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Review

Potential application and mechanism of hexanal in extending shelf life and safety of tropical fruits: A systematic review

[1]Nur, P. S., [1]Azhar, A. H., [1]*Pak-Dek, M. S., [1]Ramli, N. S., [1]Rukayadi, Y., [1]Jaafar, A. H., [2]Misran, A., [3]Mohd Rafdi, H. H., [4]Hussin, M., [5]Mohd-Zainudin M. A. and [6]Mediani, A.

[1]*Department of Food Science, Faculty of Food Science and Technology, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor, Malaysia*
[2]*Department of Crop Science, Faculty of Food Science and Technology, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor, Malaysia*
[3]*School of Fisheries and Food Science, Universiti Malaysia Terengganu, 21030 Kuala Nerus, Terengganu, Malaysia*
[4]*Food Science and Technology Research Centre, Malaysian Agricultural Research and Development Institute, MARDI Headquarters, Persiaran MARDI-UPM, 43400 Serdang, Selangor, Malaysia*
[5]*Department of Chemistry, Faculty of Engineering Technology, Universiti Malaysia Perlis, 02600 Arau, Perlis, Malaysia*
[6]*Institute of Systems Biology, Universiti Kebangsaan Malaysia, 43600 UKM Bangi, Selangor, Malaysia*

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Abstract

Post-harvest losses of tropical fruits have profound implications for food security and food safety. Hexanal has demonstrated high efficacy in reducing post-harvest losses, and extending the shelf life of temperate fruits. The protective effects of hexanal on tropical fruits are limited. The present review investigated the influence of hexanal treatment on the extension of shelf life in tropical fruits. A systematic review was conducted to collate existing data pertaining to hexanal treatment, its impact on the shelf life and safety of tropical fruits, and its potential mechanism of action. Literature was examined *via* electronic databases such as Google, Google Scholar, PubMed, and SCOPUS, spanning the period from 2012 to 2024. The findings revealed that hexanal application, at both pre- and post-harvest, had the potential to extend the shelf life, and enhance the safety of tropical fruits. Hexanal exhibits favourable effects on the physicochemical and microbial parameters during fruit storage. It was found that the effectiveness of hexanal treatment varies across species. To date, there is insufficient evidence that differentiates between tropical and temperate fruits in response to hexanal. It is suggested that the mode of action of hexanal in extending the shelf life is by affecting the calcium ion channel generating calcium signalling, subsequently inhibiting the expression of ripening-related genes such as phospholipase D. Hexanal implementation showed promising result for prolonging fruit shelf life. The transcriptomic and metabolomics studies provided information on how ripening is regulated, which is important for future shelf-life improvement through gene modification.

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Introduction

Tropical fruit production is one of the significant industries in most developing countries, and their substantial contributor to the Gross Domestic Product (GDP). From the nutritional point of view, these fruits contribute to meeting the nutritional requirement as fresh fruits possess a unique nutritional profile. Asian continent is one of the significant producers of tropical fruits, and can be considered a cradle for agricultural production. Asian tropical fresh produces such as mango, durian, jackfruit, guava, starfruits, papaya, and banana possess a unique position in the world of fruits. The international demand for these fruits is increasing at a great speed annually. However, tropical fruits are a

*Corresponding author.
Email: mhdsabri@upm.edu.my

highly perishable product, and have faster spoilage, thus leading to a high rate of post-harvest losses. These matters become a global challenge to be addressed since it causes huge economic losses estimated at billions of dollars annually. The losses are more prominent in under-developed and developing countries compared to developed countries. This happened due to developing countries having a wide range of issues related to post-harvest handling and management that need to be considered to reduce the losses (Rick *et al.,* 2010). Tropical fruits tend to have higher respiration rate due to higher temperature of tropical climate, thus leading to faster ripening and shorter shelf life (Ho *et al.,* 2018). Higher sensitivity to cold storage may cause tropical fruits to be more prone to chilling injuries such as durian (Sonkaew *et al.,* 2023). In addition, warmer climate increases the risk of fungal and bacterial infections on the tropical fruits. Poorer regions in tropical climate countries face problems on high cost of transportation and infrastructures such as cold storage facilities. Therefore, tropical fresh produces face unique challenges compared to temperate fruits. It is thus crucial to identify an effective solution to prevent the losses, and to make a significant contribution to the public health and economy of Asian countries.

The losses of tropical fruits happen due to several physiochemical changes during storage which affect the quality parameters of the fruits. The physical, chemical, biological, and environmental factors are correlated with post-harvest deterioration (Yahaya and Mardiyya, 2019). Many techniques have been developed to reduce post-harvest losses of fresh produces. The techniques from pre- and few post-harvest management systems are available to minimise the losses. For example, improvement of the storage condition can be used to minimise microbial invasion to improve the shelf life of fruits (Samarawickrama *et al.,* 2018). Besides, a wide range of post-harvest treatments such as edible coating, modified atmosphere packaging (MAP), gamma irradiation, and application of different active organic compounds have been practiced to minimise post-harvest losses. The application of organic treatments to reduce post-harvest losses is common in developed countries. For example, several studies have reported on hexanal application for enhancing the shelf life of temperate fruits. However, the application of hexanal treatment in extending the shelf life and quality of tropical fruits is limited. The organic treatment like hexanal for reducing post-harvest losses of tropical fruits may have a huge possibility in the food industries of Asia.

The United States Food and Drug Administration considers hexanal (C-6 aldehyde), which is naturally generated by the lipoxygenase pathway in plants, to be a safe food additive (Thavong *et al.,* 2011). The natural volatile component is found to have a potent antimicrobial agent, and also commercially available. Hexanal has also been approved as one of the ingredients for several food productions. Unlike hexanal, 1-methylcyclopropene (1-MCP) is a synthetic compound which competes with ethylene to bind to the ethylene receptors. Despite the safety of 1-MCP being widely reported, the long-term effects on environment and human health remain a concern. Hexanal treatment is cheaper and easier to apply compared to other post-harvest techniques such as freezing, modified atmosphere packaging, and irradiation techniques. The dual properties of hexanal as antimicrobial and shelf-life enhancer, as well as having lower production cost, offer more advantages over other compounds such as essential oils, calcium chloride, methyl jasmonate, and salicylic acid. Hexanal also reduces post-harvest losses, and enhances shelf life of fruits and vegetables. The studies and practical implementation of hexanal treatment to reduce post-harvest losses of temperate fruits such as cherry, berry, peach, and apple are extensive in comparison with the tropical fruits such as mango, banana, durian, and jackfruit. The source of information and studies on post-harvest technology of tropical fruits are also limited (Underhill and Kumar, 2018).

The objectives of the present review were to collate the data and evidence of the effective use of hexanal on tropical fruits, and to give a recommendation for using the potential treatment to minimise the post-harvest losses of tropical fruits. The present review also compared the effectiveness of hexanal treatment between tropical and temperate fruits in providing safety during the storage.

Materials and methods

Protocol

The present systematic review was conducted on research works which evaluated the effective use of hexanal treatments on tropical fruits until 2024. The research works reported for temperate fruits were also reviewed for comparison with tropical fruits from 2012 to 2024 publication year. The criteria chosen to represent data in the selected studies were objectives, related problems, collected data, and evaluation. The illustration of the findings was performed following the Preferred Reporting Items for Systematic Review and Meta-Analysis (PRISMA) guidelines (Figure 1). The publication duration from 2012 to 2024 was selected for the present review. In order to obtain the entire necessary information, electronic databases such as Google, Google Scholar, PubMed, and SCOPUS were used. The related research works entitled "Effective use of hexanal treatment" which were available in English language were primarily selected for analysis. The inclusion criteria were articles related to hexanal in extending shelf life and safety of tropical fruits, articles using English language, and articles available in free full text. In order to increase on the numbers of selected articles, for the first step of selection, all related articles were selected. In the next step, articles not available in the free full text version were excluded. After that, the abstract and title of the selected articles were carefully studied, the eligible parameters were selected, and the rest were all excluded.

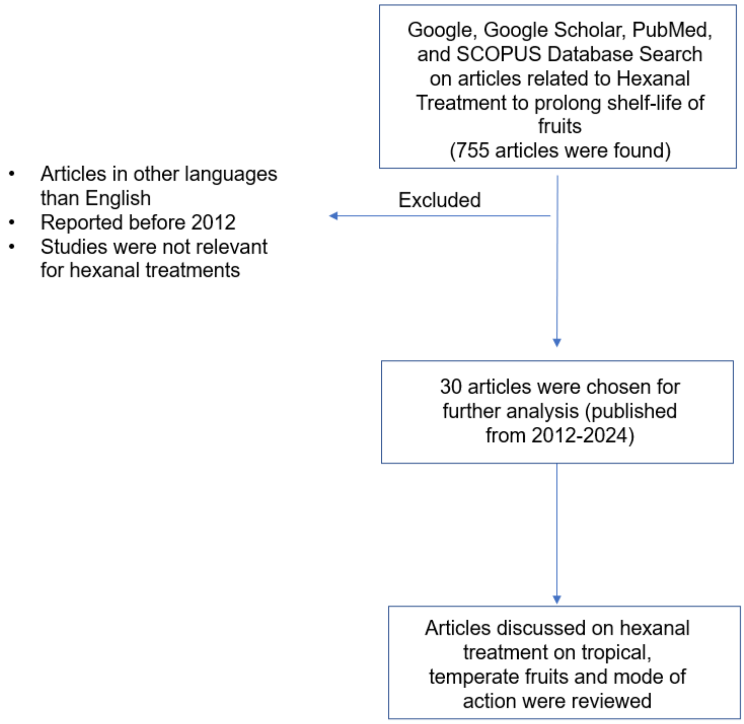

Figure 1. PRISMA flow chart for study selection process.

Search strategy

In the present review, the analysis was conducted to determine the potential use of hexanal in extending the shelf life and safety of tropical and temperate fruits. Studies related to the keyword published between 2012 and 2024 were analysed to meet the research questions. Different scientific databases Google, Google Scholar, PubMed, and SCOPUS were used. The systematic review was organised and reported following the PRISMA guidelines. The expected outcomes of the present review would answer these questions: (1) what is the effect of hexanal treatment on tropical fruits?; (2) is hexanal treatment effective enough to provide physicochemical and microbial safety to tropical fruits during storage?; and (3) what are the differences in the effectiveness of hexanal treatment between tropical and temperate fruits?

Inclusion and exclusion criteria

In general, the studies based on the following eligibility criteria were selected for analysis. First, the papers related with the effectiveness of hexanal treatments on different tropical fruits. Second, the papers were in English. Third, the papers were available for free, full-text, and original. In order to improve comprehensiveness, studies from different sources were evaluated. The most completed papers were selected if there were available different studies related to the topic. The exclusion criteria were the articles in other languages than English, the studies were reported prior to 2012, and the studies were not relevant for hexanal treatments on tropical fruits.

Results and discussion

At the beginning of the research, 755 articles were found, and after analysing the title and abstract, and removing repetitive documents, 34 were reviewed. Finally, 30 articles were chosen for further analysis. The scientific evidence showed that hexanal effectively reduced post-harvest losses, and provided safety.

Different hexanal treatments have been developed to reduce post-harvest losses, and their practicality has been proven on several fresh produces (Table 1). Pre- and post-harvest treatments of hexanal treatments were found to be effective in increasing the fruits' retention time and enhancing their shelf life under different storage conditions. The application of hexanal formulation, whether at pre- or post-harvest, was similarly effective in improving physicochemical properties such as firmness, titratable acidity, and weight loss during storage (Table 2).

Hexanal possesses a strong antimicrobial capacity. It has been successfully investigated that hexanal treatment has strong effectiveness against common microorganisms in tropical fruits. Table 3 lists the practical evidence of hexanal antimicrobial capacity that has successfully reduced post-harvest disease incidence in tropical fruits.

Mode of action of hexanal

Recently, the use of hexanal has been conducted to evaluate its efficacy in prolonging the shelf life of tropical fruits. The application of different hexanal treatments, both pre- and post-harvest, was found to be effective in delaying the fruits' retention time, and also successfully enhancing the shelf life and safety of the fruits (Figure 2). By inhibiting the phospholipase D (PLD) enzyme activity, hexanal is able to slow down the degradation of the cell membrane, which can increase the fruit retention time and shelf life. It is also able to act as a flavour enhancer. Treated fruits were found to have higher firmness, better colour, texture, and other important sensory attributes than in control fruits. Other physicochemical characteristics such as total soluble solids, total sugar, and ascorbic acid contents were higher in treated fruits than in control fruits under different storage conditions. The total titratable acidity was found to be lower in treated fruits than in control fruits. Hexanal was proven to have strong antifungal activity; it has huge potential in extending the shelf life by reducing post-harvest disease incidences. Different treatments of hexanal and their effectivity on tropical fruits' physicochemical characteristics and microbial loads are also shown in Figure 2.

The transcriptomics study of hexanal-treated apple (*Malus domestica* Borkh) showed the differential expression of 726 genes compared to the control. The genes involved in cell wall degradation, and abscisic acid (ABA) and ethylene biosyntheses were downregulated. Meanwhile, the receptor genes (*ETR2* and *ERS1*) and gibberellic acid (GA) biosyntheses were upregulated. It was also stated that hexanal may delay fruit abscission by reduction of ABA through ethylene inhibition (Sriskantharajah *et al.,* 2021). The study focussed on the effects of hexanal on the transcriptomics of fruit abscission zone (FAZ) at commercial maturity. The effects of hexanal treatment on other tissues at different development stages were unclear. It remains unknown whether the result observed was caused by hexanal alone or developmental stage effect. In addition, the effect of the upregulation of gene related to GA biosynthesis, and signalling on the fruit abscission and retention were not clearly explained. Although various studies have reported that hexanal is a potent PLD inhibitor, the downregulation of PLD expression was not explained in that study.

In banana (*Musa acuminata* Colla), similar observation reported in apple was observed in which the hexanal treatment inhibited the expression of genes involved in the biosyntheses of ethylene, aminocyclopropane-1-carboxylic acid oxidase (ACO), and cell wall degradation (polygalacturonase, endo-β-1,4-glucanase, and expansins) enzymes (Yumbya *et al.,* 2021; Sriskantharajah *et al.,* 2021). This suggested the mode of action of hexanal through the inhibition of ethylene biosynthesis and cell wall degradation.

Hexanal-treated raspberry (*Rubus* spp.) showed potential role of hexanal affecting calcium-binding proteins (El Kayal *et al.,* 2017). Calcium-binding protein acts as a sensor to detect the changes of intracellular calcium level. The expression of calmodulin-binding transcription activators was altered in hexanal-treated raspberry. Significant increases in cAMTA3 and cAMTA5 at late development stage were observed in hexanal-treated

Table 1. Effectiveness of hexanal treatments on shelf-life of tropical and temperate fruits using qualitative measurement.

Fresh produce	Pre- or post-harvest treatment method	Shelf-life extension	Reference
Banana (*Musa acuminata* Colla)	Post-harvest dip at ambient and cold temperatures	6 - 9 days	Venkatachalam *et al.* (2018)
	Pre-harvest spray and post-harvest dip (5 min, 25 ± 1°C, RH 60 ± 5%)	9 days	Yumbya *et al.* (2019)
	Post-harvest (13.5 ± 2°C)	21 days	Samarawickrama *et al.* (2018)
	Post-harvest dip (2% hexanal for 5 min)	24 days	Yumbya *et al.* (2021)
	Pre-harvest spray EFF sprays at 1.6 mM (14 ± 2°C; RH 85 - 90%)	36 - 40 days	Anusuya *et al.* (2016)
	Post-harvest dip in aqueous hexanal (0.02%) (13°C for 3 min)	28 days	Silué *et al.* (2022)
	Pre-harvest spray (0.02%) twice at 15 and 30 days before harvest (13°C)	20 days	Preethi *et al.* (2021)
Mango (*Mangifera indica* L.)	Post-harvest application of hexanal (1.0%) + hot water treatment, shelf-life studies at 12°C and 85 - 90% RH	35 days	Darshan *et al.* (2024)
	Post-harvest application of encapsulated hexanal using β-cyclodextrin, poly(vinyl alcohol), and poly(lactic-co-glycolic) acid matrices	23 days	Sundaram *et al.* (2024)
Figs (*Ficus carica* L.)	Post-harvest application of hexanal vapour (0.02%), shelf-life studies at 4 ± 1°C, 90% RH	18 days	Öz and Ali (2023)
	Post-harvest of hexanal (500 ppm + carbendazim 500 ppm + Tween 80) (12 ± 2°C; RH 80 - 85%)	27 days	Thakur *et al.* (2017)
	Post-harvest dip (2% hexanal for 5 min)	15 days	Hutchinson *et al.* (2018)
Papaya (*Carica papaya* L.)	Pre-harvest hexanal double spray (2%) at 30 + 15 days, shelf-life studies at 25 ± 1°C, 60 ± 5% RH	6 days	Hutchinson *et al.* (2022)
	Combined pre-harvest and post-harvest EFF, 20 - 22°C with 90 - 95% RH	15-18 days	Debysingh *et al.* (2018)
Guava (*Psidium guajava* L.)	Post-harvest hexanal vapour (1,400 µL/L for 3 and 4.5 h, 1,600 µL/L for 3 and 4.5 h), shelf-life studies at 10 ± 2°C, 55 -70% RH)	20 days	Ashitha *et al.* (2019)
Orange (*Citrus sinensis* L.)	Post-harvest dip with hexanal at 0.02%, 18°C	8 days	Baltazari *et al.* (2016)
	Post-harvest dip in hexanal (0.02% for 5 min), shelf-life studies at 18 ± 2°C	12 days	Baltazari *et al.* (2020)
Apple cv. Royal Delicious	Post-harvest dip in hexanal (0.03% for 3 min), shelf-life studies at 20 - 25 °C, 40 - 56% RH after 1-month cold storage	21 days	Sulaimankhil *et al.* (2024)
Persimmon (*Diospyros kaki* L.)	Post-harvest dipped hexanal (0.04%), shelf-life studies at 0°C, 80 - 90% RH	120 days	Öz *et al.* (2023)
Blueberries (*Vaccinium corymbosum* L.)	Pre-harvest spray of 0.02% hexanal, shelf-life studies at 2°C, 90% RH	35 days	Sönmez *et al.* (2024)
Strawberry (*Fragaria × ananassa*)	Pre-harvest spray and post-harvest vapour (0.02%), shelf-life studies at 2°C, 90 - 95% RH	15 days	Öz and Kafkas (2022)
	Pre-harvest spray of hexanal (4mM/0.04%), shelf-life studies at 6°C	20 days	Sah et al. (2024)
	Post-harvest dip in hexanal (2% for 2.5 min), shelf-life studies at 22 - 30°C	6 days	Datta *et al.* (2024)
Tomato (*Solanum lycopersicum* L.)	Application of electrospun hexanal nano-fibre matrix, shelf-life studies at 30 ± 2°C, 65 ± 2% RH	32 days	Gbabe *et al.* (2024)

Table 2. Different hexanal treatments in providing physicochemical safety of tropical fruits during storage.

Parameter	Overall qualitative change	
	Treated	**Control**
Ripening/appearance	Delayed in ripening found in treated fruit	Over-ripening compared with treated
Physiological loss of weight	Lower rate of weight loss	Higher rate of weight loss
Firmness	Higher firmness	Lower firmness
Total soluble solid	Higher TSS	Lower TSS
Titratable acidity	Lower TA	Higher TA
Ascorbic acid	Higher AA content	Lower AA content
Phenolic content	Higher phenolic content	Lower phenolic content
Organoleptic rating	Higher sensory acceptability	Lower sensory acceptability

Table 3. Different hexanal treatments in providing microbial safety of tropical and temperate fruits during storage.

Fresh produce	Target microorganism	Reference
Mango	*Colletotrichum gloeosporioides* and *Lasiodiplodia theobromae*	Anusha *et al*. (2016)
Banana	*Colletotrichum gloeosporioides* and *Lasiodiplodia theobromae*	Dhakshinamoorthy *et al.* (2020)
Logan fruit	*Lasiodiplodia theobromae, Pestalotiopsis* sp., *Phomopsis* sp. and *Curvularia* sp.	Thavong *et al.* (2010)
Apples	*Penicillium expansum*	Fan *et al.* (2006)
Peach	*Monilinia fructicola, M. laxa*	Baggio *et al.* (2014)
Berry	*Colletotrichum acutatum, Alternaria alternata* and *Botrytis cinerea*	Almenar *et al.* (2007)
Pears	*Penicillium expansum*	Neri *et al.* (2006)
Strawberry	*Colletotrichum acutatum*	Yuan *et al.* (2009)
Raspberry	*Botrytis cinerea*	Taghavi *et al.* (2018)

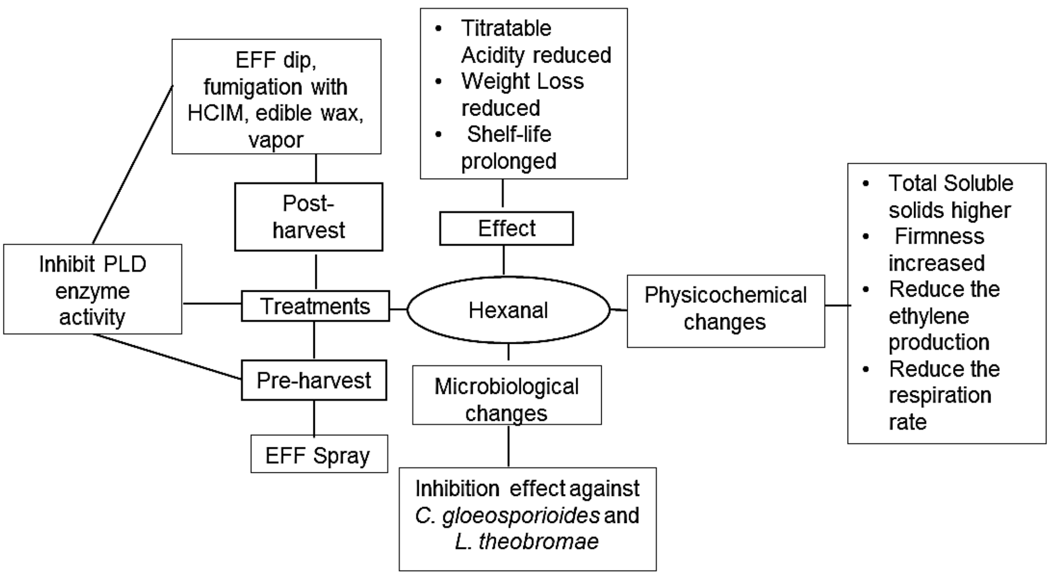

Figure 2. Hexanal treatments effect on post-harvest quality parameters of tropical fruits.

fruits (El Kayal *et al.,* 2017). Previous study reported that the inhibition of calmodulin helped to initiate ethylene-independent ripening process.

It has been proposed that ethylene promotes the increase in cytosolic Ca^{2+} during ripening (Gao *et al.,* 2019). The elevation of Ca^{2+} induces PLD and other cell wall degradation related enzyme expression, causing fruit softening and decay. The role of calcium signalling in ripening has been extensively reported (Gao *et al.,* 2019; Zhu *et al.,* 2024). However, it is unclear how hexanal affects Ca^{2+} and ABA levels to inhibit the expression of ripening-related enzymes.

Hexanal has small molecular size which can easily move across plasma membrane through simple diffusion due to its moderate hydrophobic property. It can also form hydrophobic interaction with lipid membrane, and cause changes in lipid membrane composition, thus affecting the activities of some membrane proteins such as PLD, receptors, and ion channels. Hexanal may affect the activity of Ca^{2+} channel resulting in the elevation of cytoplasmic Ca^{2+} level. This will induce calcium signalling pathway which play important role in inhibition or activation of many genes (Gao *et al.,* 2019). For example, hexanal may inhibit the expression of transcription factor (TF) for ripening-related genes involved in ethylene biosynthesis, and lipid membrane and cell wall degradation through calcium signalling, thus improving the shelf life.

Method of hexanal application

Post-harvest hexanal treatments have been proven to be as effective as pre-harvest treatments. Post-harvest hexanal dipping is the simplest and most effective treatment in retaining all the quality parameters under different storage conditions. The technology was tested in different important tropical fruits such as banana, guava, mango, and papaya. The hexanal treatments were found to be successful for each of the fruits. Enhance Freshness Formulation (EFF), edible wax, and edible coating using hexanal as an active component have been successful in reducing post-harvest losses of the fruits (Table 4). Different physicochemical parameters of post-harvest importance were also found to be positively impacted by the treatment.

Table 4. Different hexanal treatments with composition.

Hexanal treatment	Concentration	Application method
EFF formulation spray	2%, 3%	Pre-harvest
EFF formulation dip	1%, 2%	Post-harvest
Edible wax	Bee wax with 0.02% hexanal + 0.02% cinnamon bark oil	Post-harvest
Hexanal with HICM	Banana fibre (11%) + polyvinylpyrrolidone (3%) + biopolymer with tapioca starch + kappa-carrageenan (5.0%) + hexanal (15% of final weight)	Post-harvest

Hexanal treatments are unique and powerful, and possess the capacity for better quality management of fresh produce. If other factors such as storage, transportation, and handling after harvest of tropical regions go well, these treatments have been proven to be effective in order to reduce the post-harvest losses of fresh fruits. Several types of hexanal treatments, individually or in combination, were found to have potential effects on the quality attributes of tropical fruits during storage (Table 4). However, there is no specific treatment that is particularly suitable for certain fruits. According to Anusuya *et al.* (2016), EFF was evaluated as a pre-harvest treatment, and resulted in exerting the least effect on fruit yield, but a significant effect on fruit retention rate. The study also illustrated that the incidences of diseases like sooty mould and stem rot were reduced in sprayed trees. The different studies that have reported that hexanal was found to be effective in enhancing the shelf life of different fruits and vegetables are listed in Table 3.

Hexanal is a naturally occurring compound produced by linoleic acid through the lipoxygenase pathway, and it naturally has antifungal properties (Almenar *et al.,* 2007). By reducing microbial contamination, hexanal is effective in reducing fruit rot. The data reported by Anusuya *et al.* (2016) clearly showed that hexanal formulation successfully enhanced the shelf life of mango (*Mangifera indica* L.) of two different cultivars namely Alphonso (AL) and Banganapalli (BP) by four to six weeks. By inhibiting PLD in the skin of the fruits, hexanal plays an important role in enhancing the shelf life of tropical and temperate fruits (Anusuya *et al.,* 2016).

Effect of hexanal on post-harvest quality

Normally, climacteric fruits such as banana continue to respirate after harvest, which usually causes rapid spoilage. So, common post-harvest management techniques are focused on restricting the respiration of the fresh produce. The EFF dipping was found to be more effective in prolonging the shelf life of bananas by nine days than the control (Venkatachalam *et al.,* 2018). Debysingh *et al*. (2018) demonstrated that papaya treated (pre- and post-harvest) with 2% hexanal formulation (EFF) was found to have longer fruit retention period and shelf life, and improved post-harvest quality than that of control. Hutchinson *et al.* (2018) reported that post-harvest hexanal treatment was effective in enhancing the shelf life of papaya by six days. The study added that the hexanal treatment was also found to be effective to improve the other quality parameters during storage. Oranges treated with 0.02% hexanal have shown effectiveness in increasing shelf life by maintaining post-harvest quality parameters (Baltazari *et al.,* 2016). The study articulated that the use of hexanal-incorporated composite material (HICM) had a positive effect in improving the post-harvest quality materials, and was also found to be efficient to prolong the shelf life in ambient and cold storage temperatures (Samarawickrama *et al.,* 2018). A study conducted by Thakur *et al.* (2017) also evaluated the hexanal effectiveness on the post-harvest quality and shelf life of fresh mango. The study found that the post-harvest treatment using hexanal successfully reduced the post-harvest losses and disease incidences, and enhanced the shelf life of the fresh produce.

Physicochemical quality attributes of fresh fruits tend to undergo rapid changes during storage. Hexanal being investigated as an effective treatment in providing physicochemical and microbial safety of tropical and temperate fruits during storage are listed in Tables 2 and 3. Weight loss is one of the major factors in post-harvest losses, and the loss is due to moisture loss from the cell wall during maturity. This quality parameter indicates the level of freshness of the fruit during storage, and an important quality aspect in terms of safety of fresh produces. Moisture loss and physiological loss in weight (PLW) are positively correlated. The energy produced by fruits through respiration is the main cause of weight loss (Dharmasena and Kumari, 2006). According to Anusuya *et al.* (2016), hexanal successfully minimised the weight loss compared to the control at ambient temperature. However, there was no significant difference in weight loss in treated and control fruits during cold storage. In the study of pre-harvest treatment of hexanal on mango, it was found to be more effective in reducing weight loss at ambient temperature than cold storage. At low temperature, the metabolism is lower. This reduces the ability of hexanal to interact with ripening-related enzymes which causes weight loss as one of the key events in ripening. Hexanal treatment before or after cold storage may improve the effectiveness of hexanal in reducing weight loss. Post-harvest dipping with hexanal (0.03%) after one month of cold storage increased the shelf life of apple cv. Royal Delicious at 20 - 25 °C up to 21 days (Sulaimankhil *et al.,* 2024). However, this might be less effective for tropical fruits due to chilling or cold injuries. Yaptenco *et al.* (2001) reported that PLW was found to be low if they were distributed using refrigerated transportation. Anusuya *et al.* (2016) also added that the mango harvested from the treated trees showed lower ethylene production and respiration rates, which might also be responsible for higher fruit retention.

Venkatachalam *et al.* (2018) concluded that the hexanal dipped banana showed a lower rate of PLW until the end of storage. The study showed that the capacity of hexanal to reduce PLD activity resulted in lower PLW. Hutchinson *et al.* (2018) reduced the weight loss of papaya by up to 8% using the post-treatment of hexanal dip without developing any unacceptable sensory attributes. In the case of citrus fruits like oranges, weight loss occurs due to transpiration. The rate of transpiration increases simultaneously with the shrinkage rate of fresh produce during storage (Paul and Pandey, 2016). Baltazari *et al.* (2016) concluded that among all the used post-harvest treatments, 0.02% hexanal treated oranges have shown the lowest rate of weight loss during storage. According to Gunasekera *et al.* (2018), wax-coating containing hexanal was proven to be more effective in reducing the weight loss of fresh mango than the other treatments and control.

According to Muthuvel *et al.* (2019), the banana's highest weight loss was observed on bananas from different cultivars under ambient storage conditions. However, banana dipped in 2% EFF formulation was found to have the lowest PLW during the study period. The study also added that the effectiveness of hexanal formulation to reduce the PLW of banana showed a similar trend to the formulation used for the other fruits such as mango, guava, and papaya. Gill (2018) mentioned that EFF was effective in reducing the rate of weight loss in guava compared to the control condition.

Firmness is an essential quality and safety parameter of fresh produce that has an important impact on its marketability and consumer acceptance. Firmness can be defined as a response of fresh produce against physiological changes, damages, and turgidity, and this must be maintained during storage (Sousa *et al.,* 2007). The firmness of fruits can be measured by the deformation or extrusion test. Fresh produce is highly perishable. Thus, maintaining accepted level during storage is still a challenge in food quality management. The reduction of firmness is the result of cell wall degradation, and the transformation of starch into sugar (Mirshekari *et al.,* 2015). In order to minimise the losses of these parameters, different techniques have been developed. The application of hexanal to reduce post-harvest losses is common in food safety and quality. It is proven to be safe and effective in order to retain the quality parameters of fruits during storage under different storage conditions.

Anusuya *et al.* (2016) reported that hexanal was found to be effective in retaining the firmness of mango var. Alphonso and Banganapalli post-harvest. However, the study should explore more on the effect of hexanal concentration on the firmness to identify the optimal dose for maximum shelf-life extension. The effects of the treatment on broader range of mango varieties were unclear. Hexanal has been reported to be able to inhibit the enzymes that cause hemicellulose degradation and pectin development. Hexanal helps fruits to retain the firmness during storage by the reduction of these enzyme activities. There are numerous reports on the role of natural compounds in extending the shelf life by the inhibition of ripening-related enzymes, but lack of comparative analysis on their mechanism, effectiveness, practicality, and cost. For example, the inhibition mechanism of cell wall and lipid membrane degradation by hexanal seems overlapping with salicylic acid (SA), jasmonic acid (JA), and methyl jasmonate (MeJA) (Cenzano *et al.,* 2008; Krinke *et al.,* 2009; Xia *et al.,* 2024). Although hexanal inhibition of PLD is well documented, the interaction of hexanal with other enzymes remains unexplored. Transmembrane protein functions as scramblase localised at the plasma membrane, and catalyses bidirectional movement of phospholipid such as phosphatidylcholine from inner to outer leaflet of phospholipid bilayer membrane which helps to destabilise the membrane. However, this is not studied in plants (Miyata *et al.,* 2025). Hexanal may interact with this scramblase-like protein to prevent membrane degradation other than PLD. Venkatachalam *et al.* (2018) illustrated that EFF-dipped fresh banana remained fresh than control. Hexanal was found to be able to delay the peel and pulp softening of bananas during storage (Yumbya *et al.,* 2019).

Debysingh *et al.* (2018) reported that hexanal dip had a positive impact on the quality attributes of fresh produce post-harvest. Hexanal dip treatment was found to be effective in delaying the softening of papaya during storage. Hutchinson *et al.* (2018) showed that hexanal and calcium chloride treatment had a similar impact on providing firmness to fresh oranges during the study period. However, the post-harvest treatment was more effective in the retention of the firmness of fruits (Paliyath *et al.,* 2008).

Samarawickrama *et al.* (2018) reported that the release of hexanal vapour was able to retain the firmness of fruit for longer period in comparison with control during storage. As firmness is responsible for the quality structure of fruit by delaying the decrease in firmness, hexanal plays an important role in reducing post-harvest losses of fresh mango. The study added that hexanal could preserve the firmness of fresh mango without developing any unacceptable flavour and other sensory attributes. Thakur *et al.* (2017) demonstrated the analysis using different concentrations of hexanal treatment to prolong the shelf life, and retain the other quality parameters during storage. The study illustrated that by suppressing the ethylene production, hexanal potentially retained the firmness more effectively in cold storage than ambient temperature storage. Muthuvel *et al.* (2019) found that 2% hexanal EFF was able to slow down the loss of firmness of bananas of different cultivars. Study by Muthuvel *et al.* (2019) also included alum (0.2%) and carbendazim (400 ppm) to post-harvest dip treatment in addition to hexanal formulation. However, the effect of the treatment on firmness caused by hexanal was not clear. A similar result was also found in the case of other tropical fruits that have been proven by different scientific investigations. The result reported by Gill (2018) is that in the case of guava, the firmness was higher than that of the control. In the study, different treatments on Dashehari mango were evaluated under cold and ambient storage temperatures. Among the treatments, treated fruits resulted in having higher total soluble solid and total sugar, and lower ascorbic acid and total acidity.

Other important physicochemical parameters of fresh produce such as total soluble solid (TSS), total sugar (TS), total titratable acidity (TTA), and ascorbic acid (AA) were found to be positively affected by the application of hexanal treatments. According to Anusuya *et al.* (2016), the mangoes harvested from hexanal pre-treated trees had a higher amount of TSS, soluble sugar, and reducing sugar than that those harvested from untreated trees. In the case of TTA, the study reported a reverse trend. The TSS is a combination of different elements such as sugar, the soluble part of the starch, soluble pectin, and ascorbic acid. Different studies have been conducted to minimise the post-harvest losses due to the degradation of quality attributes such as TSS, TTA, TS, and AA contents of fresh produces. Sugars will eventually be exported transporters (SWEET) proteins play important roles in sugar allocation (Chen *et al.,* 2010). This protein translocates sugar such as sucrose, glucose, and fructose from source tissues (leaves) to sink tissues (fruits). SWEET protein forms a channel or pore in the membrane, facilitating the movement of sugar across plasma membrane from active photosynthetic tissue (leaves) to fruits, which helps in sugar accumulation during fruit development (Chen *et al.,* 2010). SWEET genes (*PpSWEET9a* and *PpSWEET14*) in peach (*Prunus persica*) were highly expressed in mature leaves, facilitating the sugar translocation from leaves to fruits (Luo *et al.,* 2024). The impact of hexanal treatment on SWEET protein was not reported. Since hexanal can affect the TSS, pre-harvest treatment of hexanal on the leaves and fruits may affect the sugar accumulation in fruits by affecting the SWEET protein activity.

These are the important quality parameters of fresh fruits. Several studies have illustrated that by retaining these quality attributes of fresh fruits, hexanal is effective in improving safety during storage. Reis *et al.* (2004) reported that different treatments such as calcium dip, calcium chloride treatment, and use of AA have been proven to enhance the important quality attributes during storage than untreated fruits in cold and ambient temperatures. Venkatachalam *et al.* (2018) reported that hexanal treatment was effective in retaining TSS, TA, and AA of fresh banana during storage. The study emphasised the importance of AA as a quality parameter. The AA in fresh produce rapidly increases due to enzymatic or other chemical reactions during storage. However, hexanal is proven to be effective in retarding the enzymatic deteriorations or formation of other precursors to inhibit the excessive formation of AA during storage.

Yumbya *et al.* (2018) reported two concentrations of hexanal treatment effective in inhibiting the increase in TAA in comparison with the control. The TSS is another important quality attribute that is found to increase during storage. The formation of sugar occurs due to the breakdown of carbohydrates. An increase in TSS in banana resulted from the breakdown of cellulose and pectin. Hexanal-treated bananas have shown a slower rate of TSS due to low hydrolysis of the carbohydrate into sugar. A similar finding was also observed in bananas (Ambuko *et al.,* 2006) and avocados (Ferguson *et al.,* 1999). The study resulted in hexanal capability in reducing the AA content in treated banana during storage. Hexanal treatment was not found to have any effect on improving the total sugar content for different cultivar of bananas. In the case of pH, the hexanal-treated fruits were showed to retain higher level of pH till the end of the study period across all assessed banana cultivars. Muthuvel *et al.* (2019) described the hexanal effect on ultrastructural changes of bananas through scanning electron microscopy. The study reported that there were significant differences in the structural integrity of tissue layers in treated and controlled bananas. Hexanal-treated bananas had prominent starch granules between the parenchyma cells in the pulp. That indicated a delay in the ripening process. However, there were no traces of starch granule found in the control fruits.

The result is quite similar to other studies done on hexanal effectivity on other temperate fruits. Baltazari *et al.* (2016) concluded that 0.02% hexanal treatment was able to improve the post-harvest quality attributes in both Masa and Jaffa oranges during the storage period. The study showed that hexanal-treated fruits had higher TSS and firmness, and lower acidity during the post-harvest storage time.

Samarawickrama *et al.* (2018) showed the effective use of HICM to improve the post-harvest quality parameters of mango. The study reported higher fruit firmness but lower pH in comparison with the untreated fruits.

Gill (2018) studied the effect of hexanal treatment on the post-harvest quality parameters of guava, and also showed a positive effect. Treated guava had higher TSS than the control fruit. The TTA was found to be low in treated fruits than in untreated fruits. The contents of sucrose, glucose, and fructose significantly increased by the conversion of starch and organic acids into sugars as the fruit ripened. In addition, cell wall and membrane remodelling resulted in firmness or textural changes. Then, the fruits proceeded to senescence stage caused by the decline in cell function, leading to fruit decay. These processes are regulated by complex gene expression involved in ripening and senescence. Transcriptome analysis revealed the temporary downregulations of genes such as polygalacturonase (PG), endoglucanase, xyloglucan endotransglucosylase/ hydrolase (XTH), pectate lyase (PL), phospholipase D (PLD), and expansin by the application of hexanal (Yumbya *et al.,* 2021). Techniques to permanently inhibit the expression of these genes can be developed for future research. Therefore, the fruit will never proceed to senescence stage. Gene-editing tool such as CRISPR-Cas9 can be used to change the promoter sequence of PG, XTH, PL, PLD, and expansin so that the genes will stop expressing after the fruit reach full maturity. This technique has been used in tomato, resulting in delayed softening by mutation of tomato polygalacturonase gene (*SIPG*) (Nie *et al.,* 2022). However, the study did not permanently inhibit senescence. Therefore, deeper understanding of metabolic pathways and gene regulations in fruits is required. Nevertheless, the study of hexanal treatment provides preliminary information on how ripening can be regulated.

Effect of hexanal on fruit decay

Fresh fruits are highly perishable in nature and provide favourable conditions for microbial growth and development. Microbial invasion causes post-harvest decay, thus reducing the shelf life of fruits. The use of hexanal treatments was investigated as an effective solution to minimise post-harvest decay by minimising microbial contamination (Table 3). As a six-carbon aldehyde, hexanal is a naturally occurring compound produced through the lipoxygenase pathway in plants. Hexanal possesses toxic effects against fungi which can minimise fruit decay. Moreover, some precursors of this six-carbon aldehyde are able to be converted into an abundant volatile component that can develop fruit aroma. It has been proven by a study conducted on apples that using hexanal was effective in minimising fungal decay and developing fruit aroma (Song *et al*., 1996). Hexanal has also been proven to be effective in enhancing the shelf life by minimising microbial invasion during storage under cold (4°C) and ambient temperature (15°C) (Lanciotti *et al.,* 1999).

A different study was conducted to evaluate the antifungal capacity of hexanal on tropical and temperate fresh produce. Dhakshinamoorthy *et al.* (2020) reported that hexanal was found to be efficient in minimising the pathogen *Lasiodiplodia theobromae* and *Colletotrichum gloeosporioides*. The study added graphical evidence of the effect of hexanal on the rate of incidence of disease reduction in comparison with the control. The study successfully provided evidence that hexanal treatment was effective in minimising the post-harvest microbial contamination, thus can take part in prolonging the shelf life of fresh banana up to 15 days which can be achieved by inhibiting the mycelial growth and spore germination of fungi by hexanal. Hexanal was also found to be similarly active against some of the other fungal pathogens with post-harvest importance such as *Botrytis cinerea*, *Monilinia fructicola*, *Sclerotinia sclerotium*, and *Alternaria alternata* (Song *et al.,* 2007).

Anusha *et al.* (2016) also investigated the antifungal capacity of hexanal over important post-harvest pathogens of fresh mango. In the study, hexanal was found to be successfully active in minimising the germination of *C. gloeosporioides* and *L. theobromae* compared with the untreated fruits. The study indicated that 0.10% concentration of hexanal was significantly able to reduce spore germination. The study also concluded that 0.06% hexanal was completely able to inhibit the spore formation of *C. gloeosporioides* and *L. theobromae*. Thus, hexanal was proven effective in the reduction of stem-rot disease caused by *C. gloeosporioides* and *L. theobromae* in mango. The germination of *A. alternata* and *C. gloeosporioides* was sensitive toward the antifungal volatile, and ceased completely after 12 hours of exposure. Through the electron microscope, it was revealed that hexanal ruptured and broke the mycelia of both *C. gloeosporioides* and *L. theobromae*, and was also responsible for morphological deformation of the pathogens. However, the complete inhibition of the spore germination was not reported. The study concluded that hexanal was effective to minimise the germination of the spore within 24 hours of the period rather than completely stopping it. Hexanal is effective against a wide range of fungal pathogens since it has been clearly pointed out that it possesses fungicidal and fungistatic effects that can act on the plasma cell membrane of the spores, causing morphological deterioration. However, the effectiveness of the volatile greatly depends on the concentration.

Besides acting as a fungicide, hexanal is also capable in enhancing the aroma of fresh produce by conversion of its different aroma volatile precursors. Song *et al.* (2010) showed that hexanal vapour reduced spoilage, thus improving the marketability under the controlled atmospheric condition of highbush blueberry. The vapour treatment successfully inhibited *B. cinerea,* thus extending the storage life of the fresh fruits. Another study was done on peach using hexanal, and concluded that a certain rate of hexanal had a negative impact on the sporulation and mycelial growth of *Monilinia fructicola* and *M. laxa in vitro* (Baggio *et al.,* 2014).

Hexanal has also been proven to have the capacity to inhibit the growth and production of fungi that cause brown rot disease in peach. The study defined hexanal as a promising alternative to chemical fungicide. A study reported that hexanal provided higher effectiveness against three fungi namely *A. alternata, B. cinerea,* and *C. gloeosporioides* at lower concentrations (Taghavi *et al.,* 2018). Almenar *et al.* (2007) investigated the hexanal fungicidal effectivity on berries, and concluded that hexanal had greater antifungal activity against *C. acutatum* than against *A. alternata* and *B. cinerea.* The study also mentioned that the antifungal activity of hexanal was correlated with the concentration.

Hexanal vapour has also been shown to inhibit *Penicillium expansum* (Fan *et al.,* 2006). However, the effectivity of the volatile depends on the concentration and time. Studies on hexanal as a fungicide on both tropical and temperate fruits such as mango, banana, apple, peach, and cherry also yielded potential results. Taghavi *et al.* (2018) demonstrated that hexanal significantly inhibited *P. expansum* in apple; *Colletotrichum acutatum, A. alternata*, and *B. cinerea* in berry; and *M. laxa* in peach compared to untreated fruits.

Tropical and temperate fruits' responses towards hexanal

Tropical fruits are facing unique challenges compared to temperate fruits in reducing the post-harvest losses. Tropical fruits have higher ripening rate, and are more susceptible to pathogens due to higher ambient temperature (Ho *et al.,* 2018). In addition, tropical fruits are prone to chilling injury (Sonkaew *et al.,* 2023). Hexanal treatment has been developed to enhance shelf life of many fruits. From previous studies, hexanal treatment in combination with cold storage resulted in longer shelf life of temperate fruits compared to hexanal alone, as shown in Table 1. This technique may be less effective for most tropical fruits due to sensitivity to low temperature. The difference in mechanism in response to hexanal treatment between temperate and tropical fruits are still unclear despite the hexanal treatment efficacy on wide range of fruits have been reported (Preethi *et al.,* 2021; Öz and Ali, 2023; Sulaimankhil *et al.,* 2024; Sönmez *et al.,* 2024). Hexanal treatment in different species and cultivars of both tropical and temperate fruits showed different results. Furthermore, the formulations, doses, and durations all play a significant role in the effectiveness of the treatment. Fruit is a complex plant organ evolved to adapt to various environmental stresses which is important in ensuring the biodiversity of plants. Therefore, their response to hexanal is different even within the same climatic region. In the present review, it is suggested that the response of fruits to hexanal treatment varies regardless of their climatic regions (tropical or temperate). To date, there is insufficient evidence to clearly differentiate the responses between these two groups of fruits.

Conclusion

The use of hexanal for shelf-life extension has been proven to be successful for temperate and tropical fruits. Hexanal treatment is cheaper, safer, and easier to use compared to freezing, irradiation, and modified atmosphere packaging. However, tropical fruits face unique challenges such as higher ripening rate, sensitivity to low temperature, and limited infrastructures and transportation. Previous study showed that tropical and temperate fruits share similar mechanism in response to hexanal treatment to extend the shelf life which involves the inhibition of ethylene biosynthesis, and cell wall and lipid membrane degradation. Hexanal was reported to be potent inhibitor of phospholipase D (PLD). However, direct or indirect interaction of hexanal with other enzymes, transcription factors, metabolites or microRNA (miRNA) affecting the expression of ripening-related genes remain elusive. It is suggested that hexanal may inhibit ripening-related genes through calcium signalling by affecting membrane protein such as calcium channel. Method of application, dose, and formulation are the main factors that influence the effectiveness of the treatment. The response of fruits to hexanal may differ based on their physiology rather than their climatic regions (tropical or temperate). This highlights the biodiversity of plants within the same climatic region. The study of hexanal treatment on fruits provides insights into how ripening can be regulated. Consequently, genomic and metabolic modifications could be used to improve shelf life in the future.

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