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Review Article
Alcoholic Off-Flavor Disorders in Fresh Fruits

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The off-flavor disorder is one of the most quality deteriorating and undesirable postharvest physiological disorders in fresh fruits. Over-biosynthesis and accumulation of ethanol metabolism-related metabolites such as acetaldehyde and ethanol have been associated with an alcoholic off-flavor disorder in various fresh fruits at both pre- and postharvest stages. Correspondingly, many studies have reported the association of such off-flavor disorders with several inducing factors, including anaerobic respiration, low O_2 stress, high CO_2 stress, and storage temperature stress, that upregulate ethanol metabolism in fruits. Furthermore, numerous metabolic and physiological mechanisms that govern ethanol metabolism under such factors are subsequently addressed. These mechanisms include the γ-aminobutyric acid (GABA) shunt pathway, mitochondrial energy metabolism, glycolysis, Krebs or TCA cycle, cytosolic malate metabolism, and starch and sugar metabolism. To summarize the relevant findings, the current paper reviews the literature on alcoholic off-flavor disorder, focusing on the role of significant underlying causes and key metabolic and physiological mechanisms in boosting ethanol metabolism in fresh fruits. In addition, recent measures that have been already taken or are in progress to control the higher activity of ethanol metabolism that may eventually result in limiting the alcoholic off-flavor disorder in harvested fresh fruits have also been discussed. Moreover, functions of metabolic mechanisms, including respiratory mechanisms, and other factors such as fruit genetic makeup, degree of maturity, and postharvest handling and storage conditions, are needed to be investigated in future work at both physiological and transcriptomics levels to reveal the additional relation to alcoholic off-flavor disorders in fresh fruits during ripening and storage.

1. Introduction

Fruits are one of the most desired horticulture commodities among consumers due to their high nutritional content, appealing color, and flavor [1–5]. However, due to a fluctuating ripening trend, most fresh fruits ripen rapidly after harvest, even at ambient and low temperatures. In turn, substantial-quality losses might occur in fruits, such as early fruit softening, decay incidence, weight loss, color degradation, flesh browning, skin pitting, nutritional breakdown, chilling injury, and alcoholic off-flavor development [6–8]. Such quality losses arise due to the ongoing metabolic adaptations that alter the intended qualities of fruits until they are unmarketable.

The perception of off-flavor sensations characterizes alcoholic off-flavor disorder as a result of an excess of fermentation metabolites in ethanol metabolism, such as acetaldehyde and ethanol [6, 9–11]. Acetaldehyde and ethanol concentrations in fruits are often present in trace amounts throughout normal ripening or postharvest storage but

begin accumulating as fruits tend to ripen sharply under high respiration rates, elevated temperatures, and anaerobic respiration [12]. Such metabolites are involved in maintaining the postharvest quality of the fruit under aerobic respiration, notably during the volatile aroma production stage [13]. Also, they can improve fruit flavor, suppressing ethylene production and reducing fruit firmness [14]. Conversely, increased levels of these metabolites develop physiological disorders in fruit during postharvest storage as their accumulation may impart the formation of off-flavors in various horticultural crops such as mandarins, pear, dragon fruit, grapes, and kiwifruit.

Several studies have shown that anaerobic respiration [15], low O_2 stress [16], high CO_2 stress [17], and high-temperature stress [18] have a detrimental impact on ethanol metabolism, which leads inevitably to over biosynthesis or accumulation of acetaldehyde and ethanol, resulting in alcoholic off-flavor disorder in fruits. Subsequently, numerous metabolic physiological mechanisms, including the γ-aminobutyric acid (GABA) shunt pathway [6], mitochondrial energy metabolism [19], glycolysis and Krebs (TCA) cycle [12], cytosolic malate metabolism, and starch and sugar metabolism [20, 21], tend to alter or regulate the ethanol metabolism under the consequences of such stresses. The detrimental impact of undesirable modifications in such metabolic physiological pathways in response to stress stimuli, specifically accelerated ethanol metabolism, has been demonstrated by various studies.

To date, as per our knowledge, no review article on the alcoholic off-flavor disorder in fresh fruits has been published. Hence, this review article aims to discuss the comprehensive literature regarding alcoholic off-flavor disorders in fresh fruits. This article particularly addressed the primary causing factors involving physiological and metabolic mechanisms and postharvest strategies to overcome alcoholic off-flavor disorders at an agroindustrial level. Furthermore, a research gap that needs to be investigated at a molecular level in future research has also been pointed out.

2. Ethanol Biosynthesis and Metabolism

Ethanol is an essential aroma-active volatile compound naturally synthesized in fruits and vegetables during the maturing and ripening processes via ethanol metabolism [22]. Ethanol metabolism is a two-step pathway involving the decarboxylation of pyruvate into acetaldehyde and ethanol via the activities of pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH), as depicted schematically in Figure 1. Furthermore, acetaldehyde could be further reduced to acetic acid via aldehyde dehydrogenase (ALDH) activity, and ethanol could be converted to ethyl acetate via an esterification reaction catalyzed by alcohol acetyltransferase (AAT) activity using acetyl-CoA as a key substrate [6, 23, 24]. Ethanol metabolism is concomitant with the continuous recycling and reoxidation of nicotinamide adenine dinucleotide + hydrogen (NADH) to nicotinamide adenine dinucleotide (NAD^+) to generate adenosine triphosphate (ATP) [25–27]. Studies reported that ethanol metabolism is the only alternate pathway for ATP
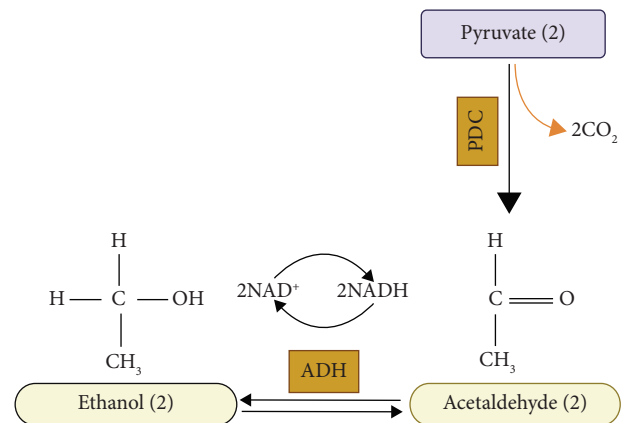

FIGURE 1: Metabolic pathway of ethanol metabolism (PDC: pyruvate decarboxylase; ADH: alcohol dehydrogenase).

biosynthesis to fulfill the plant's metabolic energy demand under hypoxic or anoxic stresses [12, 19].

Additionally, accelerated ethanol metabolism leads to over-accumulation and the induction of alcoholic off-flavor, which deteriorate the fruit flavor quality [19]. It has been reported that the high stimulation of ethanol metabolism is anticipated by cellular pH-stat. Pyruvate is catalyzed by lactate dehydrogenase (LDH) to lactic acid, and lactic acid production acidified cytoplasmic pH and consequently activates the first ethanol metabolism enzyme PDC [25, 27, 28]. The intensity of ethanol metabolism can vary based on PDC and ADH enzyme activities, resulting in desired or immature flavor development in various horticultural crops. For example, Botondi et al. [29] and Huan et al. [19] reported the correlation between excess ethanol and acetaldehyde production or accumulation due to enhanced activities of PDC and ADH, resulting in alcoholic off-flavor disorder in "Hayward" and "Bruno" kiwifruit.

Similarly, Zhang and Watkins [30] reported the occurrence of off-flavors compounds such as acetaldehyde and ethanol and enhanced PDC and ADH activity in strawberry fruit. Furthermore, Shi et al. [31] noticed enhanced acetaldehyde and ethanol contents due to upregulated PDC and ADH transcriptional levels in mandarin fruit. Our previous work also demonstrated that higher PDC and ADH activities result in higher acetaldehyde and ethanol accumulation, which leads to alcoholic off-flavor disorder in "Bruno" kiwifruit at room temperature storage [6, 12, 32].

In contrast, some previous studies negatively correlated PDC and ADH activities with acetaldehyde and ethanol biosynthesis. For example, Ponce-Valadez and Watkins [33] reported that the accumulation of acetaldehyde and ethanol negatively correlated with changes in PDC and ADH activities in "Jewel" and "Cavendish" strawberry fruit. Imahori et al. [34] reported that increased activity of PDC and ADH in bell pepper fruit was not correlated with acetaldehyde and ethanol accumulation. Our previous study concluded a negative correlation between kiwifruit fermentation metabolites and enzymatic activities [32]. Such a correlation could be based on the sensitivity range of each crop's PDC and ADH expression under various stresses [35, 36].

2.1. Factors Leading to Upregulated Ethanol Metabolism in Fresh Fruits. The development of alcoholic off-flavor is limited during normal fruit growth or ripening, even at pre- and postharvest stages. Meanwhile, due to the upregulation of ethanol metabolism, fruits may be susceptible to the occurrence of alcoholic off-flavor, which may result in the deterioration of fruit flavor quality initiated by the following inducing factors:

2.2. Anaerobic Respiration. Anaerobic respiration is a process that initiates under the effect of reduced aerobic mitochondrial activity and lower ATP biosynthesis as a result of undesired stresses, activating ethanol metabolism to regenerate ATP by using NADH [37, 38]. Plenty of ethanol contents are produced and accumulated, resulting in alcoholic off-flavor development in various fruits [12, 19, 29, 39].

Moreover, a relationship between anaerobic respiration and alcoholic off-flavor disorder is described in detail by Saltveit [15] as follows: "Anaerobic respiration is associated with the regeneration of NAD^+ and ATP to maintain the plant cell energy demand by moving the pyruvate flux to the ethanol fermentation/metabolism instead of the TCA cycle" (Figure 2). This process further leads to the accumulation of lactic acid in the lactate fermentation pathway, which results in the acidification of cells and activates the PDC in ethanol metabolism. PDC converts the pyruvate to acetaldehyde by removing the CO_2 and then to ethanol through the activity of the ADH to generate more NAD^+ content. The anaerobic pathway accounted for only 20% of the energy synthesis ability, which is insufficient for plant survival. This fact upregulated ethanol metabolism for more ATP synthesis, resulting in an over-accumulation of ethanol and alcoholic off-flavor.

2.3. Low O_2 Stress. Oxygen concentration in fruit tissues is primarily based on each cultivar's respiration rate, as the ratio of O_2 and CO_2 fluctuates continuously due to organic compounds' consistent biochemical reactions and degradation [40]. The correlation between various physiological disorders in many horticultural crops was investigated by applying different modified gas conditions during storage. However, exposure of each cultivar to different concentrations of O_2 atmosphere can be beneficial or harmful depending on various factors such as storage temperature and cultivar type. Oxygen acts as an electron acceptor in mitochondrial cytochrome oxidase during aerobic pathways. However, in a scenario of a limited O_2 atmosphere, plant cells are exposed to fermentation pathways, energy deficits, and storage disorders [17, 41]. Reduced O_2 concentration appeared to have a beneficial relationship with decreased respiration rate, senescence, ethylene synthesis, and enzymatic oxidation at a certain level. In contrast, lowered O_2 induced physiological disorders such as alcoholic off-flavor, gummosis, fruit rots, fruit discoloration, superficial scald, split and shattered pits, gel breakdown, greasiness, and pit burning in many fruits, including pear, apple, mango, and stone fruits (nectarines, plum, cherry, apricot, and peach) during storage [16, 42–44].

The oxygen limit at which ethanol metabolism initiated and accumulation occurred was named the pasture point, or lower oxygen limit, and later referred to as fermentation induction point [16]. Recently, Park et al. [45] reported that the upregulated expression of ethanol metabolism-related genes *MdPDC2* and *MdADH1* led to higher production of acetaldehyde and ethanol in "Empire" apples during storage in a 0.5 kPa O_2 atmosphere compared to a 1.5 kPa O_2 atmosphere. Burdon et al. [46] reported increased PDC and ADH activities, resulting in a sharp accumulation of fermentation metabolites in the "Hass" avocado under the storage atmosphere with less than 0.5% O_2 concentration. Each crop has a specific tolerance limit for low O_2 levels, and below that, plants adopt a fermentation pathway [47, 48]. Previously, many researchers exposed various fruits to low O_2 atmosphere for a short period and concluded beneficial effects regarding quality. Meanwhile, susceptibility to alcoholic off-flavor disorder has been observed with long-term exposure [16, 19, 49, 50].

Regarding alcoholic off-flavor disorder in fruits under low O_2 stress, Wood et al. [51] reported that exposing fruits to anoxic conditions (20.9 kPa O_2) results in a higher concentration of acetaldehyde and ethanol in apple fruit. Ntsoane et al. [43] concluded that acetaldehyde and ethanol accumulation were significantly higher in "Shelly" mango stored at 5% O_2 than at 10% O_2 in controlled atmosphere storage. Moreover, Pintó et al. [52] concluded that the change in pomegranate flavor quality is caused by the accumulation of ethanol and acetaldehyde due to a low O_2 storage atmosphere. Under low O_2 stress, acetaldehyde is produced by the decarboxylation of pyruvate by PDC and then converted to ethanol by ADH by consuming NADH. Imahori et al. [53] reported that elevated PDC and ADH transcription and translation resulted in the synthesis of new mRNA and PDC and ADH protein in a low O_2 atmosphere. Thus, under low O_2 stress, activation of PDC and ADH is a critical response. Another effect of low O_2 stress is the accumulation of lactic acid that lowers cytoplasmic pH and inhibits LDH activity. This fact further activates PDC and ADH, resulting in excessive ethanol biosynthesis, as discussed above. Boeckx et al. [23] and Botondi et al. [29] reported the accumulation of acetaldehyde and ethanol and the occurrence of alcoholic off-flavor in "Jonagold" apple and "Hayward" kiwifruit under the storage of ultra-low oxygen atmosphere. Ethanol accumulation has been reported as a low-O_2 stress biomarker during horticultural crop storage [40].

2.4. High CO_2 Stress. Optimal ranges of CO_2 levels in fruit tissue or the storage environment may regulate fruit quality [53]. However, each crop's sensitivity to elevated CO_2 injury varied according to genetic variation, resulting in different responses [54, 55]. For example, the storage atmosphere containing 20–30% CO_2 concentration resulted in maintaining the fruit firmness, ascorbic acid regulation, and titratable acidity level without deteriorating the flavor quality in several sweet cherry cultivars such as "Lapis," "Van," "Kristin," "Stella," "Sam," and "Huldra" [56, 57]. On the other hand, Cozzolino et al. [58] described the occurrence of
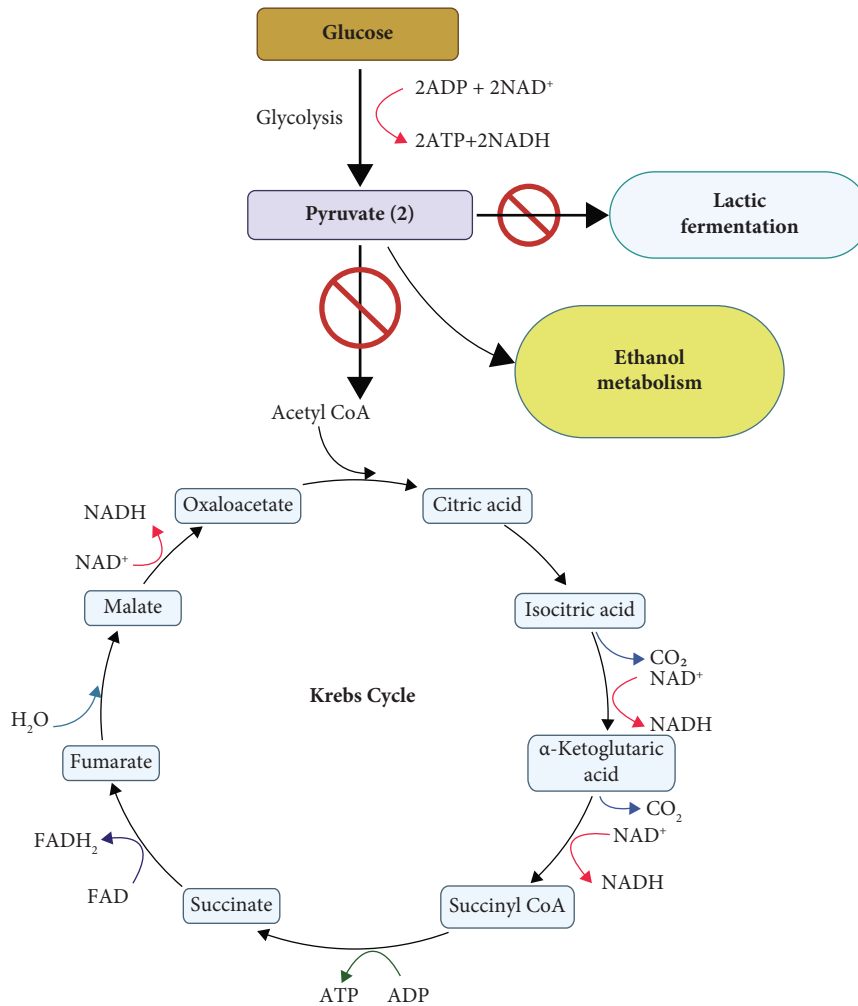
FIGURE 2: Fate of pyruvate flux under anaerobic respiration to ethanol fermentation.

off-flavor in sweet cherry cv. "Ferrovia" during storage based on the accumulation of fermentation metabolites under a 20% CO_2 storage atmosphere. The beneficial effects of increased CO_2 may inhibit respiration rate, ethylene biosynthesis, and N-assimilation in crop tissues, even while promoting carbohydrate synthesis [59–61]. In contrast, Lu et al. [62] reported the occurrence of an alcoholic off-flavor in satsuma mandarin fruit during storage in a modified atmosphere accompanied by a 15% CO_2 concentration. Harman and McDonald [63] also reported the effect of a storage atmosphere consisting of 14% CO_2 concentration on the "Hayward" kiwifruit for 16 weeks and noticed the development of the alcoholic off-flavor disorder. Surprisingly, the optimum flavor was retained when fruit was stored at a lower CO_2 concentration during storage. The off-flavor sensation was identified due to ethanol over-accumulation in "Bartlett" pears, tomatoes, and lettuce stored in an elevated CO_2 storage atmosphere [64–68]. The mango cultivar "R2E2" was similarly reported to have an alcoholic off-flavor disorder after being stored under 8% CO_2 rather than 6% CO_2 during the controlled storage atmosphere [69]. Similarly, the storage atmosphere of 10 kPa CO_2 produced less ethanol and acetaldehyde in mango fruit than the storage

atmosphere of 25 kPa CO_2 [70]. Wang et al. [71] evaluated the effect of modified atmosphere packing on the ethanol content of two sweet cherry varieties, "Lapins" and "Skeena," resulting in off-flavor disorder due to ethanol buildup in the 10% CO_2 storage atmosphere rather than the 8% CO_2 storage atmosphere. Forney et al. [72] reported the accumulation of ethanol in several blueberry cultivars (such as "Duke," "Aurora," "Brigitta," "Jersey," and "Liberty") under the storage condition of 25 kPa CO_2. The same findings were reported in the "Ottomanit" fig subjected to an elevated CO_2 atmosphere [73]. Alcoholic off-flavor was observed in the "Italia" table grapes stored in a high CO_2 (>20%) atmosphere [9]. Furthermore, increased expression of the ethanol metabolism-related gene *VvADH* was associated with increased accumulation of off-flavor aroma volatiles, including ethanol, in table grapes during storage under higher CO_2 conditions [74]. Overall, elevated CO_2 levels have mostly been associated with the deterioration of crop quality attributes, particularly flavor balance and sensory quality [75–79]. The overall impacts of O_2 and CO_2 stress conditions on ethanol metabolism-related metabolites, enzymes, and genes transcriptions in fresh fruits are summarized in Table 1.

TABLE 1: Effects of O_2 and CO_2 stress conditions on ethanol metabolism-related metabolites, enzymes, and genes transcriptions in fresh fruits.

O_2 and CO_2 stress conditions	Fruits	Effects on ethanol metabolism-related metabolites, enzymes, and genes	References
0.5 kPa O_2	"Empire" apple	Upregulated expression of ethanol metabolism-related genes *MdPDC2* and *MdADH1*	Park et al. [45]
20.9 kPa O_2	Apple (golden delicious, Jonagold, and kanzi)	Increased levels of acetaldehyde and ethanol	Wood et al. [51]
0, 0.5, 1 kPa O_2	"Jonagold" apple	Increased levels of PDC and ADH activities and enhanced acetaldehyde and ethanol contents	Boeckx et al. [23]
<0.5% O_2	"Hass" avocado	Increased PDC and ADH enzyme activities	Burdon et al. [46]
5% O_2	Mango	Increased levels of acetaldehyde and ethanol	Ntsoane et al. [43]
0.25% O_2	"Hayward" kiwifruit	Increased levels of acetaldehyde and ethanol	Botondi et al. [29]
20% CO_2	"Ferrovia" sweet cherry	Increased levels of acetaldehyde and ethanol	Cozzolino et al. [58]
15% CO_2	Mandarin	Increased levels of ethanol	Lu et al. [62]
8% CO_2	"Delta R2E2" mango	Increased levels of acetaldehyde and ethanol	Lalel and Singh [69]
10% CO_2	Sweet cherry (Lapins and Skeena)	Increased levels of ethanol	Wang et al. [71]
20 kPa CO_2	Blueberry	Increased levels of acetaldehyde and ethanol	Forney et al. [72]
>20% CO_2	"Italia" grapes	Increased levels of acetaldehyde and ethanol	Cefola et al. [9]
15 kPa CO_2	Table grapes	Upregulation of *VvADH* gene transcription	Maoz et al. [74]

O_2: oxygen; CO_2: carbon dioxide.

2.5. Storage Temperature Stress. An optimal storage temperature range is critical to maintaining fresh fruit quality and extending shelf life by reducing pathological and physiological deterioration [80]. The ideal temperature for each crop's storage varied depending on its origin or ripening behavior. Kader and Yahia [37] recognized the optimal temperature range of 20–24°C for the anticipated ripening of most harvested fruits. However, some fruits experienced alcoholic off-flavor disorder even at such temperature range (Table 2) along with others disorders such as freezing injury, heat injury, chilling injury, skin/flesh discoloration, softening, and AsA degradation [84, 85].

Studies were conducted on the effect of varied temperature environments on the alteration of volatile aromatic compounds in several fresh fruits. For example, Saberi et al. [81] noticed the alcoholic off-flavor in "Valencia" oranges at 20°C than 5°C during storage. Ali et al. [6] reported the alcoholic off-flavor occurrence in "Bruno" kiwifruit during storage at 24°C. Obenland et al. [82] reported a rapid decline in the sensory quality of "W. Murcott Afourer's" mandarins due to an excess of alcohols and ethyl esters, resulting in alcoholic off-flavor disorder at 20°C compared to 5°C and 10°C. Similarly, Yang et al. [18] also concluded that high temperatures have a deteriorative effect, particularly due to the enhanced biosynthesis of volatile aromatic compounds (primarily in ethanol) in banana fruit during storage at 30°C than 20°C. Furthermore, Petracek et al. [83] likewise reported an increase in ethanol content in sweet cherry (Prunus avium L., cv. "Sams") during storage at 20°C compared to storage at 5°C, 10°C, and 15°C, resulting in alcoholic off-flavor disorder. On the other hand, Zou et al. [86] demonstrated that lower storage temperatures ranging from 4°C to 10°C significantly impacted the transcript expression of genes ADH2, PDC1-like1, and PDC1-like2 in tomato fruit. In addition, the effects of storage temperature either on the accumulation or reduction of off-flavor compounds in a variety of fruits have been reported, including "Hort16A" kiwifruit [87], cantaloupe [88], strawberry [89], tomatoes [90], oranges [91], and nectarine [92].

3. Role of Physiological Mechanisms in Regulating Alcoholic Off-Flavor in Fresh Fruits

3.1. GABA Shunt Pathway. The GABA shunt pathway regulates many physiological mechanisms such as C : N balance, pH-stat, plant development, plant defense against insects, signal transduction, and osmoregulation [6, 93]. A short pathway generally metabolizes GABA via the TCA cycle that includes glutamate decarboxylase (GAD), GABA-transaminase (GABA-T), and succinate semialdehyde dehydrogenase (SSADH), called the GABA shunt pathway [94, 95], as depicted in Figure 3(a). So apart from GABA beneficial roles, its accumulation under stress is linked to various postharvest physiological disorders, including the incidence of pear fruit core breakdown [96], pear flesh and spathe browning [97, 98], reduced chilling tolerance in Natura zucchini fruit [99], and controlled atmosphere-related injury in "Honeycrisp" apples [100]. Enhanced GABA levels have also been linked to tomato surface pitting and soggy breakdown in "Honeycrisp" apples, respectively [101, 102].

Regarding alcoholic off-flavor disorder, Deewatthanawong et al. [103] found that lower GABA-T activity under high CO_2 storage conditions induced the synthesis and accumulation of alcoholic off-flavor compound ethanol along with GABA accumulation as a stress marker in response to a high CO_2 environment in the "jewel" strawberry cultivar. Moreover, Mae et al. [104] also reported an increase in GABA levels due to upregulated GAD and limited GABA-T gene expressions in tomatoes stored in a hypoxic atmosphere. According to the preceding discussion, the relationship between GABA accumulation is mostly similar to the results of low O_2/high CO_2 or anaerobic respiration, which resulted in an ATP deficit and reduced aerobic metabolic pathways. Interestingly, Deewatthanawong and Watkins [101] justified the interlinking of GABA enhancement with the accumulation of fermentation metabolites. Our previous research concluded that the GABA shunt pathway might initiate ethanol metabolism, thus possibly causing the alcoholic off-flavor disorder in kiwifruit cv. "Bruno" [6]. In Figures 3(b)–3(d), it has been shown that inhibited activity of the GABA-T enzyme from 12 days (d) to onward in control kiwifruit cv. "Bruno" appears to be directly linked to limited decarboxylation of GABA and thus shows a sign of suppressed GABA shunt pathway that impacts the functionality of the TCA cycle and thus leads to activation of PDC and ADH, resulting in oversynthesis or accumulation of acetaldehyde and ethanol contents. Our previous study noticed this relationship by using 1-methylcyclopropene (1-MCP) to reduce ethanol metabolism by regulating the GABA shunt pathway under reduced climacteric respiration, avoiding the occurrence of alcoholic off-flavor disorder in kiwifruit during storage [6]. However, limited research has been conducted to investigate the GABA shunt pathway concerning ethanol fermentation, suggesting the need for an integrated approach to analyzing GABA shunt pathway-related gene expression, protein level, and involved metabolites at transcriptomic, proteomics, and metabolomics levels further to reveal the GABA shunt influence on ethanol fermentation.

3.2. Mitochondrial Energy Metabolism. The cell mitochondria are a primary site for maintaining the ATP or energy status pool required for regulating the plant's physiological or biochemical reactions [105, 106]. The mitochondrial energy status is closely related to the activities of energy metabolism-related enzymes, including succinic dehydrogenase (SDH), cytochrome C oxidase (CCO), H^+-adenosine triphosphatase (H^+-ATPase), and Ca^{2+}-adenosine triphosphatase (Ca^{2+}-ATPase) [12]. Previously, decreased ATP and energy charge (EC) in various fruits were adversely associated with several physiological disorders i.e., chilling injury [107], tissue, pericarp, or peel browning [108], skin pitting [109], and ethanol accumulation or alcoholic off-flavor disorder [12, 19, 95]. An energy deficit occurs due to dysfunctional mitochondrial energy metabolism at the cellular level [19, 77].

TABLE 2: Effects of storage temperature stress on ethanol metabolism-related metabolites in fresh fruits.

| Storage temperature (°C)	Fruits	Effects on ethanol metabolism-related metabolites	References
20	"Valencia" oranges	Increased ethanol contents	Saberi et al. [81]
24	"Bruno" kiwifruit	Increased levels of acetaldehyde and ethanol	Ali et al. [6]
20	"W. Murcott Afourer's" mandarins	Increased levels of ethanol contents	Obenland et al. [82]
30	Banana	Increased levels of ethanol contents	Yang et al. [18]
20	Sweet cherry	Increased levels of ethanol contents	Petracek et al. [83]

(a)

(b)

(c)

(d)
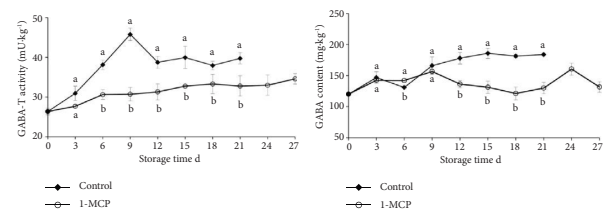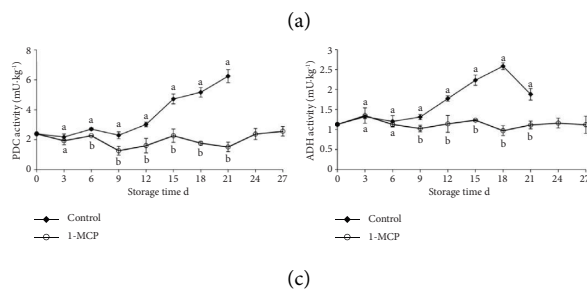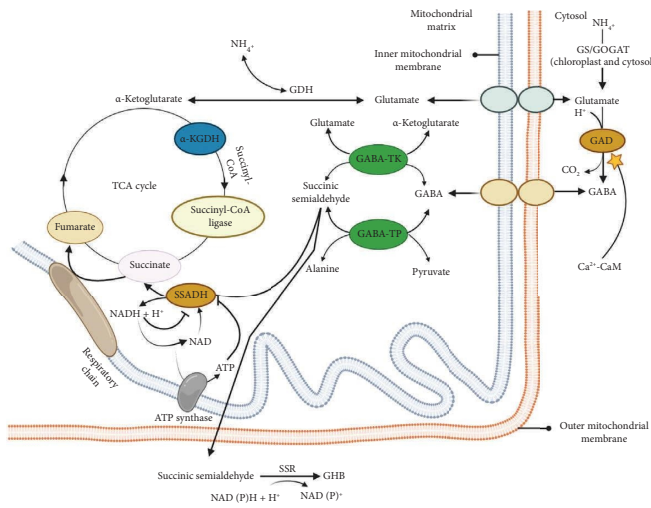
FIGURE 3: GABA shunt pathway and its possible correlation to ethanol (reprinted with permission: [6, 94]. (a) The GABA shunt pathway. (b) The GABA-T activity and GABA contents. (c) Pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH) activities. (d) Acetaldehyde and ethanol contents).

In agreement, our previous study concluded a possible correlation between dysfunctional mitochondrial energy metabolism with reduced SDH, CCO, H^+-ATPase, and Ca^{2+}-ATPase activities with upregulated ethanol metabolism [12]. Moreover, Cukrov et al. [39] also reported the occurrence of alcoholic off-flavor in kiwifruit due to downregulated mitochondrial energy metabolism during storage. Consequently, Zhang et al. [110]; Huan et al. [19]; and Blanch et al. [77] further coincided with the susceptibility of alcoholic off-flavor disorder incidence under the same circumstances in strawberry and kiwifruit during storage.

3.3. Glycolysis and TCA Cycle. Glycolysis and the TCA cycle are the central respiratory pathways in horticultural crops. These pathways are involved in maintaining the ripening or senescence processes by regulating the energy status, carbon flux, NAD(P), and NAD(P)H levels through sequential cell reactions [111]. However, research has revealed that such respiratory pathways exhibit considerable variation under different conditions. The glycolysis ended up with pyruvate formation that acts as a primary substrate for the first enzyme of the TCA cycle, pyruvate dehydrogenase (PDH), and ethanol fermentation (PDC) [11, 12]. Meanwhile, the concentration and fate of pyruvate either in the TCA cycle or ethanol fermentation are profoundly influenced by a high CO_2/low O_2 atmosphere or anaerobic metabolism. For example, Ummarat et al. [11] concluded that the off-flavor sensation caused by the over-accumulation of ethanol correlated with enhanced pyruvate content in "Pixie" mandarin during an anaerobic atmosphere generated by waxing. Interestingly, it has been reported that enhanced pyruvate is preferred for alcoholic fermentation over the TCA cycle in anaerobic respiration [112]. Mannucci et al. [113] reported that anaerobic metabolism eventually

converts pyruvate to acetaldehyde and ethanol, suggesting that pyruvate and ethanol contents are critically interlinked under stress conditions.

The increase or accumulation of glycolytic flux is interlinked with the enhanced activity of pyruvate kinases (PKs) or suppressed activities of TCA cycle enzymes that are eventually indicated by the accumulation of TCA cycle organic acid [12, 21, 114]. The functional TCA cycle is vital in generating a vast pool of ATP for regulating the cell metabolic mechanisms via oxidative phosphorylation or electron transport chains to maintain the desired ripening processes of horticultural crops [115–117]. Meanwhile, the TCA cycle has been reported to be replaced by glycolysis, which directs pyruvate to ethanol metabolism to generate sufficient ATP to keep cell functions alive under hypoxic conditions [12, 118, 119]. A number of previous research reported that ethanol metabolism occurs under stressed conditions as a result of a malfunctioned TCA cycle, which is associated with suppressed PDH, SDH, and GABA-T enzyme activities as well as increased levels of organic acids such as citric acid, succinic acid, and GABA content [12, 26, 120–122].

3.4. Cytosolic Malate Metabolism.

In plants, malate is important in regulating the cytoplasmic pH, cell acidity, and carbon metabolism. Malate is synthesized by converting the phosphoenol-pyruvate (PEP) into oxaloacetate (OAA) by the activities of cytosolic enzymes, including phosphoenol-pyruvate carboxylase (PEPC) and NAD-linked malate dehydrogenase (NAD-MDH) [33]. It has been demonstrated that both OAA and malate can enter the mitochondrial TCA cycle to generate numerous organic acids. Malate can also be converted to pyruvate by the cytosolic NADP-linked malic enzyme (NADP-ME) via a dicarboxylate carrier [123].

Little research has been done into the possible link between cytosolicmalate metabolism and ethanol metabolism. In a recent study, Huan et al. [21] reported the promising involvement of higher expression of NADP-dependent malic enzymes (NADP-MEs) in increased ethanol production that eventually develops an alcoholic off-flavor in kiwifruit cv. "Bruno" during ambient storage conditions. Malate metabolism has previously been shown to induce ethanol metabolism by converting stored malate into pyruvate under various atmospheric conditions in harvested fruit such as grapes, berries, and strawberries [20, 123]. In contrast, Ponce-Valadez and Watkins [33] found a discrepancy between ethanol metabolism-related metabolites and enzymes involved in cytosolic malate metabolism. However, more omics-based research is needed to validate the role of cytosolic-malate metabolism in causing alcoholic off-flavor. A proposed schematic diagram of the relationship between cytosolic malate and ethanol metabolism is depicted in Figure 4.

3.5. Starch and Sugar Metabolism.

Fruits primarily convert their starch stores into sugars as their primary energy source [124]. The flavor of ripe fruit is largely determined by the number of soluble sugars that accumulate during ripening [125]. Cultivars differ significantly in starch degradation and sugar composition at various stages of fruit development and ripening [126]. The starch in starch-based crops reportedly needs to be converted into simple sugars before it can be fermented into ethanol [127]. Previous research has indicated that sugars might be the most important substrates utilized by ethanol fermentation during fruit ripening [128]. β-amylase plays a crucial role in carbohydrate metabolism by depolymerizing α-glucan chains, thereby facilitating starch degradation during fruit ripening [129, 130], as evidenced in blueberries, as starch content drops at the same time as the rise in β-amylase gene expression [131]. It has been shown that the conversion of mango fruit starch to soluble sugars occurs simultaneously when the anaerobic respiration pathway is initiated [132]. Therefore, elevated starch degradation to sugars phenomenon may affect the biosynthesis of ethanol metabolism metabolites, which could initiate an off-flavor due to the over production and accumulation of ethanol content under anaerobic respiration.

Regarding this, Huan et al. [21] revealed that starch-to-sucrose metabolism (starch degradation) might induce alcoholic off-flavor disorder in "Bruno" kiwifruit during postharvest storage based on the findings associated with a dramatic decline in starch contents coincided with increased sucrose, fructose, and glucose levels accompanied with enhanced acetaldehyde and ethanol contents along with higher expressions of key genes such as starch phosphorylases (SPs), beta-amylases, UDP-glucose pyrophosphorylases (UGPases), sucrose synthases (SSs), and invertases (INVs) which are responsible for accelerating starch conversion to soluble sugars. This study provided transcriptome evidence that increased starch catabolism during fruit ripening may function as a substrate to promote ethanol fermentation, which induces an alcoholic off-flavor.

4. Measures to Control Alcoholic Off-Flavor Disorder Based on Changes in Ethanol Metabolism

4.1. Chemical Treatments.

Numerous chemical treatments have been studied and applied to various fresh fruits to eradicate the susceptibility of alcoholic off-flavor disorder via suppressing the ethanol metabolism in both pre- and postharvest stages. Our recent study indicates that 1-MCP ($1 \mu L \cdot L^{-1}$) treatment significantly reduced the occurrence of alcoholic off-flavor disorder in kiwifruit during storage at ambient conditions via inhibiting the ethanol metabolism-related enzymatic activities of PDC and ADH [12]. Subsequently, Huan et al. [133] also reported that $1 \mu L \cdot L^{-1}$ 1-MCP treatment could effectively reduce the alcoholic off-flavor disorder by suppressing ethanol metabolism in kiwifruit during ambient storage. Thewes et al. [134] concluded that applying 1-MCP together with dynamic controlled atmosphere (DCA) was particularly effective in lowering acetaldehyde and ethanol biosynthesis in apple fruit. Such findings were correlated with reduced PDC and
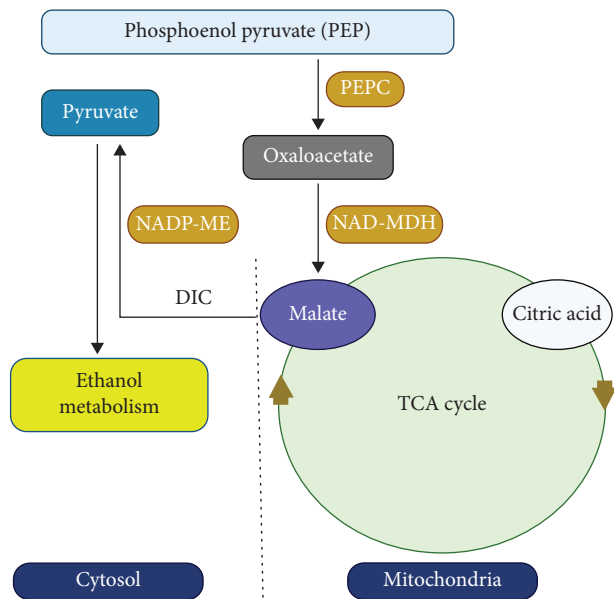
FIGURE 4: Correlation of cytosolic-malate metabolism to ethanol metabolism (PEPC: phosphoenol pyruvate carboxylase; NAD-MDH: NAD-linked malate dehydrogenase; NADP-ME: NADP-dependent malic enzyme; DIC: dicarboxylate carrier).

ADH activity in apples, except during the mature stage, regardless of the cultivar. The lower levels of acetaldehyde and ethanol contents were also noticed in "Galaxy" apples under the effect of 1-MCP treatment and a dynamically controlled atmosphere based on respiratory quotient [135]. It has also been observed that 1-MCP could substantially lower the expression of *PDC2* and *ADH*, reducing acetaldehyde and ethanol synthesis in apple fruit [136].

Recently, Lv et al. [22] demonstrated that exogenous application of $100 \, \mu mol \cdot L^{-1}$ nordihydroguaiaretic acid (NDGA) on "Nanguo" pear fruit resulted in lower acetaldehyde and ethanol contents concomitant with downregulated expressions of *PDC1, ADH1,* and *ADH2* genes. Our previous work also suppressed the ethanol metabolism via preharvest spraying of $5 \, mmol \cdot L^{-1}$ oxalic acid (OA), which resulted in the absence of alcoholic off-flavor disorder in kiwifruit "Bruno" during storage under ambient conditions [32]. In another study, Zhang et al. [137] demonstrated that fumigation with $10 \, \mu mol \cdot L^{-1}$ carbon monoxide (CO) on the winter jujube might restrain the ethanol metabolism-related metabolites (acetaldehyde and ethanol) under reduced PDC and ADH activities. Li et al. [17] reported that treating strawberries with 1 mM ATP in a 20% CO_2 storage atmosphere reduced acetaldehyde and ethanol over-accumulation (72% and 75% lower in ATP + CO_2-treated fruit, respectively) that was linked to lower PDC and ADH activities during fruit storage. In a recent study, the effects of melatonin on ethanol metabolism in kiwifruit were also investigated, resulting in reduced acetaldehyde and ethanol

contents under suppressed PDC and ADH activities and downregulated expressions of potential genes such as *AdADH1, AdPDC1,* and *AdPDC2* during storage [138]. These changes may eventually result in decreased synthesis of aromatic compounds such as acetaldehyde and ethanol, thus controlling the alcoholic off-flavor disorder in fresh fruits during storage.

4.2. Hypobaric and Other Treatments. Several studies have found that hypobaric treatments can help suppress or delay various physiological disorders in fresh fruits. To suppress the alcoholic off-flavor disorder, Huan et al. [19] reported the significant effects of hypobaric treatment (25 ± 5 kPa for 30 min/twice treatment) in alleviating the alcoholic off-flavor disorder by inhibiting the activities of PDC and ADH in kiwifruit during storage. Previously, it had been demonstrated that fresh fruits could reduce the occurrence of alcoholic off-flavor by reducing the ethanol metabolism metabolites during storage under modified super-atmospheric O_2 exposure [44, 139]. Similarly, Wood et al. [51] observed a decrease in acetaldehyde and ethanol levels under controlled storage conditions (O_2 kPa^{-1} CO_2 $kPa^{-2.5}$) for "Golden Delicious" and "Jonagold" apple fruit. Furthermore, Chen et al. [140] reported the decrease in ethanol and acetaldehyde production in "Benihoppe" strawberries under low oxygen application (2 kPa O_2) during storage. Zuo et al. [141] investigated the effects of high relative humidity (RH: $98 \pm 2\%$) on ethanol metabolism in zucchini fruit, identifying that it inhibited the activities of PDC and ADH, as well as *CpPDC1* and *CpADH1* gene transcripts, resulting in decreased acetaldehyde and ethanol levels during cold storage. Previously, certain coating formulations were reported to initiate ethanol metabolism, resulting in off-flavor disorder in various fruits due to a change in the internal gas atmosphere of the fruit.

Meanwhile, a recent study showed that Carnauba wax nano-emulsion (attributed to being an effective moisture barrier and relatively permeable to gases) as a coating material had the least impact on the occurrence of alcoholic off-flavor by avoiding the production of ethanol above the threshold level in citrus fruit during storage [142]. Moreover, Velazco et al. [143] also concluded that Brillaqua_{F6} (18% solids (9.35% oxidized polyethylene wax and 5.7% shellac)), Citrosol_{AK} (18% solids (Carnauba E903 and shellac)), and Teycer_{GLK} (18% solids (Carnauba and shellac)) coatings on citrus fruit had promising effects about reduced acetaldehyde and ethanol contents, thus decreasing the susceptibility to alcoholic off-flavor disorder. The overall impacts of chemical, hypobaric, and other treatments on ethanol metabolism to suppress the alcoholic off-flavor disorder in fresh fruits are summarized in Table 3.

TABLE 3: Effects of treatments to control the ethanol metabolism to overcome alcoholic off-flavor disorder in fresh fruits.

Treatments	Fruits	Effects on ethanol metabolism to control alcohol off-flavor	References
1-MCP (1.0 $\mu L \cdot L^{-1}$)	"Bruno" kiwifruit	Reduced acetaldehyde and ethanol biosynthesis via suppressing the PDC and ADH enzymatic activities	Ali et al. [6]
1-MCP (0.625 $\mu L \cdot L^{-1}$ and 1.0 $\mu L \cdot L^{-1}$) + DCA-RQ1.5	Apple (galaxy, fuji, and pink lady)	Restrained the ethanol metabolism	Thewes et al. [134]; Anese et al. [135]
1-MCP (1.0 $\mu L \cdot L^{-1}$)	"Golden delicious" apple	Reduced transcriptomic expression of *PDC2* and *ADH* genes	Yang et al. [136]
NDGA (100 $\mu mol \cdot L^{-1}$)	"Nanguo" pear	Reduced acetaldehyde and ethanol contents concomitant with downregulated expressions of *PDC1*, *ADH1*, and *ADH2*	Lv et al. [22]
OA (5 mmol·L^{-1})	"Bruno" kiwifruit	Reduced acetaldehyde and ethanol contents	Ali et al. [32]
CO (10 $\mu mol \cdot L^{-1}$)	Winter jujube	Restrained the ethanol metabolism	Zhang et al. [137]
ATP (1 mM)	Strawberry	Restrained the ethanol metabolism	Li et al. [17]
Melatonin (100 $\mu mol \cdot L^{-1}$)	"Bruno" kiwifruit	Reduced acetaldehyde and ethanol contents and downregulated expressions of potential genes including *AdADH1*, *AdPDC1*, and *AdPDC2*	Cheng et al. [138]
1-MCP (0.5 $\mu L \cdot L^{-1}$) and storage temperature (4°C–10°C)	Tomato	Lowered transcript expression of genes *ADH2*, *PDC1-like1*, and *PDC1-like2*	Zou et al. [86]
Hypobaric atmosphere (25 ± 5 kPa for 30 min)	"Bruno" kiwifruit	Restrained the ethanol metabolism	Huan et al. [19]
Coating (Carnauba wax)	Citrus	Prevented the above threshold level biosynthesis of ethanol	Miranda et al. [142]
Coatings (Brillaqua$_{F6}$, Citrosol$_{AK}$, and Teycer$_{GLK}$)	Citrus	Reduced the production of acetaldehyde and ethanol contents	Velazco et al. [143]
High relative humidity (RH: 98 ± 2%)	Zucchini	Decreased acetaldehyde and ethanol levels under inhibited activities of PDC and ADH enzymes and *CpPDC1* and *CpADH1* gene transcripts	Zuo et al. [141]
O_2 (2 kPa)	"Benihoppe" strawberries	Reduced acetaldehyde and ethanol contents	Chen et al. [140]

1-MCP: 1-methylcyclopropene; NDGA: nordihydroguaiaretic acid; OA: oxalic acid; CO: carbon monoxide; ATP: adenosine triphosphate; O_2: oxygen.
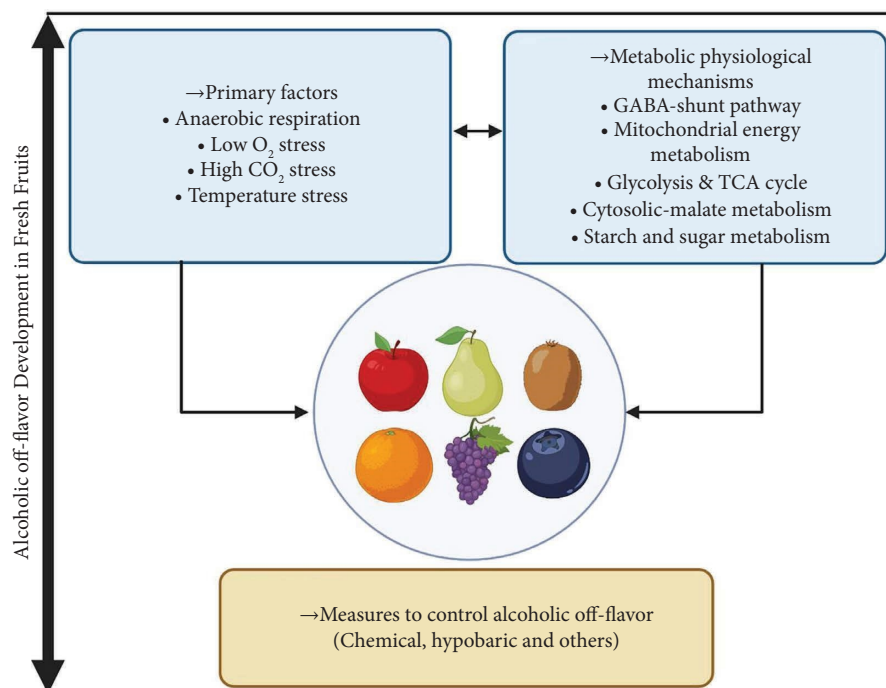
Figure 5: Alcoholic off-flavor causing factors, regulating metabolic physiological mechanisms and its control measure.

5. Conclusion and Future Work

Anaerobic respiration, low O_2 stress, high CO_2 stress, and storage temperature stress are the most important factors for inducing alcoholic off-flavor disorder by upregulating ethanol metabolism in fresh fruits. These factors further cause undesirable metabolic changes at cellular levels by altering physiological mechanisms such as the GABA shunt pathway, mitochondrial energy metabolism, glycolysis and TCA cycles, cytosolic-malate metabolism, and starch and sugar metabolism. These physiological metabolic mechanisms might further activate ethanol metabolism, resulting in over-biosynthesis and the accumulation of alcoholic off-flavor-related metabolites such as acetaldehyde and ethanol in fresh fruits. Several chemicals, hypobaric, and coatings treatments have been practiced to overcome alcoholic off-flavor disorders in fresh fruits during storage. Despite this, a wide research gap still prevails that needs further investigation at the omics level to evaluate or validate the impact of numerous physiological mechanisms on ethanol metabolism and reveal the detailed mechanistic relation. In addition, other mechanisms and factors, including respiratory mechanisms, fruit genetic makeup, degree of maturity, and postharvest handling and storage conditions, are also recommended for future work concerning the alcoholic off-flavor disorder in fresh fruits during storage. The overall thematic scheme representing the current review is shown in Figure 5.

Data Availability

The dataset supporting the conclusions of this article is included within the article.

Conflicts of Interest

The authors declare that there are no conflicts of interest.

Authors' Contributions

Maratab Ali conceptualized the study and wrote the original draft. Sara Batool, Muhammad Faisal Manzoor, Rana Muhammad Aadil, and Xiuming Zhao wrote, reviewed, and edited the article was responsible for writing and review and editing. Nauman Khalid and Fujun Li performed visualization and wrote, reviewed, and edited the paper. Xiaoan Li was responsible for validation, writing, reviewing, and editing. Xinhua Zhang was responsible for conceptualization, writing and review, editing, funding, and supervision.

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