177]. However, when fruit Ca content decreases to levels where the deficiency occurs, the plasma membrane becomes weaker, thus making the fruit cells more prone to cellular breakdown [50,174]. These Ca deficit conditions lead

to a decline in the pool of free Ca available exterior to the cell membrane, which in turn drastically disrupts the signalling and leads to dysfunctional cellular activity [50].

Because of its relationship with cell wall stability, fruit Ca content is positively correlated with fruit firmness [178]. According to Marcelle [179], Ca plays an essential role in retarding senescence and ripening in apples by slowing down the respiration rate and decreasing ethylene emission; therefore, it may considerably influence harvest maturity. Moreover, Ca has been found to be negatively correlated with various maturity indices such as soluble sugars, refractometric index, and dry matter content [35]. Over-mature fruit of ‘Cripps’ Pink’ has been reported to undergo membrane disruption followed by expression of DFB [180]; this fruit also recorded increased levels of lipid peroxidation and decreased ascorbic acid and linolenic acid content. De Castro et al. [27] reported a high incidence of CO₂ injury in fruit with low levels of Ca; they also found that the antioxidant ascorbic acid was negatively associated with CO₂ injury. Hence, antioxidants are responsible for protecting the plasma membrane from the oxidative breakdown of fruit tissue. Ca, along with ascorbic acid, plays a role in maintaining cell membrane stability; thus, deficiency of Ca and ascorbic acid in fruit during storage could be considered one of the causes of IFB-related disorders [35,180].

However, in a recent study, Wood et al. [181] reported contradictory results to previous studies, finding that fruit Ca content was positively correlated with CO₂ injury in ‘Braeburn’ apples, backing their findings with the industry observations of McCormick et al. [34] that the seasons with higher bitter pit (related to Ca deficiency) incidence recorded lower incidence of BBD and vice versa. The above-described literature is summarised in Table 2.

Table 2. Pre-harvest factors responsible for the development of different internal fruit browning (IFB) related disorders in various apple cultivars.

Pre-Harvest Factor	Intensity of Factor	IFB Risk/Incidence	Cultivar	Reference
Tree/fruit factors				
Fruit size	Large fruit	↑ RFB & DFB	‘Cripps Pink’	Butler [35]
	Large fruit 250 to 350 g	↑ Senescent breakdown	‘Honeycrisp’ ‘Royal Gala’	Prange et al. [100] Lee et al. [108]
	Medium/average fruit (173–176 g)	↑ CO ₂ injury	‘Cripps Pink’	De Castro et al. [40]
Crop load	Light (3.1 to 3.8 fruit cm ^{−2} TCSA)	↑ BBD	‘Braeburn’	Elgar et al. [38]
	Light	↑ RFB	‘Cripps Pink’	Jobling et al. [29] James [37], Bergman et al. [36]
	Light	↑ IFB related disorders & BBD	–	Little and Holmes [65] Volz et al. [127]
	Heavy (36 to 44 tonnes/ha)	↑ CO ₂ injury	‘Cripps Pink’	De Castro et al. [40]
	No effect of crop load	↔ CO ₂ injury	‘Cripps Pink’	Brown et al. [25]
	Light (50% of standard crop load)	↑ BBD	‘Braeburn’	McCormick et al. [34]
	Late harvest (1 week after normal)	↑ BBD	‘Braeburn’	Lau [32] Streif [45]
Maturity at harvest	Late harvest (1 week after commercial)	↑ RFB & DFB	‘Cripps Pink’	Brown et al. [26]
	Late harvest (>50% starch breakdown)	↑ RFB & DFB	‘Rosy Glow’	Doe et al. [43]
	Late harvest	↑ RFB	‘Cripps Pink’	Moggia et al. [42]
	Late harvest (210 DAFB)	↑ CO ₂ injury	‘Fuji’	Volz et al. [46]

Table 2. Cont.

Pre-Harvest Factor	Intensity of Factor	IFB Risk/Incidence	Cultivar	Reference
	Late harvest (2 to 3 weeks after commercial or 72% starch breakdown)	↑ DFB	‘Cripps Pink’	Elgar et al. [38], Crouch et al. [44]
	Both early and late harvest	↑ CO ₂ injury	‘Braeburn’ ‘Cripps Pink’	Elgar et al. [38] De Castro et al. [40]
	Early harvesting	↓ FFB	‘Empire’	James et al. [47] Doerflinger et al. [134] Doerflinger et al. [68]
Cultivar	Susceptible	↑ IFB related disorders	‘Jonagold’ ‘Cox’s Orange Pippin’ ‘Jonathan’ ‘Delicious’	Meheriuk et al. [78]
	Less susceptible	↓ CO ₂ injury	‘Jonagold’, ‘Kanzi’ ‘Fuji Superma’ ‘Golden Delicious’	Saquet et al. [141] Ho et al. [89] Hatoum et al. [24] Argenta et al. [144]
	Highly susceptible	↑ BBD	‘Braeburn’	Ho et al. [89] Hatoum et al. [24]
	Highly susceptible	↑ CI	‘McIntosh’ ‘Boskoop’ ‘Elstar’	Little and Holmes [65] Watkins [101]
	Less susceptible	↓ CI	‘Delicious’ ‘Granny Smith’	Little and Holmes [65] Watkins [101]
	Susceptible	↑ CO ₂ injury	‘Braeburn’ ‘Fuji’ ‘Rosy Glow’ ‘Han Fu’	Elgar et al. [31] Lau [32] Volz et al. [83] Little and Holmes [65] Watkins [101] Williamson et al. [143] Li et al. [145]
Climate				
Seasonal temperatures	Warmer climate 4–6 weeks before harvest	↓ LTB & CB	–	Bramlage [39]
	Higher temperatures before harvest	↑ RFB & DFB	‘Cripps Pink’	Brown et al. [26]
	Cooler climate 50 days post flowering	↑ CO ₂ injury	‘Braeburn’	Lau [32] Little and Holmes [65]
	Warmer average daily temperatures from 90 to 210 DAFB	↓ CO ₂ injury	‘Fuji’	Corrêa et al. [150]
	Warmer night temperatures (>10 °C) four weeks before harvest	↓ BBD	‘Braeburn’	McCormick et al. [34]
	Cold growing region	↑ CO ₂ injury	‘Fuji’	Argenta et al. [149]
Growing degree days	GDD _{>10 °C} below 1100	↑ DFB		
	GDD _{>10 °C} between 1100 to 1700	↑ RFB	‘Cripps Pink’	James and Jobling [28] James et al. [103]
	GDD _{>10 °C} below 500 (during 50 to 60 DAFB)	↑ DFB	‘Honeycrisp’	Tong et al. [64]

Table 2. Cont.

Pre-Harvest Factor	Intensity of Factor	IFB Risk/Incidence	Cultivar	Reference
Mineral nutrition				
Nitrogen	Higher fruit N	↑ Internal breakdown & CB	–	Sharples [157] Bramlage [39]
	High fruit N (>400 mg kg ^{−1} fresh weight)	Senescent & internal breakdown	‘Lobo’	Dris et al. [159]
		Internal breakdown & CB	‘Raika’ ‘Red Atlas’	
Phosphorus	Low fruit P (<110 ppm) at whole fruit less seeds and stem basis	↑ LTB	‘Cox’s Orange Pippin’	Sharples [157]
	Low fruit P (<0.011%)	↑ LTB & senescent breakdown	–	Bergmann [171] Bramlage [39] Marcelle [155]
	Higher fruit P (>90 ppm) at whole fruit less seeds and stem basis	↓ LTB	‘McIntosh’	Bramlage et al. [163] Webster and Lidster [77]
	Higher fruit P (18–19 mg 100 g ^{−1} fresh weight)	↓ LTB	‘Cox’s Orange Pippin’ ‘McIntosh’	Johnson and Yogaratnam [76]
	Low fruit P (<85 ppm) at whole fruit less seeds and stem basis	↑ LTB	‘McIntosh’	Webster and Lidster [77]
	High fruit P	↑ BBD	‘Braeburn’	Neuwald et al. [165]
	Low fruit K	↑ LTB	–	Sharples [157] Bergmann [171] Bramlage [39]
Potassium	Higher fruit K	↓ CI & LTB (induces resistance to CI and LTB)	–	Hakerlerler et al. [168] Singer and El-Tohamy [169]
	Higher fruit K (>0.12–0.15%)	↑ CB or Core flush		Sharples [157] Bergmann [171]
	Higher fruit K	↑ CO ₂ injury & BBD	‘Santana’ ‘Braeburn’	Neuwald et al. [165,170]
Calcium	Higher fruit Ca (~80 mg per gram fresh weight)	↓ CO ₂ injury	‘Cripps Pink’	De Castro et al. [40]
	High Ca (~110 mg kg ^{−1} fresh weight) or low Ca:K ratio (15.8)	↓ DFB	‘Cripps Pink’	James and Jobling [57]
	Higher fruit Ca (>4 mg 100 mg ^{−1} fresh weight)	↑ CO ₂ injury	‘Braeburn’	Wood et al. [181]
	Lower fruit Ca	↑ CO ₂ injury	‘Cripps Pink’	De Castro et al. [27]
	Lower fruit Ca (<40–60 mg kg ^{−1} fresh weight)	↑ flesh breakdown & other disorders	–	Dris et al. [159] Suzuki and Basso [182]
	Lower fruit Ca (<80 mg kg ^{−1} fresh weight)	↑ CO ₂ injury	‘Fuji’	Corrêa et al. [175]

RFB = radial flesh browning, DFB = diffuse flesh browning, TCSA = trunk cross-sectional area, BBD = ‘Braeburn’ browning disorder, DAFB = days after full bloom, FFB = firm flesh browning, CI = chilling injury, LTB = low temperature breakdown, CB = core browning, GDD = growing degree days. [Descriptors: ↑ = increases, ↓ = decreases and ↔ = no effect].

4. Commercially Available Pre-Harvest Technologies and Their Effectiveness against IFB-Related Disorders

4.1. 1-Methylcyclopropene (1-MCP)

The chemical 1-methylcyclopropene (1-MCP) is an ethylene inhibitor extensively used in the horticulture industry across a wide range of fruits and vegetables in order to maintain post-harvest quality and prolong storage life [183,184]. 1-MCP competes with ethylene for binding sites with a 10 times higher affinity than ethylene [185,186], consequently reducing ethylene biosynthesis [187]. It aids in extending the post-harvest life of apple fruit by reducing ethylene production, lowering the respiration rate, and delaying the ripening process [180,188–190]. Post-harvest treatment with 1-MCP formulations, such as Smart Fresh™ (AgroFresh Solutions, Philadelphia, PA, USA), is common in the apple industry [191]. The effectiveness of post-harvest applications of 1-MCP in preventing different physiological disorders varies considerably depending upon the role of ethylene in the development of the particular disorder [183,192–194]. 1-MCP has been reported to reduce the incidence of senescent breakdown in ‘Macoun’ [195], DFB in ‘Royal Gala’ [196], and chilling injury in ‘Gala’ apples but Lee et al. [196] found that it tended to increase sensitivity to stem-end IFB in ‘Royal Gala’. Lafer [197] noted that overripe ‘Golden Delicious’ fruit treated with 1-MCP developed a higher incidence of IFB-related disorders than untreated fruit. Similarly, Lafer [198] observed a greater incidence of BBD in 1-MCP treated fruit stored under CA, or dynamic CA conditions and Köpcke [142] reported a higher incidence of CO₂ injury in 1-MCP treated ‘Elstar’ apples; however, the incidence was reduced when 1-MCP treated fruit was stored under dynamic CA conditions. Argenta et al. [199], Hatoum et al. [24], and Al Shoffe et al. [200] observed increased CO₂ injury in ‘Braeburn’ and ‘Honeycrisp’ apples with post-harvest 1-MCP treatments while De Castro et al. [201] and Deyman et al. [104] observed no effect on CO₂ injury. DeEll et al. [202] found that the incidence of core browning was reduced in ‘Empire’ but increased in ‘Delicious’ apples following treatment with 1-MCP, but there was no effect on IFB in either of these cultivars. DeEll and Lum [203] also found that 1-MCP treatment increased core browning in ‘Northern Spy’ apples.

Research in ‘Empire’ apples revealed that post-harvest 1-MCP treatment increased the incidence and severity of firm flesh browning under CA conditions, and incidence was particularly enhanced when apples were stored at warmer temperatures (3 to 4 °C) in order to prevent chilling injury at lower storage temperatures (0 or 0.5 °C) [66,67,69,71–73,204]. This could be associated with higher polyphenol oxidase activity in the flesh of treated fruit [67,133,205]. Treatment with 1-MCP under low O₂ storage conditions can induce greater physiological alterations in metabolic activity indicated by higher levels of volatile aromatic compounds and amino acids in the stem-end than calyx-end region [71].

More recently, a pre-harvest formulation of 1-MCP (Harvista™, 1.3% 1-MCP as a soluble concentrate, Agrofresh Solutions, Philadelphia, PA, USA) has gained considerable popularity in the horticulture industry. Applied as a spray before harvest, this product is easy to use and can help in extending the harvest window by delaying fruit maturity and ripening and reducing pre-harvest fruit drop [206,207]. It has also been found to be effective in retaining flesh firmness during storage [47,208] and reported to positively influence fruit quality characteristics, such as total soluble solids, titratable acidity, and colour development [209].

However, the effectiveness of pre-harvest 1-MCP in controlling physiological disorders related to IFB has not been extensively studied. A few studies investigating the role of pre-harvest 1-MCP for IFB-related disorders reported a reduction in the incidence of both soggy and senescent breakdown in ‘Honeycrisp’ [200,210] and stem-end IFB in ‘Gala’ apples [211,212]. Similarly, DeEll et al. [213] reported that pre-harvest 1-MCP in combination with post-harvest 1-MCP treatment reduced the incidence of IFB in ‘Gala’ apples. In general, previous studies have reported that both pre- and post-harvest 1-MCP treatments are effective in reducing senescent-related IFB disorders, but they can also increase the incidence and severity of chilling and CO₂ injury-related IFB disorders [187].

Given the contrasting reports on the impact of post-harvest 1-MCP treatments on IFB-related disorders and the limited information available on the influence and effectiveness of pre-harvest 1-MCP formulations on different IFB-related disorders, there is a need for research to determine how effective pre-harvest 1-MCP formulations are in controlling IFB-related disorders, particularly in highly susceptible apple cultivars.

4.2. Aminoethoxyvinylglycine (AVG)

Aminoethoxyvinylglycine (AVG) is another ethylene biosynthesis inhibitor that is widely used in the apple industry to delay fruit maturity and extend the harvest period [214]. According to Robinson et al. [215] and Costa [216], AVG can increase yields when applied two to four weeks prior to harvest as a result of reduced fruit drop and increased fruit size due to delayed ripening through extension of the harvest window; it also provides flexibility in scheduling of harvest operations [216,217]. Multiple studies on pre-harvest application of AVG to apple trees confirm that AVG can decrease fruit drop [215,217], reduce ethylene production and slow down fruit ripening and starch breakdown [197,217–222], delay yellowing and red colour development [218,222–225], and reduce flesh firmness loss during storage [197,217,226]. The effectiveness of AVG in relation to different fruit quality parameters may vary depending upon time and concentration of application, fruit maturity stage at the time of application, cultivar, and seasonal climate [197,215,217,218,224].

Although benefits of AVG application have been reported, pre-harvest application of AVG has been reported to have little or no effect on senescent-related IFB and rate of fruit softening in ‘Gala’, ‘Royal Gala’, and ‘Imperial Gala’ [218] or on stem-end IFB in ‘Gala’ apples [211]. Application, four weeks prior to optimal harvest in ‘Golden Delicious’, saw no clear effect on IFB-related disorders [197]. According to Robinson et al. [215], a higher incidence of IFB was observed in AVG-treated ‘Mcintosh’ apples compared to untreated fruit following eight months of CA storage.

4.3. Diphenylamine (DPA)

Diphenylamine (DPA) is an arylamine antioxidant that has been used commercially in the apple industry since the early 1960s to inhibit the development of superficial scald during storage [227]. Unlike 1-MCP and AVG, which are inhibitors of ethylene biosynthesis, DPA treatment increases the expression of two metabolic pathways related to ethylene production; thus, the action of DPA could be associated with increased ethylene production [187], which in turn can provide tolerance to various abiotic stresses [228]. In addition to effective control of superficial scald, DPA treatment has been reported to effectively inhibit CO₂ injury in ‘Delicious’ [229], ‘Cortland’ and ‘Law Rome’ [230], ‘Fuji’ [231], ‘Pink Lady’ [27,40], ‘Braeburn’ and ‘Gala’ [232–234], and ‘Honeycrisp’ [98].

Despite its effectiveness against the development of superficial scald and various other IFB-related disorders of apples, the detection of residues and metabolites of DPA, which may be toxic and carcinogenic to humans in treated produce, has led to uncertainty about its future use in the industry [227]. Associated adverse effects have led to the imposition of a ban by the European Commission on all existing authorisations and products comprising DPA above the maximum residue limit (MRL); however, DPA products with detectable MRL of 0.1 mg kg^{−1} or below can still be used.

4.4. Other Technologies

Other technologies to mitigate the risk of IFB disorders include the pre-harvest application of gamma-aminobutyric acid which is thought to improve the levels of ATP and nicotinamide adenine dinucleotide (reduced form; NADH) and reduce active oxygen species levels. In a three-year study by Al Shoffe et al. [235], the application of gamma-aminobutyric acid two weeks before harvest reduced senescent breakdown in ‘Honeycrisp’ during one season of the study, suggesting a need for further investigation of its effectiveness. Pre-harvest Ca fertilisation (both soil and foliar) and application of triazole fungicide can influence proteome in ‘Braeburn’ apple; Buts et al. [236] noted that Ca fertilisation

enhanced the expression of proteins related to antioxidant enzymes and can be associated with the reduction of BBD. Whereas triazole fungicide made alterations in the proteins related to respiration and ethylene biosynthesis, hence, could be associated with increased incidence of BBD.

5. Conclusions

This review demonstrates that IFB-related disorders occur in erratic patterns and can be region and/or cultivar-specific, with incidence varying between seasons, orchards, blocks and even between trees within the same orchard or block. The development of IFB-related disorders are greatly influenced by a range of pre-harvest tree and fruit conditions such as fruit size, level of crop load, fruit maturity at harvest, cultivar, growing climatic conditions and other factors, such as content of mineral nutrients, especially N, P, K and Ca. Research gaps have been highlighted, particularly in relation to the role of pre-harvest factors such as crop load, fruit size, and mineral nutrition. Although IFB disorders have been studied in depth in apple cultivars such as ‘Cripps Pink’, ‘Braeburn’, and ‘Empire’ there is further need for comprehensive research in other susceptible apple cultivars to better understand the types, causes, and predisposing factors of IFB. Attempts should also be made to standardise the terminology used for different expressions of IFB-related disorders in different cultivars. Hence, future studies should focus on cultivar-specific comprehensive investigations considering all the pre- or post-harvest factors to isolate the best predictors of IFB-related disorders. This would help in the development of cultivar specific strategies to prevent damaging and erratic physiological disorders, such as IFB-related disorders. This review also examined the effectiveness of commercially available pre-harvest technologies such as 1-MCP, AVG and DPA against IFB-related disorders. As results varied greatly between cultivars with contradictory findings and increased incidence of IFB-related disorders in some cases, the effectiveness of these technologies is not yet confirmed.

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