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Postharvest Biology and Handling of Banana Fruit

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ABSTRACT

Banana (*Musa* sp.) is one of the most economically important fruit crops in the world. The banana fruit is generally harvested and stored in a mature green state. Fruit ripening involves a transient burst in ethylene production that coordinates ripening-associated process. These processes include the respiratory climacteric, pulp softening, peel de-greening, and production of aroma compounds. Avoidance of exposure to ethylene and control of endogenous ethylene synthesis are key measures for banana storage. Other important factors that influence banana fruit storage life are pathogen development, mechanical damage, and variable maturity. The interaction of these factors can lead to uneven and unpredictable ripening that has adverse implications for marketability. Low temperature storage is highly effective in reducing decay and extending the storage life of harvested banana. However, banana fruit are chilling sensitive and storage at sub-optimal temperatures results in injury symptoms that include peel discoloration and abnormal ripening. These symptoms are common when banana fruit are stored at temperatures below about 13°C. Controlled atmosphere (CA) storage or modified atmosphere (MA) packaging constitute adjunct or alternative technologies to extend the green life of harvested fruit. These technologies can be effective at ambient temperatures, particularly in combination with the use of ethylene absorbing compounds and/or treatments that prevent ethylene action or inhibit rots. However, if CO_2 concentrations become too high, the fruit may fail to ripen normally. The relatively recently introduced ethylene binding site blocker, 1-methylcyclopropene (1-MCP), can effectively inhibit ethylene action on banana fruit. Applied as a gas, like ethylene, 1-MCP has demonstrated potential for the modulation of ripening and senescence processes in banana fruit. Overall, postharvest research on banana fruit remains focused on control of ethylene synthesis and action and on suppression of disease development, including by chemical-free means.

Keywords: disease, ethylene, physiology, ripening, storage
Abbreviations: 1-MCP, 1-methylcyclopropene; **ABA**, abscisic acid; **ACC**, 1-aminocyclopropane-1-carboxylic acid; **ACO**, 1-amino-cyclopropane-1-carboxylic acid oxidase; **ACS**, 1-aminocyclopropane-1-carboxylic acid synthase; **ATP**, Adenosine triphosphate; **CA**, controlled atmosphere; **Chl**, chlorophyll; **CI**, chilling injury; **GA**, gibberellic acid; **IAA**, indole-3-acetic acid; **MA**, modified atmosphere; **N_2O**, nitrous oxide; **NO**, nitric oxide; **PAL**, phenylalanine ammonia lyase; **PEP**, phosphoenolpyruvate; **PG**, polygalacturonase; **PEL**, pectate lyase; **PME**, pectin methylesterase; **PPO**, polyphenol oxidase; **RH**, relative humidity; **SPS**, sucrose phosphate synthase and **SuSy**, sucrose synthase

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Invited Review

INTRODUCTION

Banana is one of the most economically important fruit crops. Banana production in the world was about 68 million metric tons in 2005, with India, Brazil, China, the Philippines, Ecuador, and Indonesia contributing 63% of the total production (**Table 1**; FAO 2005). In the international fruit trade, banana ranked 1st and 2nd among all fruits in terms of quantity and value, respectively. Ecuador was the biggest banana exporter, followed by the Philippines, Costa Rica and Columbia. These four countries accounted for 54% of total export quantity in 2005 (FAO 2005).

Bananas are perennials grown and harvested year-round. Banana fruit have a short postharvest life of approximate 10-15 days at ambient temperatures. This short postharvest longevity limits trade and consumption, especially in developing countries. In places such as China and India, there is a shortage of cold chain facilities. The main factors affecting banana fruit quality are rapid physiological deterioration, physical damage, decay, chilling injury and uneven and unpredictable ripening. Postharvest technologies have been developed to maintain postharvest quality and extend the postharvest life of banana fruit. Moreover, research on postharvest biology and technology for banana fruit continues at a rapid pace. This overview considers the current status of postharvest research on banana fruit, with an emphasis on postharvest handling.

POSTHARVEST BIOLOGY

Respiration

Banana is a typical climacteric fruit. It undergoes a rapid increase in ethylene synthesis, followed by a 4- to 5-fold increase in respiration rate as indicated by CO_2 production during ripening (Barket and Solomos 1962; Pathak *et al*. 2003). CO_2 production by banana fruit in the climacteric phase is attributed to an increased flux of carbon through the glycolytic pathway to mitochondria, accompanied by conversion of starch to sucrose (Beaudry *et al*. 1987, 1989; Hubbard *et al*. 1990; Liu *et al*. 2004). The enhanced glycolytic flux in association with mitochondrial respiration rise in the climacteric period can generate adenosine triphosphate (ATP) for the conversion of starch to sucrose (Hill and Rees 1994).

Initiation of the respiratory climacteric in bananas fruit during ripening is correlated with activation of cytosolic pyruvate kinase and/or PEP carboxylase, which control phosphoenolpyruvate (PEP) and pyruvate contents, respectively (Beaudry *et al*. 1989; Ball *et al*. 1991). Complex allosteric control of pyruvate kinase and PEP carboxylase is the model for control of cytosolic glycolysis and PEP partitioning during banana fruit ripening (Law and Plaxton 1995, 1997; Turner and Plaxton 2000). Another important respiration rate-controlling step in glycolysis in banana fruit is reversible phosphorylation, i.e. fructose 6-phosphate to fructose 1,6-bisphosphate by fructose 1,6-bisphosphatase, ATP-dependent phosphofructokinase and/or PPi-dependent phosphofructokinase (Beaudry *et al*. 1987, 1989; Ball *et al*. 1991). Turner and Plaxton (2003) suggested that the primary and secondary control of glycolytic flux in banana cultivar 'Cavendish' during ripening is exerted as the level of PEP and fructose 6-phosphate metabolism, respectively. In banana fruit, there appears to be little or no contribution to electron transport by the alternate oxidase in the climacteric phase (Theologis and Laties 1978). The mechanisms of the initiation of the respiratory climacteric in harvested bananas fruit, concerning respiration pathways, merits further investigation.

Ethylene

Ethylene plays an important role in ripening and senescence of harvested fruits. Ethylene, applied at as low as 0.1 μl/l for 1 day is normally sufficient to initiate banana ripening (Chang and Hwang 1990). Two ethylene production systems operate in harvested banana fruit. The low basal rate of ethylene production is contributed to System 1 ethylene. System 2 ethylene is responsible for the autocatalytic climacteric rise in ethylene production (McMurchie *et al*. 1972). In higher plants, ethylene is biosynthesized from methionine via a pathway in which 1-aminocyclopropane-1-carboxylic acid synthase (ACS) and 1-aminocyclopropane-1-carboxylic acid oxidase (ACO) catalyze the reactions of *S*-adenosylmethionine conversion to 1-aminocyclopropane-1-carboxylic acid (ACC) and ACC conversion to ethylene, respectively (Yang and Hoffman 1984; Wang *et al*. 2002). ACS and ACO have been isolated and purified from banana fruit, and both enzymes appear to be encoded by multigene families (Liu *et al*. 1999; Do *et al*. 2005; Huang *et al*. 2006). In banana fruit cultivar 'Grand Nain', ethylene production is at least partially regulated by transcriptional

Table 1 Total production, area harvested, export quantity and export value of bananas in the major producing countries in 2005 (data from FAO 2005).

Country	Total production (1000 tonnes)	Area harvested (1000 Ha)	Export quantity (1000 tonnes)	Export value (million $)
India	11,710	404	13	4
Brazil	6,703	491	211	51
China	6,667	274	42	18
Philippines	6,298	417	1,964	735
Ecuador	6,118	221	4,085	1260
Indonesia	4,503	315	3	1
Costa Rica	2,353	48	1,597	513
Mexico	2,250	76	64	22
Thailand	1,865	140	25	7
Colombia	1,765	64	1381	453
Burundi	1,539	303	0	0

levels of *MA-ACS1* until the climacteric rise and by reduction of ACC oxidase activity possibly through limited *in situ* availability of its cofactors once ripening has commenced, which in turn characterizes the sharp peak of ethylene production (Liu *et al*. 1999). Golding *et al*. (1998) showed an involvement of a negative feedback regulatory mechanism in ethylene biosynthesis in banana fruit once ripening commenced. Inaba *et al*. (2007) found that exposure of 'Grande Naine' banana fruit ripened previously by propylene treatment to 1-MCP increased ethylene production concomitantly with an increase in ACS activity and ACC content, and prevented a transient decrease at the *MA-ACS1* transcript in the pulp. In contrast, in the peel of ripened fruit, 1-MCP treatment delayed the increase in ethylene production with subsequent ripening by reduction of the increase in the *MA-ACS1* and *MA-ACO1* transcript levels and inhibition of ACS and ACO activities. Therefore, it was suggested that ethylene biosynthesis in ripening banana fruit may be negatively controlled in the pulp tissues, but positively in the peel tissues at the transcriptional level. As with the respiratory climacteric, the detailed mechanism of regulation of ethylene production in the banana fruit still needs to be fully elucidated.

Volatiles

The aroma compounds of banana fruit consist mainly of 3-methylbutyl esters, acetates, butanoates, pentan-2-one, esters, alcoholic compounds, esters, alcohols, aldehyde, ketone, heptyl-acetate, isoamyl acetate, 2-methylbutyl acetate, and 2-heptyl acetate (Tressl *et al*. 1970; Shiota 1993; Nogueira *et al*. 2003; Pino *et al*. 2003). Perez *et al*. (1997) found 25 free volatiles and 25 glycosidically bound volatiles from 'Valery' and 'Pequena Enana' banana pulp using an Amberlite XAD-2 column. The free volatiles were identified as an ester, 14 alcohols, 2 aldehydes, 4 acids, 2 ketones and 2 terpenes (**Table 2**). Aromatic compounds are synthesized during banana fruit ripening (Salmon *et al*. 1996). For green 'Grande Naine' banana fruit, only two major peaks identified as isoamyl acetate and butyl acetate were found, whereas many peaks were detected for overripe banana fruit (Boudhrioua *et al*. 2003). Constituent volatile compounds in banana fruit may vary with differences in cultivars, geographic origin and postharvest handling protocol.

Starch and sugar

Starch is the principal component of green banana fruit. It constitutes approximately 20-25% of the fresh weight or about 85% of the dry weight of the pulp tissues in mature unripe fruit. During the climacteric phase, starch is rapidly degraded and most of the polysaccharide is converted into soluble sugars, mainly sucrose (Lii *et al*. 1982; Cordenunsi and Lajolo 1995).

Starch–sucrose transformation during banana fruit ripening involves a series of enzymes and their related pathways (Zhang *et al*. 2005). It is generally accepted that β-amylases play a key role in starch degradation in banana fruit. These amylases hydrolyze β-1,4-glucosidic linkages in starch and remove successive maltose units from the non-reducing ends of the chains. Garcia and Lajolo (1988) found that β-amylase activity increased before the initiation of the respiration climacteric, paralleling with the decrease in starch, while activities of α-amylase and glucosidase increased significantly only at the climacteric peak when the starch had already been degraded. Nascimento *et al*. (2006) reported that β-amylase activity in 'Nanicao' banana fruit was well correlated to the decrease in starch, suggesting the primary up-regulation by *de novo* synthesis. In 1-MCP-treated fruit, the amount of β-amylase protein was almost undetectable even though there was a strong induction of transcription. Similar results were found by Purgatto *et al*. (2001) and Rosecler *et al*. (2003) in 'Nanicao' banana fruit treated with indole-3-acetic acid (IAA) and gibberellic acid (GA). These findings confirmed that activity of β-amylases is essential for starch degradation in banana fruit during ripening.

Sucrose synthase (SuSy) and sucrose phosphate synthase (SPS) are key enzymes in sucrose metabolism. Cordenunsi and Lajolo (1995), Nascimento *et al*. (1997) and Nascimento *et al*. (2000) investigated the changes in SuSy and SPS activities during development and ripening of harvested 'Nanicao' banana fruit and also the changes in carbohydrates in fruit left to ripen on the plant. SPS was present during fruit development, but at a very low activity level. SuSy activity was high and remained constant throughout the entire starch synthesis phase, followed by a reduction during starch breakdown and disappearance in the post-climacteric phase. Slower starch breakdown was related to lower sucrose content and SPS activity, but higher SuSy

Table 2 Free and glycosidically bound volatile compounds in 'Pequena Enana' banana fruit (data from Perez *et al*. 1997).

Free volatile compounds	ng/g (FW)	Glycosidically bound volatiles	ng/g (FW)
Methyl acetate	2.62	3-Methylbutanoic acid	12.2
Ethyl acetate	0.48	4-Methylhydroxypentan-2-one	2.74
Butan-2-one	0.17	Hexanol	1.18
Benzene	0.13	Hexanoic acid	10.52
Pentan-2-one	1.27	Hex-3-enoic acid	6.54
Butyl acetate	0.15	Hex-2-enoic acid	
Toluene	0.10	2-(2-Ethoxyethoxy)ethanol	4.16
3-Methylbutyl acetate	0.76	Benzoic acid	5.42
2-Methylpropanol	0.22	2-Phenylethydecane	7.08
Pentyl acetate	0.03	2,5,6-Trimethyldecane	4.72
Pentan-2-ol	0.75	Phenylacetic acid	2.10
2-Methybutyl butanoate	0.01	Decan-1-ol	12.36
Butan-1-ol	0.18	3-Oxo-pentanoic acid	12.64
Hex-2-enal	0.04	Eugenol	8.00
2-Pentyl 2-methylpropanoate	0.04	γ-Decalactone	9.70
2-Butyl butanoate	0.01	9-Oxononanoic acid	1.68
3-Methylbutanol	0.19	Dodecanoic acid	1.92
3-Methylbutyl butanoate	0.01	Elimicine	5.42
2-Buthoxyethanol	0.10	3,4-Dimethoxyacetopenone	4.18
Acetic acid	0.38	Methyleugenol	0.94
Methyl decanoate		2-Furyloctanoic acid	13.38
Propanoic acid	0.12	Jasmonic acid	3.46
3-Methylbutanoic acid	0.08	3,4,5-Trimethoxyacetophenoone	2.36
Butanoic acid	0.14	Tetradecanoic acid	8.22
Pentanoic acid	0.19	Hexadecanoic acid	

activity, for attached fruits as compared to detached fruits. Therefore, it seems that SPS is more important than SuSy for starch degradation during banana ripening.

During natural ripening of banana fruit, there is modulation of the activity for starch-metabolized enzymes related to sucrose biosynthesis, such as SuSy and SPS (Cordenunsi and Lajolo 1995). The conversion of starch to sucrose is the result of the combined action of these enzymes. Purgatto *et al*. (2001) reported that GA treatment delayed starch degradation and sucrose formation of harvested 'Nanicao' banana. However, SuSy and SPS activities and their transcript levels were not affected, indicating no direct relation of these sucrose-metabolizing enzymes to prevention of sucrose accumulation. Impairment of sucrose synthesis could be a consequence of lack of substrate, since starch degradation was inhibited. Nascimento *et al*. (1997, 2000) suggested that substrate limitation could play an important role in the regulation of starch breakdown of harvested 'Nanicao' banana because SPS and SuSy activities were shown to be up- and down-regulated, respectively. Thus, starch degradation and sugar biosynthesis in banana fruit during ripening might be, at least partially, controlled at the transcriptional level.

Texture

Texture is usually expressed as fruit firmness and is an important quality attribute of harvested banana fruit. Textural changes during ripening of banana fruit result from the structural and compositional modification in cellular walls. Decrease in fruit texture (softening) is mainly attributed to solubilisation and depolymerisation of cell wall polysaccharides, including pectins, hemicellulose and cellulose by a series of activities of hydrolase, transglycosylase and proteins, such as expansins. The major enzymes, involved in fruit firmness changes during ripening of banana fruit, are polygalacturonase (PG), pectin methylesterase (PME), pectate lyase (PL), cellulose, β-glucanase, and β-galactosidase (Prabha and Bhagyalakshmi 1998; Peumans *et al*. 2000; Pua *et al*. 2001; Marin-Rodriguez *et al*. 2003; Payasi and Sanwal 2003; Ali *et al*. 2004; Lohani *et al*. 2004; Asif and Nath 2005; Imsabai *et al*. 2006). Ali *et al*. (2004) suggested that PG, PME, (1→4)-β-glucanase and β-galactosidase might contribute importantly to 'Mas' banana fruit softening. However, Lohani *et al*. (2004) reported that the activities of PG and cellulase increased sharply during softening of 'Harichhal' banana fruit but PME activity increased gradually. Recent study indicated that fruit softening in 'Harichhal' banana results from the downstream effects of at least four PG genes which are differentially expressed at various ripening stages. *MAPG3* and *MAPG4* are believed to be ripening-related and regulated by ethylene, whereas *MAPG2* was associated more with senescence (Asif and Nath 2005).

Degradation of pectins requires the combined action of methylesterases, which remove methoxy groups from pectin, and depolymerases, which cleave the bonds between galacturonate units. Pectate lyase (PEL) catalyzes the cleavage of (1→4) galacturonan linkages of pectate by a β-elimination reaction, generating 4,5-unsaturated oligo-galacturonates. Payasi and Sanwal (2003) reported that PEL activity was not detected in preclimacteric 'Harichhal' banana fruits, but increased progressively from the early climacteric phase, then reached maximum level at climacteric peak, and finally declined in postclimacteric phase, indicating that PEL might play a role in fruit softening. PELs have been purified and characterized from banana fruit (Payasi and Sanwal 2003). Pua *et al*. (2001) and Marin-Rodriguez *et al*. (2003) cloned PEL genes in 'Williams' and 'Grande Naine' banana pulp and found that transcripts of two PEL cDNAs were not detectable in unripe preclimacteric fruits. However, they began to accumulate as ripening progressed and remained at a high level in overripe fruit, which supports the role of PEL in fruit softening.

Apart from the hydrolases discussed above, expansins, a class of proteins inducing extension of cellular walls in a pH-dependent manner, are required for fruit softening (Brummell and Harpster 2001; Hayama *et al*. 2003; Sane *et al*. 2005). Expansins have been identified from 'Harichhal' and 'Williams' banana fruits and they are associated with fruit maturation and softening (Trivedi and Nath 2004; Wang *et al*. 2006). However, as with most aspects of banana ripening physiology and biochemistry, the detailed mechanistic role of expansins in fruit softening needs to be further investigated.

Colour

Peel colour is the most obvious character that changes during banana fruit ripening and is the major eating criterion for consumers. The typical change during ripening is loss of green and appearance of yellow. The loss of green colour is due to chlorophyll (Chl) degradation from approximate 50-100 mg/g fresh weight (FW) to almost zero in ripe fruit (Seymour 1993). The Chl degradation pathway in higher plants has been largely elucidated (Matile *et al*. 1999; Hortensteiner 2006). There might be two Chl degradation pathways in banana fruit, the chlorophyllase and chlorophyll oxidase pathways (Janave 1997). Janave and Sharma (2004) confirmed the presence of chlorophyllase, magnesium-dechelatase, pheophorbide a oxygenase, red fluorescent catabolite reductase and Chl oxidase in banana peel tissues.

Chl catabolism of banana fruit may differ somewhat when the fruit is held at high temperature, which inhibits Chl degradation (Seymour *et al*. 1987). Matile *et al*. (1996) suggested that Chl should be solubilized from the thylakoid membranes prior to degradation and is apparently transported to the chloroplast envelope, where chlorophyllase is located. Ultrastructure studies of banana fruit peel tissues reveals that thylakoid membranes are retained to degree in the fruit ripened at high temperature, which may hinder release of Chl from thylakiod membranes to the chloroplast envelope, resulting in inhibition of the Chl degradation (Blackbourn *et al*. 1990). Drury *et al*. (1999) reported that the colour-degraded products of 'Grande Nain' banana fruit, chlorophyllide and pheophorbide, were not detected at any stage of fruit ripening at 20 or 35°C. However, a non-fluorescent Chl product accumulated to a higher concentration at 20°C than at 35°C, indicating that the 'stay-green' effect of fruit ripening at 35°C was not due to inhibition of pheophorbide a oxygenase. The biochemical mechanism of Chl breakdown in banana fruit skin during ripening at high temperature requires a full investigation.

Chilling injury

Chilling injury (CI) is a physiological disorder in banana and other subtropical and tropical fruit, which occurs upon exposure to low, but non-freezing, temperatures. Storage of banana below 13°C can lead to the development of CI (Wills *et al*. 1998). The CI symptoms depend on cultivar, maturity, and temperature by time of low temperature exposure (Nguyen *et al*. 2003; Wang *et al*. 2006). The most common visual symptoms of CI on banana fruit are a dull yellow skin, browning of the skin, failure to ripen, hardening of the central placenta, increased susceptibility to mechanical injury, and in severe cases, flesh browning (Jiang *et al*. 2004; Ratule *et al*. 2006).

Cellular membrane damage is typically an early CI response (Marangoni *et al*. 1996). Low temperature-induced changes in the physical properties of cell membranes, due to modifications in the physical state of membrane lipids, cause imbalances in metabolism. Consequences of disruption to the various membranes are breakdown of cellular compartmentalization, loss of function of membrane-associated proteins, death of the cells and the appearance of CI symptoms (Marangoni *et al*. 1996; Wills *et al*. 1998). Ethylene binding is intrinsic to cellular membranes and CI of 'Williams' banana fruit appears to be associated with suppressed ethylene binding capacity, resulting in a failure of

fruit ripening and softening (Jiang *et al*. 2004). Wang *et al*. (2006) suggested that ethylene might alleviate CI of 'Williams' banana fruit. Increased tolerance of banana fruit pretreated with propylene to low temperature-induced chilling was related to higher post-storage ethylene production rates and enhanced expression of *MaExp*1 and *MaExp*2.

When subjected to chilling, browning of the banana fruit is associated with oxidation of phenolic compounds. Nguyen *et al*. (2003) reported that CI development in 'Kluai Khai' and 'Kluai Hom Thong' banana fruit peel was highly and inversely correlated with the level of free phenolic compounds, and highly and positively correlated with the activities of polyphenol oxidase (PPO) and phenylalanine ammonia lyase (PAL). Modified atmosphere conditions reduced CI symptoms, which was related to the decreases of PAL and PPO activities in peel tissues (Nguyen *et al*. 2004). The increase of membrane permeability was responsible for decompartmentalization between PPO (enzyme) and phenolic compounds (substrates), and peel browning (Nguyen *et al*. 2003; Ratule *et al*. 2006). Some pretreatments, including with abscisic acid (ABA), jasmonic acid derivative and putrescine, help maintain partial membrane integrity in banana fruit peel at low temperature and, thereby, alleviate CI (Chaiprasart *et al*. 2002; Wang *et al*. 2003). The degree of CI may be mediated by the level of endogenous antioxidant activity. Wang *et al.* (2003) found that infiltration treatment with 200 µM ABA and 5 mM putrescine enhanced superoxide dismutase and peroxidase activities, and delayed the appearance of CI of 'Brazil' banana fruit stored at 8°C. Kondo *et al*. (2005) suggested that the concentrations of endogenous jasmonate, total phenolics and ascorbic acid, superoxide dismutase activity were linked to the degree of CI of 'Namwa' banana.

FACTORS AFFECTING STORAGE LIFE

Fruit maturity

Maturity at harvest determines the potential storage life and final banana fruit quality. Bananas are harvested at green mature stage and are ripened at or near the marketplace. The more mature banana fruit is at harvest, the shorter it is ripening period (Madamba 1977). Immature fruit are more subject to shrivelling and mechanical damage, and are of inferior flavour quality when ripe (Kader 1999; Ahmas *et al*. 2001). They also constitute reduced yield in terms of saleable weight. Moreover, fruit picked either too early or too late in their season are more susceptible to postharvest physiological disorders than fruit picked at optimum maturity (Kader 1999). Within the harvest maturity band, the green mature stage at which bananas are harvested is determined by the time required to get them to market.

As banana fruit matures, their cross-sectional diameter increases. Fruit angularity also changes during growth and maturation. As fruit approach full maturity, the angles become less acute. Fruit angularity can be used to predict the optimum harvest date (Sommer and Arpaia 1992).

Temperature

Temperature is generally the most important factor determining the postharvest life of fruits and vegetables, and markedly affects their rates of respiration and general metabolism. Typically, for every 10ºC increase, respiration rate increases between 2- and 4-fold (Wills *et al*. 1998).

Bananas storage life decreased as external temperature increased over the range 15-35ºC. The relationship was logarithmic and described by the equation: $\log g = mT + c$; where, g = preclimacteric period at temperature T, and m and c are constants. A 1ºC reduction increased storage period by 1-2 days (Marriott 1980). Trakulnaleumsai *et al*. (2006) reported that low temperature significantly reduced the senescence symptom of peel spotting, which starts with small browned spots and then becomes large area with advanced ripening, in 'Sucrier' banana fruit. Holding ripening bananas at 15 and 18ºC instead of room temperature (26-27°C) only temporarily reduced spotting. However, peel spotting was completely prevented at 12°C.

To delay ripening and reduce losses, green bananas are shipped and stored at 13-14°C (Sommer and Arpaia 1992). Symptoms of CI generally occur at below 13°C (Hewage *et al*. 1996). Exposure to temperatures higher than 30°C causes heat injury. Some symptoms of heat injury are similar to those of CI, such as browning of the peel and increased moisture loss. Jiang *et al*. (2002) reported that exposure of 'Williams' banana fruit to 45°C for 45 min caused skin browning. High temperature treatment also resulted in increased mass loss. For 'Cavendish' banana fruit, the time leading to a 70% mass loss (wet basis) at 30°C was about twice at 40°C (Nguyen and Price 2007). Furthermore, the skin of heat-injured fruit may fail to turn yellow due to suppressed chlorophyll breakdown. The pulp becomes watery and translucent. The conversion of starch into sugars may not be triggered, and thus the pulp may not sweeten (Blackbourn *et al*. 1990; Zhang *et al*. 1993; Janave 1997).

Water loss and humidity

Water loss can be highly problematical as it results not only in direct quantitative losses in weight, but also in deterioration in appearance, texture and nutritional quality in addition to accelerated and/or exacerbated expression of symptoms of injuries (Akkaravessapong *et al*. 1992; Wills *et al*. 1998). Losses of water reduce turgor (Banks and Joseph 1991), which contribute to decreased firmness and may accelerate the ripening of banana fruit (Burdon *et al*. 1994).

The rate of water loss depends on external and internal factors. External factors include temperature, relative humidity (RH), air movement and atmospheric pressure. At an ambient RH of 95-100%, fruit lose little or no moisture and the ripening period is maximal. As humidity decreases, the rate of water loss increases and the ripening period reduces. Ahmad *et al*. (2006) and Ullah *et al*. (2006) reported that high RH delayed ripening and produced good eating quality of 'Cavendish' banana fruit compared with those held at low humidity. However, wetting (free moisture) can lead to peel splitting and encourage microbial decay (Ullah *et al*. 2006). Thus, the optimum RH for storage of banana fruit is 90-95%.

Internal factors that modulate the rate of water loss include morphological and anatomical characteristics (e.g. surface-to-volume ratio), and surface injury (Wills *et al*. 1998). The greater the surface area to volume ratio, the shorter the postharvest life. Typically, large fruit lose less water than small fruit. Fruit with thin skins lose more water. Higher peel permeability leads to a higher rate of water loss. Also, a higher density of stomata may lead to a higher rate of water loss, which in turn can accelerate ripening (Shaun and Ferris 1998).

Ethylene

As mentioned earlier, the postharvest physiology of banana is characterized by a green life phase followed by a burst in ethylene production that signals the beginning of ripening-associated processes. These processes include the respiratory burst, fruit softening, peel degreening and production of aroma compounds. Ethylene production is essential for ripening of banana fruit, and determines the time from harvest to the respiratory climacteric. That is, it determines the green life or preclimacteric period (Clendennen and May 1997). An atmospheric ethylene concentration of 0.1 µl/l can trigger internal ethylene production and the respiratory climacteric, and thereby shorten the pre-climacteric period (Chang and Hwang 1990).

Exogenous ethylene application is routinely used to initiate uniform ripening of bananas. Conversely, commercial strategies for banana fruit handling, transport and storage are based on avoiding exposure to ethylene and/or attemp-

ting to minimize ethylene production and action. These strategies include temperature and atmosphere control (Wills *et al*. 1998; Marchal 1998; Watkins 2002; Wang 2006). A relatively new strategy for controlling ethylene binding and thus ripening and senescence of fruit is treatment with 1-methylcyclopropene (1-MCP) (Sisler and Serek 2003). 1-MCP effectively delayed banana fruit ripening and thereby extended their green life (Jiang *et al*. 1999b; Sisler and Serek 2003; Watkins 2006). However, the response of harvested banana fruit to 1-MCP is dependent upon fruit maturity, treatment temperature and concentration, and exposure time (Jiang *et al*. 1999b; Harris *et al*. 2000; Bagnato *et al*. 2003; Pelayo *et al*. 2003). One hour exposure at 20ºC to 1000 nl/l 1-MCP gas essentially eliminated ethylene-stimulated ripening effects of mature green 'Cavendish' banana while exposure for 12 h at 20ºC to just 50 nl/l 1-MCP had a similar effect (Jiang *et al*. 1999b).

Mechanical damage

Mechanical damage is a factor contributing to postharvest deterioration of banana fruit. Fruit damage during handling is beneficial for ethylene production. If ethylene production is sufficient to initiate the climacteric response, fruit can ripen prematurely. Loss of fruit weight is another result of mechanical injury, with consequences of lower market quality and price. Accelerated weight loss is due to breakdown of cellular walls and increased permeability of the outer tissue layers to water vapour. Damage can also lead to secondary infection, which further increases the rate of water loss and reduces quality (Dadzie and Orchard 1997; Liado and Domingues 1998; Wills *et al*. 1998).

Disease

Crown rots

Crown rot is a severe postharvest disease in banana-growing areas around the world. It is caused by a complex of fungi, including *Fusarium roseum*, *F. proliferatum*, *Lasiodiplodia theobromae*, *Thielaviopsis paradoxa*, *Verticillium theobromae*, *Nigrospora sphaerica*, *Deightoniella torulosa*, and *Colletotrichum musae* (Sommer *et al*. 1992; Ploetz 1998; Ranasingle *et al*. 2002). Inoculations with various combinations of fungi show that the greatest damage results from combinations of *T. paradoxa*, *L. theobromae*, *C. musae* and *D. torulosa* (Sommer *et al*. 1992). The disease is characterized by darkening of the hand and adjacent peduncle and loss of the ability of the hand to support the fruit (Sommer *et al*. 1992). Specific visual symptoms of this disease include blackening of tissues at the cut crown surfaces and a spreading grayish-white, pink or white mold on the cut crown surface (Ploetz 1998). Banana leaves, flowers, bracts, and transitional leaves are commonly colonized by the causal fungi. When the banana hands are harvested in the field, latex flows from the cut surface of the crown and spores of the fungi may enter the wound and initiate disease development. Once initiated, infection can progress from the crown into the pedicels and eventually into the fingers (Krauss and Johanson 2000).

Anthracnose

Anthracnose is another important postharvest disease of banana fruit that occurs in all producing areas. This disease is caused by *Colletotrichum musae*, which infects both green and ripe fruit. However, the symptom becomes evident as the fruit ripen, especially in wounds (Ploetz 1998).

C. musae typically establishes a subcuticular latent infection. Both flower parts and the last bunch (proximal) bract are potential sources of *C. musae* inoculum. Conidia of *C. musae* contaminate bananas during the month after flowering and may spread in rainwater trickling over the bunch. Conidia quickly germinate and may form a melanized appressorium (Muirhead and Deverall 1981; De Lapeyre De Bellaire and Mourichon 1997b; De Lapeyre De Bellaire *et al*. 2000a). Appressoria send out infection pegs and form limited infection hyphae, giving rise to quiescent anthracnose (Swinburne and Brown 1983; de Lapeyre de Bellaire and Mourichon 1997b; Chillet *et al*. 2006). If the bananas are bruised, rot can develop in green banana fruit and then the lesions expand as the fruit ripens (Chillet *et al*. 2006). This wound anthracnose form can trigger an early fruit ripening (Peacock 1973).

It has been reported that ethylene can trigger *C. musae* infections, accelerate conidial germination and increase appressorial number in relation to banana anthracnose (Flaishman and Kolattukudy 1994; de Lapeyre de Bellaire *et al*. 2000b). However, Chillet *et al*. (2006) determined that ethylene was not directly involved in triggering rot development as quiescent anthracnose symptoms appeared only after 'Grande Naine' banana fruit began ripening. In contrast, wound anthracnose developed just as quickly in 'green 1-MCP-treated bananas' as in 'yellow ripening bananas'. For wound anthracnose, contrary to quiescent anthracnose, rot development was not dependent on the degree of peel ripeness.

Other postharvest diseases

Other commercially postharvest disease of banana fruit include cigar-end rot (*Trachysphaera fructigena* and *V. theobromae*), finger or stem-end rot (*L. theobromae*), thielaviopsis or ceratocystis rot (*T. paradoxa*), pitting disease (*Pyricularia grisea*), squirter disease (*N. sphaerica*) and speckle and black tip (*D. torulosa*) (Sommer *et al*. 1992; Ploetz 1998). All of these diseases can reduce the quality and postharvest longevity of the fruit.

POSTHARVEST TECHNOLOGY

Modified atmosphere (MA) and controlled atmosphere (CA)

The biochemical basis of MA/CA is to extend the longevity of fruit by slowing metabolic processes at high CO_2 concentrations and low O_2 levels (Yahia 1998; Wang 2006). Optimal compositions of CA and MA storage for fresh produce vary according to its genotype and maturity or ripeness stage, and treatment temperature and duration (Wills *et al*. 1998).

MA storage has been used for several decades for marine shipment of bananas (Scott and Roberts 1966; Woodruff 1969). Storage of bananas under the MA condition is primarily achieved using low-density polyethylene (LPDE) bags (Truter and Combrink 1990; Stiles 1991; Chamara *et al*. 2000). Green mature 'Cavendish' bananas may be stored in LDPE bags (0.05 mm thickness) for up to 30 days at 14°C with ripening and sensory quality during shelf not being adversely affected (Hewage *et al*. 1995). Polyvinyl chloride film (0.01 mm thickness) packaging also prolonged the shelf life of 'Sucrier' banana fruit at peel stage 3 (more green than yellow) to 6-7 days at 20°C, compared with 3-4 days in the control (Choehom *et al*. 2004; Romphophak *et al*. 2004). Longevity may be extended using an ethylene absorber, such as potassium permanganate in combination with polymer films (Scott *et al*. 1970; Jiang *et al*. 1999a; Chamara *et al*. 2000). Ketsa *et al*. (2000) reported that bulk packaged 'Sucrier' bananas stored in non-perforated polyethylene (PE) bags with an ethylene absorbent and carbon dioxide scrubber remained green for 6 weeks at 14°C. Thus, MA has repeatedly been shown to be beneficial for long-term storage of banana fruit at low temperature. Apart from conventional MA packaging for bananas, Stemart *et al*. (2005) evaluated the potential of passive silicone membrane and diffusion channel systems to preserve the quality and extend the shelf life of 'Cavendish' banana fruit. Banana fruit could be stored for 42 days at 15°C under MA conditions achieved using these novel systems.

Controlled atmospheres of 2-5% O_2 and 2-5% CO_2 are

considered effective for delaying banana ripening and reducing respiration and the effects of ethylene (Kader 1997). The storage life of green banana fruit was up to 180 days at 20°C when they were ventilated continuously with an atmosphere of 3% O_2, 5% CO_2 and 92% N_2 (Wills *et al*. 1998). However, care must be taken to ensure that sufficient O_2 and not too much CO_2 is retained in the atmosphere. Exposure of banana fruit to less than 1% O_2 and/or more than 7% CO_2 may undesirably affect texture and flavour (Kader 1997). Application of CA to delay ripening during transport has facilitated the picking of bananas at the fully green mature stage.

Coatings

Fruit coatings can modify internal fruit atmospheres and reduce transpiration like MA films and thereby reduce respiratory activity and water loss without adversely affecting fruit taste. Kittur *et al*. (2001) investigated that the effects of four different polysaccharide-based composite coating formulations (chitosan, *N,O*-carboxymethyl chitosan, carboxymethyl derivatives of cellulose and starch, and hydroxylmethyl starch and hydroxypropyl starch) on banana quality maintenance. The fruit treated with polysaccharide-based coatings had retarded colour development, lower acidity and greater firmness compared to the control. CO_2 evolution and loss in weight were also reduced significantly. Coating 'Drawf Cavendish' banana fruit with 'PRO-LONG' inhibited ethylene production in associated with reduction of ACO activity under restricted O_2 and thereby delayed fruit ripening (Dillon *et al*. 1989; Zhang *et al*. 1996). The combination of calcium chloride infiltration with 'Semperfresh' coating achieved more efficient effects than the coating alone (Chukwu *et al*. 1995). Coatings may also form a physical barrier against pathogenic infection, thereby reducing postharvest disease incidence (Ben-Yehoshua 1966; Amarante and Banks 2001).

Anoxia or low oxygen

Anaerobic conditions may occur somewhat during postharvest handling, storage and transport of fruit, for example, during CA or MA storage, or after coating with various waxes. Anaerobiosis can result in off-flavour and generally poor fruit quality. When bananas are held in sealed polyethylene bags for a relatively long time, a green ripe disorder may occur. This disorder is characterized by green remaining in the skin along with pulp softening and off-flavour development (Satyan *et al*. 1992). However, short-term anaerobic conditions might be beneficial for postharvest fruit quality under certain circumstances. Wills *et al*. (1982) reported that exposure of preclimacteric banana fruit to low O_2 for 2-3 days prior to storage in air extended the time required for the fruit to ripen. 2% O_2 stress for 48 h was effective in preventing decay after shelf life. This low O_2 treatment also retarded 'Ziv' banana ripening processes (viz. colour, firmness, respiration and ethylene production) and reduced CI symptoms, without impairing the taste (Pesis *et al*. 2001). Exposure of banana fruit to <1% O_2 or 100% N_2 resulted in a significant reduction in the formation of ethyl acetate, an important volatile compound (Wendakoon *et al*. 2004). Yi *et al*. (2006) found that exposure of 'Brazil' banana fruit to pure N_2 gas for 9 h reduced the rates of ethylene production and respiration, as well as the activities of polygalacturonase and pectin methyl esterase during storage, and thereby effectively inhibited fruit ripening (**Fig. 1**). The ripening retardation may be related to induction of acetaldehyde and ethanol production, which could in turn inhibit ethylene production and action. This process is known to alleviate CI of harvested fruits and vegetables (Duan *et al*. 2003; Pesis 2005). However, anaerobic treatments should be applied carefully and optimised for individual species and temperature regimes.

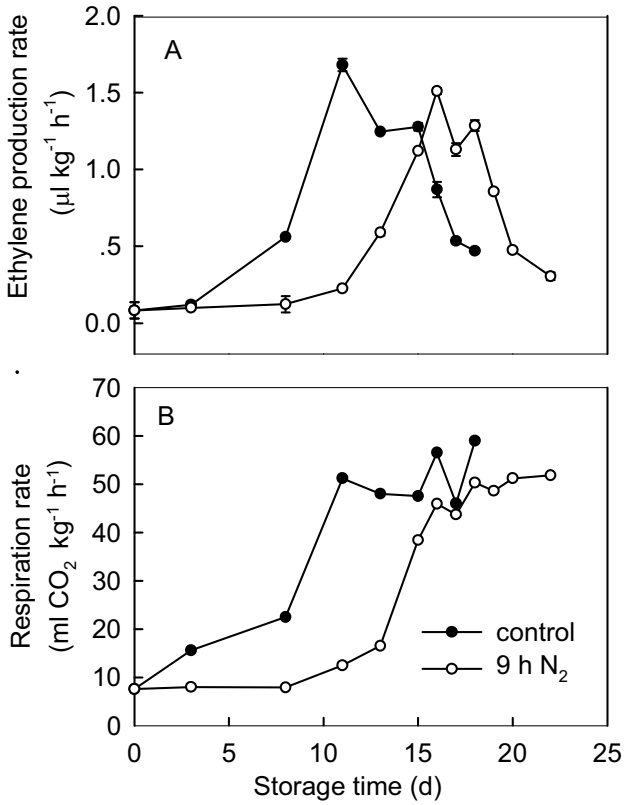

Fig. 1 Changes in the rates of C_2H_4 production (A) and respiration (B) during storage of 9 h N_2-treated and control 'Brazil' banana fruit. Each value is the mean ± standard error (n = 3). Vertical bars indicate the standard errors of the means where they exceed the symbol size (data from Yi *et al*. 2006).

1-Methylcyclopropene (1-MCP)

The ethylene antagonist 1-MCP binds irreversibly to ethylene receptors in plant cells and prevents the ethylene molecule from binding. 1-MCP thereby inhibits ethylene signal transduction and downstream action, effectively delaying ripening and senescence of ethylene sensitive fruits and vegetables. This gaseous compound has been approved for use commercially as a postharvest treatment for a range of climacteric fruits. Exposure to 1-MCP increases the longevity of harvested banana fruit (**Fig. 2**). However, the response is dependent upon fruit maturity, treatment tempera-

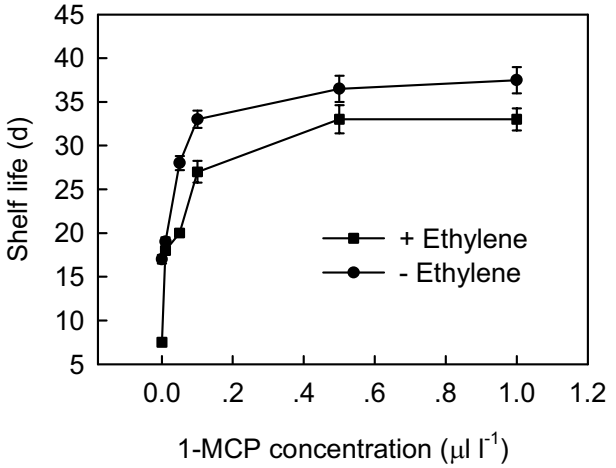

Fig. 2 Changes in the shelf life at 20°C of harvested 'Cavendish' banana fruit treated with 1-MCP for 24 h at various concentrations without (-) or with (+) subsequent ethephon treatment. Each value is the mean for nine fruit, and vertical bars indicate the standard error (data from Jiang *et al*. 1999a).

ture and duration, and 1-MCP concentration (Jiang *et al*. 1999b; Harris *et al*. 2000; Bagnato *et al*. 2003; Pelayo *et al*. 2003). It is now well established that 1-MCP treatment lowers ethylene production and respiration rates (Golding *et al*. 1998, 1999; Pathak *et al*. 2003; Pelayo *et al*. 2003; Lohani *et al*. 2004) and inhibits softening (Jiang *et al*. 1999a, 1999b; Macnish *et al*. 2000; Pelayo *et al*. 2003; Lohani *et al*. 2004) of harvested banana fruit. Colour changes are also delayed in 1-MCP treated banana fruit. A potential concern is that yellowing of banana fruit can be disrupted (i.e. incomplete and uneven), even in the presence of the ethylene analogue propylene (Golding *et al*. 1998; Harris *et al*. 2000; Macnish *et al*. 2000). Moreover, total volatile production of fruit may be inhibited by 1-MCP treatment. Quantitatively, ester concentrations were lower, while concentrations of alcohols were higher in treated fruit (Golding *et al*. 1998). The sugar content was not affected by 1-MCP treatment (Golding *et al*. 1998). 1-MCP treatment may increase the susceptibility to CI of banana fruit. Jiang *et al*. (2004) concluded that the development of CI was associated with decreased ethylene binding.

As noted, the action of 1-MCP is mediated through interacting with receptors and competing with ethylene for these binding sites (Sisler and Serek 2003). The ripening response of fruit treated with 1-MCP and subsequently treated with ethylene varies with the interval of time between 1-MCP and ethylene treatments. As the time lag is increased, new binding sites are synthesised and delayed ripening effect weakens (Jiang *et al*. 1999b). Synthesis of new binding sites can be affected by temperature. Temperature between 30 and 40°C result in faster recovery of 'Williams' banana fruit ripening capacity. Also based on the temperature action, application of 1-MCP at 2.5°C is less effective than at 15 and 20°C. This observation suggests that binding of 1-MCP at low temperatures was incomplete (Jiang *et al*. 2002, 2004).

ACO and ACS are the rate-controlled enzymes of the ethylene biosynthetic pathway. In banana fruit, inhibition of ethylene production by 1-MCP was associated with both lower expression and lower activities of ACO and ACS (Pathak *et al*. 2003; Zhang *et al*. 2006). In addition, delayed softening in 1-MCP treated banana is related to lower expression of an ethylene induced expansin (*Maexp1*) gene (Trivedi and Nath 2004) and lower activities of pectin methylesterase, polygalacturonase, endo-β-1,4-glucanase and pectate lyase (Lohani *et al*. 2004).

Plant growth regulators

On the basis of ethylene evolution and respiration, it was found that ripening of banana fruit was hastened by ABA and 2,4-dichlorophenoxy acetic acid and delayed by IAA and GA treatments (Pathak and Sanwal 1999; Jiang *et al*. 2000; Lohani *et al*. 2004). Climacteric respiration of 'Nanicao' banana was reduced and starch degradation and sucrose formation were delayed by the action of IAA. However, SuSy and SPS activities and transcript levels were not affected, the increase in the activity and transcript level of β-amylase was delayed by IAA treatment. Thus, prevention of sucrose accumulation by IAA was not related to sucrose-metabolizing enzymes, but was apparently a consequence of lack of substrate due to inhibition of starch degradation (Purgatto *et al*. 2001). GA delayed sucrose synthesis of 'Nanicao' banana by disturbance of sucrose-phosphate synthesis, but it had no effect on sucrose synthase (Rosecler *et al*. 2003). Application of the secondary messenger compound salicylic acid (SA) at 500 μmol/l and 1000 μmol/l also delayed ripening of 'HariChhal' banana fruit in association with decreases in respiration rate, fruit softening and the activities of major cell wall degrading enzymes (Srivastava and Dwivedi 2000).

Nitric oxide (NO) and nitrous oxide (N_2O)

N_2O is a naturally occurring atmospheric gas, the primary source of which is soil containing aerobic denitrifying bacteria (Firestone and Davidson 1989). NO is synthesized in animals, plants and microorganisms (Crawford 2006). Recently, N_2O and NO have been shown to have anti-senescence and ripening properties. N_2O and NO treatments have been found to extend the storage and marketing life of a range of fruits, vegetables and flowers (Gouble *et al*. 1995; Bowyer *et al*. 2003; Badiyan *et al*. 2004; Soegiarto and Wills 2004).

Palomer *et al*. (2005) reported that 'Cavendish' banana fruit ripening was significantly delayed by N_2O within the concentration range from 20 to 80%. Delayed ripening was judged by effects on both ethylene synthesis and respiration rate in association with changes in fruit colour, acidity and softening. This response to N_2O was dose- and time-dependent. Combinations of N_2O with low O_2 (8 and 12%) in controlled atmospheres had a synergistic effect on the ripening-delay capacity of N_2O. The ability of N_2O to slow down fruit ripening is thought to be due to inhibition of ethylene synthesis and action (Gouble *et al*. 1995).

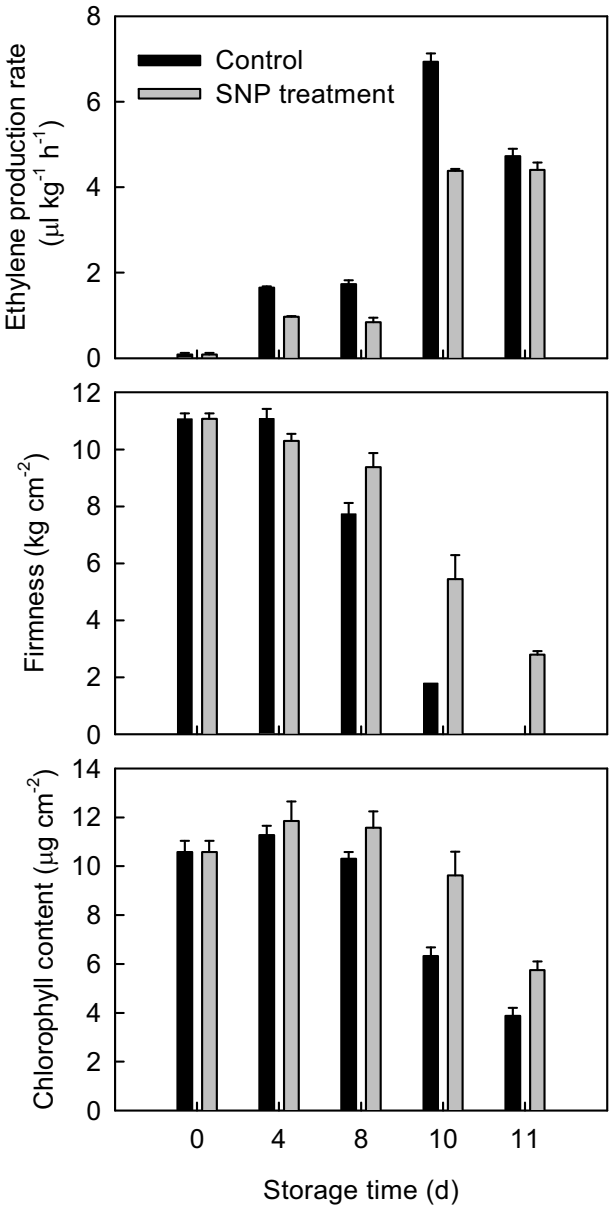

Fig. 3 Effect of the NO donor, sodium nitroprusside (SNP) on ethylene production rate (A), firmness (B), and chlorophyll content (C) of 'Brazil' banana fruit during storage at 28°C. SNP was used in 5 mM concentration. Each data point represents a mean ± standard error (n = 3) (data from Duan *et al*., unpublished).

Evidence of interplay between NO and ethylene in the maturation and senescence of fruit suggests an antagonistic effect of these gases. Unripe green banana fruit contain high NO and low ethylene concentrations. The maturation process is accompanied by a marked decrease in NO concomitant with an increase in ethylene (Leshem *et al*. 1998). Certainly, NO treatment can significantly decrease ethylene biosynthesis, delay pulp softening and peel degreening, and prolong the shelf life of 'Brazil' banana fruit (**Fig. 3**).

Control of postharvest disease

Chemicals

Control of most postharvest diseases in banana fruit is through application of fungicides as a dip or spray (Wills *et al*. 1998; Krauss and Johanson 2000). In the past, the most commonly used fungicides were benzimidazoles, such as benomyl and thiabendazole (TBZ). This class of fungicides inhibits spore germination, interferes with mycelial growth and affects conidia formation by interrupting polymerization of the tubulin protein (Wills *et al*. 1998). However, *C. musae* has developed resistance to these fungicides (de Lapeyre de Bellaire and Dubois 1997a). When control breaks down, trizaoles such as imazalil and prochloraz may be used, usually alternated with TBZ. Trizaoles inhibit demethylation processes during ergosterol biosynthesis within the fungus (Wills *et al*. 1998; Krauss and Johanson 2000; Khan *et al*. 2001).

Considering potential adverse environmental and health effects and also resistance development by pathogens to fungicides, it is desirable to develop alternatives to conventional fungicides. Alvindia *et al*. (2004) reported that spore germination of *L. theobromae*, *T. paradoxa*, *C. musae*, *C. gloeosporioides*, *F. verticillioides*, and *F. oxysporum* was completely inhibited by NaClO at 5 g/l and each of $NaHCO_3$ and $CaCl_2$ at 6 g/l. Dipping banana fruit for 10-15 min in these concentrations reduced the incidence of crown rot compared with the untreated fruits. Incidence at 17 days after harvest was reduced with NaClO by 67%, $NaHCO_3$ by 62%, and $CaCl_2$ by 33%. Postharvest acid (acetic acid and citric acid) treatments may increase 'Embul' banana fruit resistance to anthracnose, thereby reducing the benomyl concentration needed to control this disease when acid and fungicide are combined (Perera and Karunaratne 2001).

Natural extracts

Plant extracts are emerging as alternatives to conventional fungicides for the control of plant disease. They are generally regarded as safe (GRAS) to humans and environmentally friendly. Some plant extracts have been shown to effectively control various plant diseases (Wilson *et al*. 1997; Sarma *et al*. 1999; Bowers and Locke 2000).

There are examples of successful control of postharvest banana diseases with plant extracts. Ranasinghe *et al*. (2002) reported that cinnamon and clove essential oils were effective *in vitro* at low concentration against pathogenic organisms isolated from banana, including *C. musae*, *L. theobromae* and *F. proliferatum*. The major constituent of cinnamon bark oil was cinnamaldehyde. Furthermore, treatments with cinnamon bark and leaf oils controlled crown rot. However, clove oil treatment did not affect development of this disease. Treatment with emulsions of cinnamon oils combined with MA packaging can be synergistically effective for extending the storage life of 'Embul' banana fruit. This combination gave a storage lives of up to 21 days in a cold room and 14 days at 28 ± 2ºC without adversely affecting the organoleptic and physico-chemical properties of the fruit (Ranasinghe *et al*. 2005). Thangavelu *et al*. (2004) noted that extracts of *S. torvum* at 25 and 50% concentration (w/v) completely inhibited mycelial growth of *C. musae*. The same extracts were found effective in reducing the incidence of anthracnose disease on the three banana cultivars ('Robusta', 'Rasthali', 'Ney Poovan') compared to a standard benomyl (0.1%) fungicide treatment. *Cymbopogon nardus* and *Ocimum basilicum* oils also had fungicidal activity against *C. musae* and *F. proliferatum* when tested at between 0.2-0.6% (v/v) in a poisoned food bioassay (Anthony *et al*. 2004). Application of *Ocimum basilicum* essential oils (0.16% v/v) effectively suppressed crown rot and anthracnose diseases, enabling 'Embul' banana fruit to be stored for up to 21 days at 13.5 ± 1°C without any detrimental effect on their organoleptic properties. The efficacy was comparable to treatment with benomyl (Anthony *et al*. 2003).

Heat treatment

Hot water treatment (HWT) is an effective non-chemical method of postharvest pest and disease control if combinations of suitable temperatures and exposure times are selected that prevent the loss of produce quality (Lurie 1998). HWT has the potential to replace chemical fungicides to control crown rot of banana. HWT at 45°C for 20 min reduced crown rot of 'Santa Catarina Prata' and 'Williams' banana fruits inoculated with *Chalara paradoxa* spore suspension from 100 to less than 15%. When fruit were exposed to hot water at 50°C for 20 min, crown rot was reduced to < 3% (Reyes *et al*. 1998). Hassan *et al*. (2004) found that disease severity in banana fruit was significantly reduced by HWT (50 ± 2°C for 5 min) and fungicide application. Similarly, combining HWT with a bacterial antagonist gave more effective control of anthracnose, crown rot and blossom end rot of 'Emon' and 'Kolikuttu' bananas than using the two treatments individually (de Costa and Erabadupitiya 2005).

Biological control

Biological control antagonists can be used as a single application using existing delivery systems (e.g. drenches, line sprayers and on-line dips) and can significantly reduce fruit decay (Janisiewicz and Korsten 2002). Moreover, biocontrol agents may be applied directly to the targeted area (e.g. fruit wounds). Biocontrol systems for reducing decay have been successfully established for pome and citrus fruits (Janisiewicz and Korsten 2002).

For banana fruit, Brown and Swinburne (1980) found that culture filtrates or cell wall fragments of *C. musae* can induce production of antifungal components in the peel of green banana fruit, which inhibited conidial germination of *C. musae* on the treated skin. Several mycoparasites of the crown rot complex and one antagonistic bacterium were identified by Krauss *et al*. (1998). Some of these attacked the whole range of fungi involved in this disease complex, including structures considered relatively inaccessible to fungicidal attack (i.e. conidia and haustoria). Other control organisms showed tolerance to fungicides and thus could be combined with reduced concentrations of fungicide in an integrated disease management system (Krauss and Johanson 2000). Furthermore, Krauss *et al*. (2001) suggested the existence of mycoparasite discrimination between different strains of *C. musae*, the principal pathogen. The discrimination was thought to be associated with different mechanisms of action by different mycoparasites; viz. parasitism, antibiosis, competition. Accordingly, combinations of different mycoparasite strains belonging to different species enhanced biocontrol efficacy against mixed infection.

A member of the *Burkholderia cepacia* complex, isolated from the fructosphere of banana, has been shown to be effective as an antagonist of postharvest pathogens even after 5 years of storage in sterile distilled water at ambient temperature. The most effective concentration of *B. cepacia* was determined to be 10^{10} CFU/ml for *in vivo* control of anthracnose and crown rot (de Costa and Subasinghe 1998; de Costa and Erabadupitiya 2005). Taechowisan and Lumyong (2003) isolated a novel endophytic actinomycete from the root tissues of *Zingiber officinale*. The *Streptomyces aureofaciens* CMUAc130 isolate was determined to have

potential against phytopathogenic fungi. Furthermore, both the culture filtrate and crude extract from this strain had inhibitory effects against *C. musae* from banana fruit. The major active ingredients from the culture filtrate of *S. aureofaciens* CMUAc130 were identified as 5,7-dimethoxy-4-p-methoxylphenylcoumarin and 5,7-dimethoxy-4-phenylcoumarin (Taechowisan *et al*. 2005). Gunasinghe *et al*. (2004) reported that two local isolates of the biocontrol agents *Flavobacterium* sp. W5481 and *Pantoea agglomerans* W5482 reduced crown rot development on 'Embul' banana hands and, therefore, showed potential for the biocontrol of banana pathogens.

CONCLUSIONS

The published literature on mechanisms of quality maintenance of harvested fruit, including bananas is extensive. Nonetheless, our understanding is still incomplete. Further progress will be associated with even better understanding of the postharvest biology of banana fruit and more comprehensive knowledge of factors that govern major rates of quality maintenance. Particularly important advances have been made over the past decade or so in the field of ethylene perception, synthesis and transduction pathways (Sisler and Serek 1997; Marchal 1998; Jiang and Fu 2000; Adams-Phillips *et al*. 2004). The tool 1-MCP provided opportunities for postharvest scientists to gain further insight into the fundamental processes involved in ripening and senescence of the fruit (Sisler and Serek 2003). Moreover, 1-MCP has clear practical utility for extending longevity and maintaining the quality of harvested banana fruit (Jiang *et al*. 1999b; Harris *et al*. 2000; Bagnato *et al*. 2003; Pelayo *et al*. 2003). However, under commercial conditions, treatment and handling practices will need to take many variables into account. These variables include cultivar, fruit maturity or ripeness stage, the time between harvest and treatment, treatment temperature, and desired and/or acceptable effects on quality (Watkins 2006). Suppression of ethylene biosynthesis by genetic modifications is a demonstrably efficient way to extend longevity of climacteric fruit. Such technology has successfully applied in tomato (Oller *et al*. 1991). The potential of genetic manipulation to extend the shelf life of banana fruit should be explored scientifically. However, as this approach has fallen from favour with the general public, it could not a practical measure in the short to medium term.

Temperature management (the cool chain) is the most important postharvest technology for global distribution of banana fruit. However, MA and CA are sustainable postharvest technologies that also effectively extend longevity and decrease decay development. These technologies are a valuable adjunct for relatively long distance marine transport of bananas in reefers. For optimum efficacy of MA, differences in cultivar, stage of maturity, type of film, sealing method, size of package, and temperature and relative humidity should be investigated. In addition to conventional MA and CA, treatments with volatiles, anoxia, ultra-high O_2 and other non-conventional gas mixtures, including N_2O and NO have all shown promise as technologies to extend the postharvest longevity of banana fruit. However, such novel approaches all require further investigation with a view to understanding and optimization of their effects. Combining CA with complementary strategies such as decay or humidity control, delayed CA, 1-MCP and other ethylene antagonists is another potentially fertile research area.

Decay is a major postharvest problem of banana fruit. Fungicides have provided effective control in the past. However, considering present day issues, such as potential carcinogenic risk, environmental pollution and development of pathogen resistance, the quest for effective commercially viable alternative approaches for postharvest banana disease management is a research priority. Promising approaches include treatments with natural extracts, GRAS chemicals, disinfectants, biological control agents, hot water and heat shock, and modified and controlled atmospheres. However, for the most part, these approaches have not yet been adopted commercially. The key to adoption may lay in developing high efficacy integrated disease management programs. In the future, it is expected that the use of novel approaches will accelerate as more stringent international standards and requirements concerning conventional fungicides becomes the global norm.

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