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New promising molecules for ethylene management in fruit crops, 1-MCP and nitric oxide: A review

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Abstract
The gaseous plant hormone ethylene plays a key regulatory role in fruit ripening and also know as ripening hormone. Autocatalytic production of ethylene causes detrimental effects by increasing rate of respiration, accelerate senescence and chemical changes which affect post-harvest life and quality of fruits. Various tools are used for management of ethylene during post-harvest stage are control atmospheric storage, modified atmospheric storage but it has its own limitations and most of the time leads to disorders like superficial scald, melting flesh, chilling injury etc. The 1-MCP is competitive inhibitor of ethylene action which maintain fruit quality by delaying senescence. It is a gaseous chemical that can be easily applied, non-toxic mode of action and activity at very low concentration increases its commercial importance. The 1-MCP is registered by more 37 countries for use in various fruits after approval by Environmental Protection Agency from USA. A treated fruit have lowered ethylene production, slow rate of respiration and maintained physiochemical properties during both ambient and cold storage. Various genotypes, cultivars and maturity stages at time of treatment give varying response to the 1-MCP. It has effects on different physiological disorders; the proneness of fruits to various disorders can be increased or decreased by inhibition of ethylene production. The Nitric oxide (NO) known to act as a biological messenger and plays important role in Inhibition of ethylene biosynthesis and its related detrimental effect on fruits during post-harvest storage. The production of ethylene in fruits were reduced by the use of Nitric oxide as ACC oxidase–Nitric oxide complex is formed after the treatment of Nitric Oxide. It is concluded from review, that NO & 1-MCP are multifunctional signalling molecules plays significant role in postharvest physiology of fruits by reducing ethylene biosynthesis and rate of respiration.

Keywords: Ethylene; 1-MCP; Nitric oxide; Fruit ripening

Introduction
The gaseous hormone ethylene has significance in the practical agriculture, basic biochemistry and physiology of plants have been studied for many decades. The complex biosynthetic pathway of ethylene was discovered by Adams and Yang (1979), which accelerated stimulated research in this area [1, 2]. The ripening of climacteric fruits serve as the unique systematization of developmental and biochemical pathways governing to the changes in colour, texture, aroma and nutritive quality of fruits. The aeriform plant hormone ethylene governs key role in fruit ripening, hence known as ripening hormone. Rapid ripening of climacteric fruits during storage causes about 15% losses. The reason behind the losses during storage and post-harvest is autocatalytic production of ethylene, which leads to loss of sensory properties of fruits and ultimately market value. Autocatalytic production of ethylene causes detrimental effects by increasing rate of respiration, accelerate senescence and chemical changes which affect post-harvest life and quality of fruits. Various tools used for management of ethylene during post-harvest stage are control atmospheric storage, modified atmospheric storage but it has its own limitations and most of the time leads to disorders like superficial scald, melting flesh, chilling injury etc.

Fruit ripening is defined as the integrated sequence of changes, including softening, change in colour and accumulation of sugars and aromatics, coupled with a degeneration in organic acids [3]. It is considered to begin during the later stages of fruit maturation and it transforms a fully grown mature but inedible plant organ into an attractive fruit to eat. While maturation and development are completed only when fruit are attached to the plant, ripening and senescence can proceed on or off the plant [4].

Fruit are divided into two groups based on their ripening pattern: climacteric and non-climacteric fruit. In climacteric fruit, ripening is accompanied by a peak in respiration which coincides with a burst in ethylene production while ripening in non-climacteric fruit does not show a peak in respiration and ethylene production rates remain low. Some species show clear climacteric (e.g., apple, tomato and banana) or non-climacteric (orange and pineapple) behaviour, while others (like melon) comprise both climacteric and non-climacteric genotypes [5].

Ethylene is the most extrusive ripening regulating hormone. There are two systems involved in its biosynthesis, System-1 functions during vegetative growth, is auto inhibited by ethylene. This is responsible for the production of basal levels of ethylene synthesized by plant tissues, including non-climacteric fruit. System-2 comes into play during the ripening of climacteric fruit and is characterized by an autocatalytic ethylene response [6]. The main difference between system-1 and system-2 is the negative and respectively positive feedback regulation of ethylene.

Softening is for the major part regulated by ethylene, as is abscission, chlorophyll degradation, aroma volatiles production and climacteric respiration and ethylene production. The climacteric ethylene production is triggered by an ethylene independent process. The different ethylene dependent processes can differ strongly in sensitivity levels to ethylene and internal production of ethylene [7]. The higher ethylene production also have some detrimental effect like accelerates senescence, enhances excessive softening of fruits, promotes discolouration, stimulates phenylpropanoid metabolism, stimulates chlorophyll loss and induces many physiological disorders during storage.

Post-harvest losses of major fruits in India during 2010 and 2015 are as follows.

Sr. No.	Name of Crops	% Average loss (CIPHT Nanda *et al.* 2010)	% Average loss (CIPHT Jha *et al.* 2015)
1	Apple	12.26	10.39
2	Banana	6.60	7.76
3	Citrus	6.38	9.69
4	Grapes	8.30	8.63
5	Guava	18.05	15.88
6	Mango	12.74	9.16
7	Papaya	7.36	6.70
8	Sapota	5.77	9.73

[8]

Inhibitors of ethylene action

Most of the effects of ethylene can be antagonized by specific ethylene inhibitors. Silver ions (Ag+) applied as silver nitrate (AgNO3) or as silver thiosulfate (Ag $(S2O3)2^{3-}$) are potent inhibitors of ethylene action. Carbon dioxide at high concentrations (in the range of 5 to 10%) also inhibits many effects of ethylene, such as the initiation of fruit ripening, although CO_2 is less efficient than Ag+. This effect of CO_2 has often been exploited in the storage of fruits, whose ripening is delayed at elevated CO_2 concentrations. The volatile compound *trans*-cyclooctene, is a strong competitive inhibitor of ethylene binding to the receptor.

1-methylecyclopropene

The 1-MCP is competitive inhibitor of ethylene action used to maintain fruit quality by delaying senescence. It is a gaseous chemical that can be easily applied. The 1-MCP has non-toxic mode of action and activity at very low concentration increases its commercial importance. It binds irreversibly to the ethylene receptor and inhibits further processes that are controlled by ethylene [9].

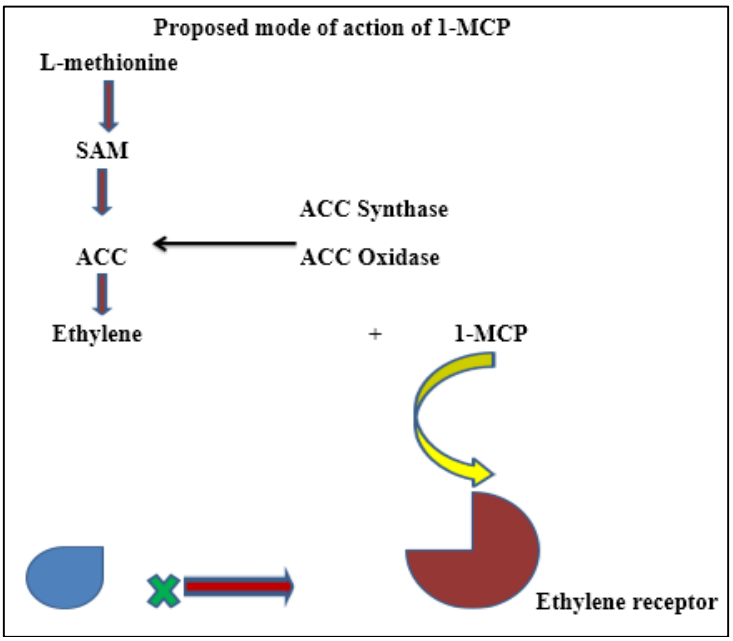
The 1-MCP is registered by more than 37 countries for use in apple, peach, plum, pear, mango, banana, papaya etc., after approval by Environmental Protection Agency of USA. A treated fruit have lowered ethylene production, slow rate of respiration and maintained physiochemical properties during both ambient and cold storage. The response of 1-MCP typically dependent on concentration and exposure time. Various genotypes, cultivars and maturity stages at time of treatment give varying response to the 1-MCP. 1-Methylcyclopropene (1-MCP) is an inhibitor of ethylene perception, has been commercialized as SmartFresh™ technology for postharvest use on fruits and vegetables around the world. 1-MCP is used widely on apple fruit in North America; its successful commercial uptake has occurred because the technology helps to maintain quality of the fruit, not only during storage, but also through the entire marketing chain including the consumers' homes. 1-MCP can reduce a number of serious storage disorders that cause fruit loss, such as senescent breakdown and superficial scald, but the incidence of others including carbon dioxide injury and flesh browning, can be increased by 1-MCP.

As far as applications of 1-MCP are concerned, the 1-MCP prevents effects of ethylene in a wider range of fruits, vegetables and floriculture crops. The low concentrations are effective and ranges from 2.5 nlL^{-1} to 1 ml L^{-1}. The interaction of concentration with temperature such that low concentrations of 1-MCP applied over longer durations may be as effective as high concentrations. 1-MCP is most commonly applied at 68-/77 ^{0}F (20-25 ^{0}C), also can be used at lower temperatures in some commodities. Generally, treatment durations of 12-24 h were sufficient to achieve a full response. The various factors required to be considered at time of using 1-MCP including cultivar, developmental stage, time from harvest to treatment, and multiple applications. Depending on the species being treated, 1-MCP shows a variety of effects on respiration, ethylene production, volatile production, chlorophyll degradation and other colour changes, protein and membrane changes, softening, disorders and diseases, acidity and sugars [10].

The ripening in mango cv. Alphonso was a potently determent by 1-methylcyclopropene. It can increases shelf life of fruits, by retarding biochemical changes and enhancing shelf life of fruits without losing quality during cold storage. The chemical and sensory properties of Alphonso mango fruits was maintained by the treatment of Cel-fresh 0.18% (1-MCP)-1tablet/$2M^3$ under cold storage conditions [11].

The 1-MCP treatment leads to decreased levels of H_2O_2 and lipid peroxidation, coordinated with increased activities and isozymes of catalase (CAT) and superoxide dismutase (SOD). Whereas the ethrel treatment causes an increase in H_2O_2 and lipid peroxidation, concomitant with a decrease in the

activities and isozymes of catalase and SOD. The treatment of ethylene increases activity of ascorbate peroxidase (APX) while 1-MCP treatment only increase in marginal APX [12].



Recommendations for use of 1-MCP in important fruit crops

Fruit	Concentrati-on	Treatment Temperature (ºC)	Treatme-nt time	Effects	Reference
Apple	0.6-2 ml/L	0, 5, 10, 15, 20,25	7 -20 h	Maintained firmness, maintain titratable acidity, reduced volatiles, slowed loss of chlorophyll and starch, inhibited ethylene, reduced respiration and decay. Prevented disorders like superficial scald.	[13-17].
	937 nL/L	15-17	20-21 h	The treatment of 'Granny Smith' apples with 1-MCP can extend the storage (0–1 ^{0}C, 90–95% RH) time for 3 months without significantly losing freshness even two weeks after removal from cold storage. It is more effective in preserving sensory attributes related to apple freshness when compared with the DPA (diphenylamine) treatment.	[18]
Banana	5 -500 nl/L, 0.1 ml /L	20,24	6 -24 h	Delayed ripening and peel colour change.	[19-20]
Banana	50 mL L^{-1} ethephon with 400 nL L^{-1} 1-MCP	20,24	16 h	Improper concentration of 1-MCP, and treatment time affect vital components of banana fruit quality. The treatment affect rate of respiration and ethylene production. The 1-MCP reduces the activity of pectin lyase, pectin methylesterase, cellulose and Polygalactouronase, and delayed the peak activity of ACC synthase and ACC oxidase. The combined treatment significantly delayed the formation of volatile compounds, ripening of fruits, which ultimately prolonged the post harvest life of banana without affecting its normal coloring and volatile development, which maintained the marketability of banana fruit.	[21]
Papaya	50-1000 nL/L	22	5-24 h	Reduces rate of respiration and ethylene production, maintain firmness and texture.	[22]
Sapota	300nL /L	25	12 h	Delayed softening, Inhibition of cell wall degrading enzymes	[23]
Plum	1, 13, 26 or 39 ml /L	20	6,20, 24 h	Reduced ethylene and respiration, maintained firmness, slowed colour change, decreased internal flesh browning	[24-25]
Plum (*Prunus salicina* Lindl.) cv. Tegan Blue	0, 0.5, 1.0 or 2.0 µLL^{-1}	20±1	24 h	Fruit were allowed to ripen at ambient temperature (20±1 ^{0}C). The reducing activities of ethylene biosynthesis enzymes ACS, ACO and ACC content with postharvest treatments of 1-MCP. The reduction in fruit softening enzymes (PE, EGase, exo-PG and endo-PG) in fruit skin and in pulp tissues were more pronounced with increased concentrations of 1-MCP.	[26]
Peach	20 nl/L, 0.1 ml /L, 0.5 ml/L	20-24	4, 18, 24 h	Maintained firmness, delayed ethylene production and reduced activity of ethylene associated enzymes	[27-29]

Pineapple	0.1 ppm (4.5 nmol l^{-1})	20	18 h	Effectively controlled internal browning, a chilling injury symptom, in pineapples stored at 10°C for 4 weeks. Delayed ascorbic acid decline, and arrested the decline in both total soluble solids and ethylene synthesis. 1-MCP could be considered for use commercially to control this important postharvest physiological disorder in pineapples.	[30]

Ripening of mango fruit is characterized by softening of flesh which limits its shelf life. 1-MCP is nontoxic gas that delays fruit softening and improves quality of several fruit. The role of 1-MCP in regulating fruit softening and quality of 'Kensington Pride' mango was investigated by, treating physiological mature fruits treated with 1-MCP (1 mL L^{-1}), ethylene (10 mL L^{-1}) or 1-MCP+ethylene for 12 h at ambient condition (20 ± 1 ^{0}C). Fruits were allowed to ripe at ambient temperature (20 ± 1 ^{0}C) for 10 days. Climacteric peaks of ethylene production and respiration rate were significantly supressed by 1-MCP application as compared to ethylene-treated and control fruit. Exogenous application of ethylene accelerated the development of fruit colour, fruit softening with increased activities of exo-Polygalacturonase, endo-Polygalacturonase and endo-1, 4-β-d-glucanase (EGase) enzymes in the pulp tissues. Whereas, activities of fruit softening enzymes were significantly delayed and/or suppressed in 1-MCP-treated fruit. 1-MCP treated fruit showed improved rheological properties (i.e. firmness, springiness and stiffness), decreased level of citric acid, malic acid, succinic acid, total organic acids, total sugars and sucrose than other treatments. 1-MCP inhibited the activities of fruit softening enzymes which consequently delayed the ripening and ripening related changes in 'Kensington Pride' mango [31].

Tatsuki *et al.* (2007) studied expression patterns of genes for ethylene biosynthesis, enzymes and ethylene receptor in two apple cultivars, Orin and Fuji. Both cultivars responds in different manner but the ultimate storage life and firmness was improved by 1-MCP. The potential for commercial application of 1-methylcyclopropene (1-MCP) to maintain quality of 'McIntosh', 'Empire', 'Delicious' and 'Law Rome' (early, mid and late season) apples under air and controlled atmosphere (CA) storage conditions. These cultivars represent early, mid and late season apples with ripening rates ranging from fast to slow. 1-MCP gas concentrations used were 0.5, 1 and 2 ml/L, generated from Ethylbloc™ powder. Effects of 1-MCP were greater in CA than air storage. A dose response of internal ethylene concentrations and flesh firmness to 1-MCP was found in 'McIntosh' and 'Law Rome', but 'Delicious' and 'Empire' ripening was generally prevented by all 1-MCP concentrations. 1-MCP reduced superficial scald incidence and accumulations of a-farnesene and conjugated trienols during air storage. The results indicate that the efficacy of 1-MCP is affected by cultivar and storage conditions [13].

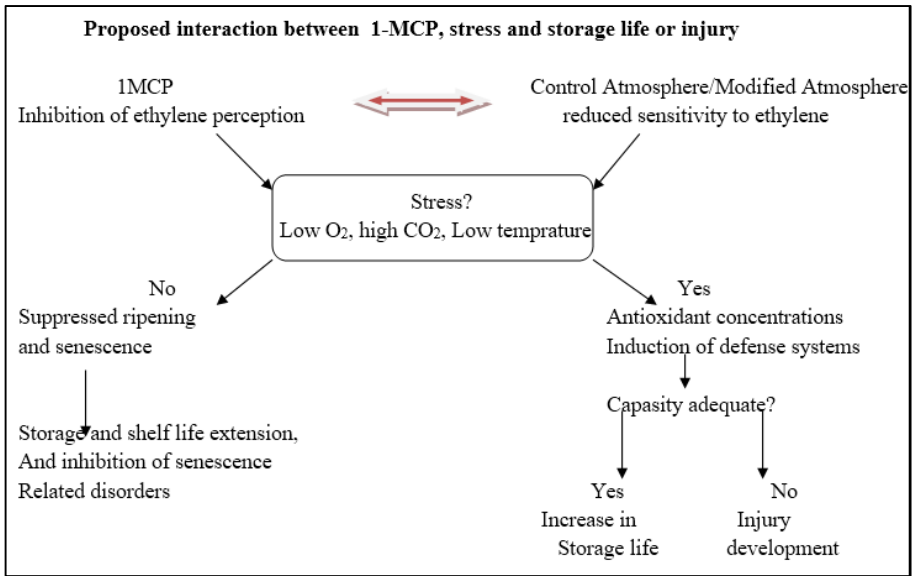
The losses due to compression during transport are heavy in the fruits like, plum due to its delicate nature and requires massive post-harvest managements for enhancing its shelf-life so as to make it available in the market for longer time. The effect of 1-MCP treatment on Santa Rosa plums of two maturity groups (climacteric and pre-climacteric) during transportation. Plums of both maturity stages were subjected to 1-MCP treatments 1-MCP @ 1.5 µl $l^{-1}$for 24 h at 20 ºC, then packed in CFB boxes and transported by road. The losses were higher in climacteric stage (25.0%) than pre-climacteric (9.0%) stage, whereas the 1-MCP (1.5 µl l-1) treatments had significantly reduced compression injury, being the least (0.0). There was significant losses reported in quality parameters like fruit firmness, AOX capacity, TSS, acidity and ascorbic acid in untreated plums. Similarly, respiration and ethylene evolution rates were higher in untreated plums than those, which were treated with 1-MCP, being the least in treated fruits [32].

Interactions between control atmospheric storage and multiple treatments of 1-MCP showed that second application of 1-MCP after 4 months storage in CA may improve firmness [14]. The treatment of 'Granny Smith' apple with 1-MCP can extend storage time without losing freshness and sensory properties even two weeks after removal from cold storage [18]. 1-MCP significantly delayed ripening of banana fruits over control which help in export of fruits [19].

The activities of pectin methyl esterase (PME), polygalacturonase (PG), pectate lyase (PL) and cellulase in banana cv. dwarf Cavendish fruit were measured over a period of 7 days after ripening was initiated with ethylene. Effects of treatments with 1-methylcyclopropene (1-MCP), abscisic acid (ABA) and indole acetic acid (IAA) on activities of these hydrolases were measured in order to help elucidate their roles during banana ripening. Ethylene stimulated activities of all four enzymes, at best differentially. 1-MCP and IAA suppressed the ethylene effects [33].

The papaya fruit treated with 1-MCP when more than 25% ripe had a delay in softening. The 1-MCP maintained fruit firmness and texture that may have commercial utility [22].

The influence of 1-methylcyclopropene (1-MCP) on the physiological and biochemical changes that sapodilla cell wall undergoes during ripening and evaluated its potential to preserve sapodilla fruits at postharvest. Fruits were treated with ethylene antagonist 1-MCP at 300 nL L^{-1} for 12 h and then stored under a modified atmosphere at 25 ºC for 23 d. 1-MCP significantly delayed softening of sapodilla for 11 d as a consequence of inhibition of cell wall degrading enzyme activities, and thus 1-MCP-treated fruit exhibited a less extensive solubilisation of polyuronides, hemicellulose and of free neutral sugar when compared to control fruit [23].



The Nitric oxide (NO) discovered by Joseph Priestly (1772) and called it "Nitrous air". Wilson *et al.* (2008) reported the various routes of nitric oxide (NO) production in plants cells. NO can be synthesized enzymatically from nitrite (NO_2^-) by nitrate reductase (NR). There is also considerable evidence for l-arginine-dependent NO synthase (NOS) activity in plant cells, although the protein At NOS1 is no longer considered to be a NOS and no other plant candidate for the role has been identified. Evidence also exists for the activity of a nitrite: NO reductase in roots and for the ability of both chloroplasts and mitochondria to convert NO_2^- to NO. Nitric Oxide is first gas known to act as a biological messenger and plays important role in inhibition of ethylene biosynthesis and its related detrimental effect on fruits during post-harvest storage.

Monitoring ethylene is crucial in regulating post-harvest life of fruits. The concept of nitric oxide (NO) involvement in regulating ethylene is new. NO mediated physiologies casted through regulation of plant hormones are widely reported during developmental and stress chemistry having no direct link with ripening. Research in NO biology and understanding its interplay with other signal molecules in ripening fruits suggest ways of achieving greater synergies with NO applications. Experiments focused at convincingly demonstrating the involvement of NO in altering ripening-related ethylene profile of fruits, would help develop new processes for shelf life extension. The putative mechanisms of NO intricacies with other primary and secondary signals are hypothesized. The advantage of eliciting NO endogenously may open up various biotechnological opportunities for its precise delivery into the target tissues [34].

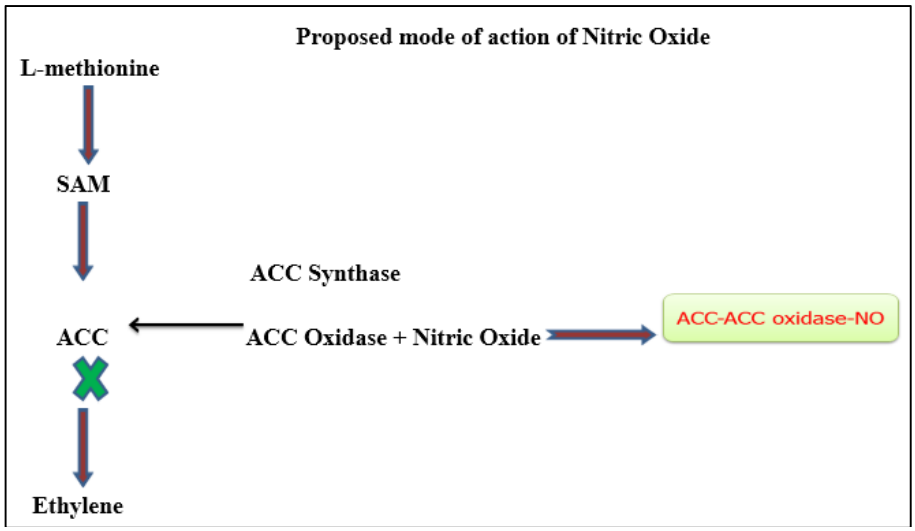
Various routes of nitric oxide (NO) production within plant cells					
Pathways	**1**	**2**	**3**	**4**	**5**
Precursors	**NO^-_2**	**NO^-_2**	**NO^-_2**	**NO^-_2**	**L-Arginine**
Site of synthesis	Plasma membrane (root)	Cytoplasm	Mitochondria	Chloroplast	Cytoplasm Mitochondria Chloroplast
Enzymes	Nitrite NO reductase (Ni-NOR)	Nitrate reductase (NR)	--	--	AtNOS1 AtNOA1

[35]

Application of NO for shelf life extension

Crop/fruit	Treatment	Extent of shelf life extension (%)	Specific conditions	Reference
Kiwi	NO gas	160	Not specified	[36]
Strawberry fruit	NO gas in the concentration range 5–10 ml l^{-1}	>50	No significance of storage temperature	[37]
Plum	1 mM Sodium nitroprusside	Up to 120 days (Slower flesh Reddening and lower levels of athocyanins)	Storage at 2 °C with 85–90% RH	[38]
Apple	DETANO dipping for 60 s in a solution of 10 mg l^{-1}	170	Treatment solution preferably acidic pH 6.5.	[39]

The ethylene production and respiratory rate of peach cv. Rojo Rito treated with NO were lower than those of control fruits. Treated fruits underwent a lesser loss of firmness during storage. A possible mechanism is proposed that NO is bound to ACC oxidase to form an ACC oxidase–NO complex, leading to a decrease in ethylene production [40]. The increase in concentration of ACC in NO-treated peaches may result in the redirection of ethylene to MACC production [41]. The similar result in Chausa mango and also reported the nitric oxide reduce pericarp browning and reserve bioactive antioxidants in litchi [42]. The mode of action of nitric oxide (NO) in inhibiting ethylene biosynthesis and fruit softening during ripening and cool storage of mango fruits. Hard mature green mango (Mangifera indica L. cv. 'Kensington Pride') fruits were fumigated with 20 uL L^{-1} NO for 2 h at 21 ^{0}C and allowed to ripen at 21±1 ^{0}C for 10 d, or stored at 13±1 ◦C for 21 d. NO fumigation inhibited ethylene biosynthesis through inhibition of ACS and ACO activities leading to reduced ACC content in the fruit pulp which consequently, reduced the activities of fruit softening enzymes during ripening and cool storage [43].



NO associated post-harvest biochemical changes

Commodity	Treatment type	Biochemical effects	References
Strawberry	NO gas	Inhibition of ethylene production.	[36]
Bartlett Pears	NO gas	Yellowing was delayed 2 days.	[44]
Peaches	NO gas	Inhibition of ACC oxidase, thus redirection of ethylene to MACC production and inhibition of lipoxygenase.	[41]
Strawberry	5 µmol l^{-1} SNP aqueous solution	Inhibition of ethylene production, respiration rate, activity of ACC synthase and reduction of ACC content.	[45]
	SNP at 10 µmol l^{-1}	Higher concentration harmed the fruits.	
	1 µmol l^{-1} SNP	It's too low to significantly extend strawberry storage life.	
Longan	5 min dip in 1 mM sodium nitroprusside (SNP)	Modulation of the phenolic metabolism for reduced browning. Inhibition of the *in vitro* activities of PPO and POD.	[46]
Plum fruit	SNP donor	Inhibition of pectin solubilisation and depolymerisation, reduced phenolic content, increase in titratable acidity, lower DPPH Radical scavenging activity, chilling injury protection.	[38]
Apple slices	DETANO	Inhibition browning of fruits	[39]
Banana slices	SNP	Inhibition of ACO activity and transcription of gene MA-ACO1, PG, PME, and endo-β-1,4-glucanase and maintained higher contents of ASP and starch	[47]
Jujube fruit	NO fumigation	Inhibition of PPO and PAL activities, maintained a low total anthocyanin content and a high total phenol content, and delayed the increase of soluble solids and decrease of vitamin C.	[48]

The effects of nitric oxide (NO) on enzymatic browning of harvested longan fruit in relation to phenolic metabolisms. Fruits were dipped for 5 min in 1 mM sodium nitroprusside (SNP), a nitric oxide donor, then packed in 0.03 mm thick polyethylene bags, and finally stored for 6 days at 28 ^{0}C. SNP treatment delayed pericarp browning, inhibited activities of PPO, POD and PAL and maintained a high total phenol content of longan fruit during storage. Furthermore, NO showed a significant inhibition of the *in vitro* activities of PPO and POD, indicating that the beneficial effect of NO was direct. Moreover, application of NO resulted in a lower pulp breakdown and maintained relatively high levels of total soluble solids and ascorbic acid [46].

Conclusion

It can be concluded that Nitric Oxide & 1-MCP plays significant role in postharvest physiology of fruits by reducing ethylene biosynthesis and rate of respiration. The functional qualities of fruit can be preserved by application of both Nitric Oxide & 1-MCP. Fruit quality attributes (firmness, TSS, acidity etc.) can be maintained by Nitric Oxide & 1-MCP treatments during postharvest storage. Exogenous application of Nitric Oxide & 1-MCP reduces browning in tropical and subtropical fruits and disease incidence during storage.

Future Prospectus

The future line of work should be to understand its mechanism of action in postharvest physiology of fruits. Research should be done for specific recommendations according to crop and variety as the internal ethylene production and responses are changes accordingly.

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