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The role of ethylene in kiwifruit ripening and senescence

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Abstract

Purpose of review: Kiwifruit cv. 'Hayward' is considered a fruit with typical climacteric behaviour. Healthy fruit display climacteric behaviour at ambient temperature (~20ºC) and non-climacteric behaviour at temperatures ≤10ºC. However, it is extremely sensitive to ethylene action even at low temperatures. The behaviour of kiwifruit in relation to ethylene sensitivity and ethylene production is of great importance for long-term storage. This paper discusses the most recent findings concerning the role of ethylene in kiwifruit ripening and senescence.

Main findings: Kiwifruit senses propylene at temperatures ranging from 15 to 34ºC by advancing the onset of ripening and respiration, while the ethylene burst occurs late in the ripening process. The main reason for late ethylene production is the tardy increase of 1-aminocyclopropane-1-carboxylate synthase (ACCS) activity. The lag period for ethylene production decreases as temperature increases. Propylene-treated kiwifruit show reduced ethylene production at 38ºC and almost none at 40ºC. 1-Aminocyclopropane-1-carboxylate oxidase (ACCO) is the first enzyme to be affected at high temperatures, followed by ACCS. Below a critical temperature range (11–14.5ºC), kiwifruit lacks the ability to produce ethylene even when treated with propylene. The main reasons for the inhibition of ethylene production at 10ºC are primarily due to the suppression of the propylene-induced ACCS gene expression and low ACCO activity. However, wounded or *Botrytis*-infected fruits produce ethylene at low temperatures. A period of about 12 days at low temperature induces autocatalysis of ethylene upon re-warming of kiwifruit, while around 19 days are required when fruit is held continuously at ambient temperatures. Low temperatures slow ripening, while high temperatures block or cause abnormal ripening. Controlled atmosphere (CA) storage in 2% O_2 + 5% CO_2 and ultra low oxygen (ULO) storage with 1% O_2 + 1% CO_2 increases storage life compared with conventional storage (CS). Prolonged storage for 60 days at 0ºC induces ACCS activity but not that of ACCO. Upon re-warming, only fruit stored under CS and CA produced ethylene. ULO-treated fruit lost the ability to produce ethylene, mostly due to reduced ACCO activity.

Directions for future research: The atypical behaviour of kiwifruit in relation to ethylene sensitivity and ethylene production at different temperatures and atmosphere compositions makes this fruit a good system for studying the ethylene biosynthetic pathway, and its regulation and action on fruit ripening and senescence. Although some efforts have been made to clarify this behaviour at the physiological level, the means by which the genes of the enzymes of ethylene biosynthesis pathway are regulated in kiwifruit need further research.

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Abbreviations

ACCO	1-Aminocyclopropane-1-carboxylate Oxidase
ACCS	1-Aminocyclopropane-1-carboxylate Synthase
CA	Controlled Atmosphere
CS	Conventional Storage
ULO	Ultra Low Oxygen

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Introduction

Kiwifruit (*Actinidia deliciosa* [A Chev.] CF Liang et AR Ferguson var. *deliciosa* 'Hayward') is one of the most important commercial fruits. The success of kiwifruit as an export crop depends on the ability to store the fruit for extended periods and to transport them over long distances. Thus, substantial research efforts have been put into its postharvest behaviour in relation to storage quality.

Ripening of kiwifruit is associated with changes in respiration, texture, carbohydrates, organic acids, ethylene production and volatile compounds, which give the characteristic aroma [1*]. Kiwifruit is harvested unripe and ripening can be initiated by exposure to exogenous ethylene. Ethylene triggers rapid and dramatic changes in fruit firmness, and advances ripening and subsequent senescence [2**]. The simple gas ethylene is an endogenous regulator of a variety of stress responses and developmental processes [3]. Tucker [4] reported that the conversion of methionine to S-adenosyl-L-methionine is constant throughout the development and ripening of the fruit. Thus, the two key control enzymes for the biosynthesis of ethylene are 1-aminocyclopropane-1-carboxylate synthase (ACCS) and 1-aminocyclopropane-1-carboxylate oxidase (ACCO). Tucker [4] and Atta-Aly *et al.* [5] reported that ACCS may be the key enzyme in the control of ethylene synthesis. Although ACCO is expressed constitutively in most tissues, its synthesis increases during ripening in some fruit [6].

Kiwifruit was believed to be a climacteric fruit whose ripening was mediated by ethylene [7]. The rate of ethylene production by mature kiwifruit at harvest is very low and increases markedly with ripening after 17±7 days [7, 8]. Ethylene plays a crucial role in ripening of kiwifruit [7], and the elucidation of the controlling factors in ethylene biosynthesis is important in prolonging the storage life and maintaining fruit quality during postharvest handling operations. Kiwifruit is highly sensitive to ethylene and concentrations as low as 5-10 ppb are sufficient to induce premature ripening and advance senescence [9]. Many factors can initiate autocatalysis of ethylene production in the harvested fruit and the control of these factors can be of significance in prolonging the storage life and keeping quality.

Kiwifruit has an atypical climacteric behaviour, behaving as a climacteric fruit at ambient temperature and non-climacteric at temperatures ≤10ºC, if the fruits are healthy [2**]. This atypical behaviour in relation to ethylene sensitivity and production, and the lack of ability to produce ethylene at low temperatures makes it a good system for analysing the role of ethylene in fruit ripening. This paper discusses the main factors affecting ripening and senescence of kiwifruit, as well as technologies for increasing its storage capacity.

Ethylene and fruit ripening

Ethylene is a plant hormone that plays a major role in fruit ripening and advances senescence of harvested horticultural crops. It is synthesised in response to different types of stimuli such as wounding, alternate temperatures, treatments with other hormones and attack by pathogens, and by climacteric fruit during ripening [10].

During ripening, several structural and biochemical changes occur in fruit that confer specific organoleptic qualities, such as modifications in the external aspect, texture and flavour of the fruit. Several studies have already demonstrated that ethylene controls most of the events associated with the fruit ripening process [11].

Fruits can be classified into two major groups based on the intervention of ethylene during ripening. Climacteric fruit are characterised by an increased rate of respiration, which occurs at an early stage in the ripening process and is associated with a similar pattern of increased ethylene production. Non-climacteric fruit do not show any increase in respiration and ethylene during ripening [2, 12]. The application of exogenous ethylene to non-climacteric fruit results in an increased respiration rate proportional to the concentration of ethylene applied and declines to basal levels upon removal of the ethylene. The main effect of applied ethylene, in climacteric fruit, providing fruit are mature enough, is the advancement in time of the fruit's respiration and ethylene climacteric, whose effect is proportional to the concentration of applied ethylene [2, 13]. Once autocatalytic synthesis is triggered, ethylene levels will increase so that the final respiration rate is independent of the original exogenous ethylene concentration. Although non-climacteric fruit do not produce autocatalytic ethylene, they respond to exogenous ethylene advancing ripening in a climacteric-like manner.

Ethylene in kiwifruit ripening

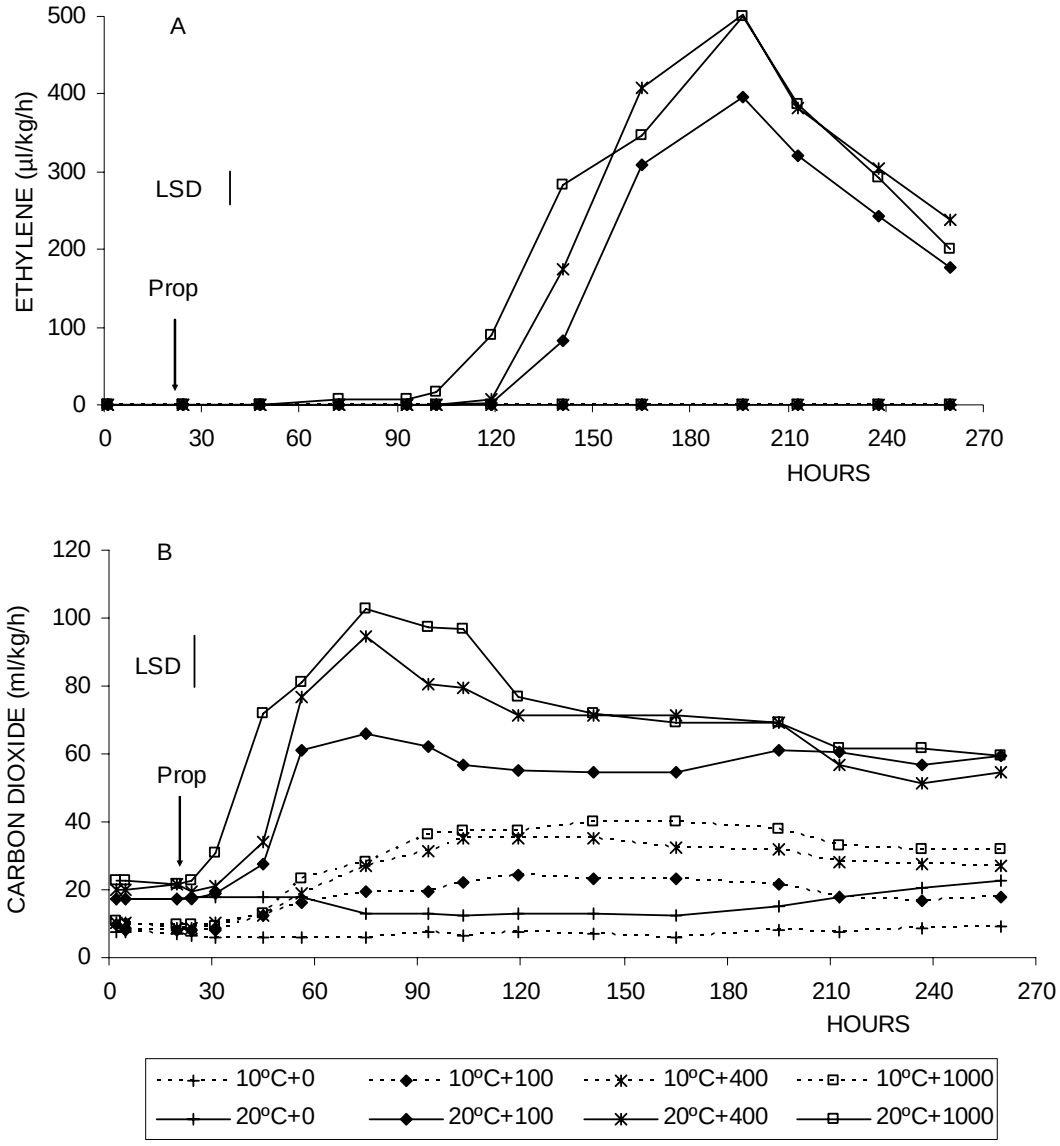
Kiwifruit produces very small amounts of ethylene on the vine and, unlike other climacteric fruit, there is no climacteric rise of ethylene production when it is attached to the tree [1*]. However, the fruit shows a tendency to soften and soluble solids content increases on the tree, which is attributed to the conversion of starch to sugars rather than as a result of the ethylene effect [1, 14].

Kiwifruit has been classified as a climacteric fruit [7, 15, 16]. Antunes *et al.* [2**] confirmed that kiwifruit cv. 'Hayward' behaves as a climacteric fruit at ambient temperature (~20ºC) by starting autocatalysis of ethylene production, respiration climacteric and ripening approximately 19 days after harvest, reaching a peak in 24 days with almost a 20,000-fold increase in the rate of ethylene production. Respiration of kiwifruit did not change significantly before autocatalysis of ethylene production, and also had a 2.5-fold increase of the rate of CO_2 production, which was closely associated with the increase in ethylene production. The same authors proposed that, in the absence of external ethylene, kiwifruit belongs to the group of climacteric fruit that show the respiration rise concomitantly with the rise in ethylene production [4].

It has been reported that the application of increasing concentrations of propylene to kiwifruit at 20°C advanced the respiration climacteric and the autocatalysis of ethylene production [2**] (Figure 1) in the same way as for other climacteric fruit [13]. However, the application of propylene changed the climacteric pattern; the rise in respiration rate and ripening-associated changes started after 4–10 h, while ethylene burst initiated late in the ripening process, after a lag period of 68–80 h, just preceding fruit senescence [2, 17], making kiwifruit different from most climacteric fruit as reported by Whittaker *et al.* [16]. Autocatalysis involved an increase in both ACCS and ACCO activities, as well as ACC content [2, 18]. In this respect, kiwifruit differs from avocado and tomato, for instance, which are characterised by a surge in ethylene production, respiration and ripening upon exposure of mature fruit to external ethylene [3, 19]. The temporal separation of ethylene sensitivity and climacteric ethylene production confirms that kiwifruit senses ethylene prior to its autocatalysis and are regulated by two independent mechanisms [2, 17, 18].

The removal of propylene after 24 h exposure did not affect autocatalysis of ethylene production, but did decrease respiration, which rose again when autocatalysis of ethylene

Figure1. Ethylene (A) and CO_2 (B) production of harvested 'Hayward' kiwifruit kept at 10 and 20°C in a continuous, humidified, air stream with different propylene concentrations: 0, 100, 400 and 1,000µL/L. The arrow shows when propylene treatments (Prop) started after the setting of the experiment. LSD at α=0.05. Adapted from [2].**



started [2**]. The burst in CO_2 production that occurred immediately after propylene application seems to be a response to the stress induced by exogenous propylene and the second increase a response to the endogenous ethylene production [4].

Thermoregulation of ethylene production in kiwifruit

Stavroulakis and Sfakiotakis [18*] treated kiwifruit with propylene, which is an ethylene analog, at temperatures from 0 to 35°C and found that below a critical temperature (11–14.8°C), ethylene biosynthesis in the propylene-treated kiwifruit did not occur. Above the critical range, autocatalysis of ethylene proceeded normally. The same authors reported that kiwifruit is a unique climacteric fruit which, at low temperatures, lacks the ability for autocatalysis of ethylene production, availability of ACC being the limiting factor rather than ACCO activity.

Interestingly, kiwifruit producing ethylene, induced by propylene at 20ºC, had drastically reduced ethylene production rate and ACC content, when transferred to 0ºC, but showed small changes in ACCO activity [17*]. Ethylene climacteric proceeded upon transfer to 20ºC.

A temperature of 10°C inhibited drastically autocatalysis of ethylene production, induced by propylene (Figure 1A), although it only slightly slowed down the ripening process [2, 18]. Antunes *et al.* [2**] found an immediate rise in the CO_2 production rate in kiwifruit at 10ºC, which was dependent on the concentration of the propylene applied (Figure 1B). Also, removal of propylene decreased the respiration rate, which recovered upon re-exposure. This behaviour is characteristic of non-climacteric fruits [4, 13].

Antunes *et al.* [2**] found transcripts of ACCS and ACCO genes after 192 h of propylene treatment at 20°C, corresponding to the climacteric rise of ethylene production. Similar results were obtained by Ikoma *et al.* [20] for ACCS and Whittaker *et al.* [16] for ACCS and ACCO in kiwifruit. In addition, the latter found ACCS gene transcription to increase with climacteric ethylene production in ripe fruit, while ACCO transcripts were induced earlier, immediately after treatment with exogenous ethylene, reaching a maximum before the ethylene burst. This may explain the fact that ACCO activity starts immediately after propylene treatment, while ACCS needs a lag period before commencement of its activity. It seems that ACCS is responsible for the lag period needed by propylene-treated kiwifruit to start autocatalytic ethylene production at ~20ºC [2, 16].

Ikoma *et al.* [20] found that transcription of KWACC1 (an ACCS gene induced by ethylene in kiwifruit) after 48 h exposure to ethylene increased until 144 h. Whittaker *et al.* [16] support the concept that ACCS has a controlling role in ethylene biosynthesis early in the climacteric. Later in the post-climacteric, ACCS transcript levels remain high, suggesting that ACCO activity is impaired late in ripening as for other fruit [3]. Antunes *et al.* [2**] reported that late in the climacteric the decline in ethylene production was due to decreased ACCS and ACCO activities. However, it is still possible that ACCO is impaired before ACCS since there was some accumulation of ACC in the post-climacteric phase. Mature unripe kiwifruit that were not treated with propylene did not show transcription of ACCS or ACCO for up to 192 h at 10 or 20°C. Thus, in kiwifruit, as for ACCS [21–23], ACCO is not a constitutive enzyme as presumed by Yang and Hoffman [24], but is induced by ethylene treatment or other stimuli as in a range of other tissues [22, 25].

Antunes *et al.* [2**] showed that inhibition of ethylene production at 10°C was associated with low activities of ACCS and ACCO. An interesting observation was the fact that there was no transcription of the ACCS gene in kiwifruit treated with propylene at 10°C, while there was transcription of ACCO. It seems that temperature plays a crucial role in controlling the ethylene induced ACCS gene and, as a consequence, the biosynthesis of endogenous ethylene in kiwifruit, making it different from other climacteric fruit.

However, it was found that kiwifruit infected with *Botrytis cinerea* or wounded produced ethylene and showed increased levels of ethylene at 0 and 10°C [1, 26], suggesting that the gene for wound-induced ACCS is not affected by low temperature. It was found that ACCS and ACCO are encoded by highly divergent multigene families differentially expressed in response to different stimuli [21, 27, 28]. Ikoma *et al.* [20] isolated two ACCS genes from kiwifruit; KWACC1, which was expressed after wounding and ethylene treatment and, KWACC2, which was expressed only after wounding.

Antunes *et al.* [2**] suggested that temperature as low as 10°C may inhibit the expression of the ACCS gene that is induced by propylene, and this was the main reason for the non-climacteric pattern displayed by kiwifruit at low temperatures. For ACCO, low temperature exerts its effect mostly on reducing enzyme activity or maybe by inhibiting translation of the mRNA and the synthesis of the enzyme or simply its activity.

Ethylene production and ripening of kiwifruit under stress conditions

High temperature stress

Propylene induced normal ripening and maximum ethylene and CO_2 production in kiwifruit at 30–35°C [1, 18, 29]. The lag period for the propylene induced autocatalytic ethylene production was shorter (24 h) than at 20ºC [2, 29].

Antunes and Sfakiotakis [29*] reported that high temperature stress (38–45°C) decreased the ripening rate and ethylene production in kiwifruit, while respiration was increased as for

other climacteric fruits [30, 31]. The small differences in respiration rate between fruit treated with or without propylene at 38°C and the absence of any differences over 40°C suggest that kiwifruit do not sense ethylene at high temperatures. A temperature of 38°C inhibited normal ripening of kiwifruit induced by propylene since the core was still hard when flesh had softened to eating ripeness. The failure of kiwifruit to ripen normally at temperatures above 38°C was probably due to the inhibition of the synthesis or activity of the ethylene biosynthetic pathway and cell-wall degrading enzymes [29, 31].

Although peak respiration rate increased as temperature increased from 30 to 45°C, ethylene production induced by propylene was inhibited at temperatures over 38°C [29*]. At 45°C, the respiration rate of kiwifruit was highest, indicating that severe stress was occurring, resulting in severe tissue injury and decreased respiration rate after 48 h exposure [29*], showing alteration of the physiological processes with exposure time as for other fruits [30, 32].

Biggs *et al.* [33] reported a reduction in ACCS and ACCO activities in tomatoes at high temperatures, the decline in ACCS being faster than that of ACCO. Since ACCO activity in kiwifruit decreased at a faster rate than ACCS when fruit temperatures were above 30°C [29*], it is likely that ACCO in kiwifruit is more affected by high temperatures than ACCS as reported for other fruits [33]. This explains the accumulation of ACC at 38°C when ethylene production was very low [29*].

Low temperature stress

Various plants respond differently to chilling stress regarding the stimulation of ethylene production [34]. In some fruits ethylene production increases during chilling stress [35, 36], while in others stimulation does not occur until after transfer to warmer temperatures [37].

Kiwifruit placed at 0–15ºC for 5 days were not able to induce autocatalytic ethylene production upon transfer to 20°C [8*]. A period of 12 days at 0–10°C satisfied the requirement for kiwifruit to autocatalytically produce ethylene 24 h after re-warming. Fruit pre-stored at 15°C needed 72 h at 20°C to start ethylene autocatalysis and took more time to ripen. After 17 days, ethylene production and ripening of kiwifruit stored at 0–15ºC began, with no delay, during re-warming of the fruit. Hyodo and Fukasawa [38] and Arpaia *et al.* [7] reported that the lag period for kiwifruit to produce ethylene at room temperature became shorter as the storage period at 0°C is extended. In addition, Antunes and Sfakiotakis [8*] report that as temperature decreases from 15 to 0ºC, the lag period for ethylene autocatalysis and kiwifruit ripening decreases upon re-warming of the fruits.

The effect of low temperature on the capacity of the fruit to produce ethylene depends on the time of exposure. After 12 days, kiwifruit kept at 0°C had a greater capacity to produce ethylene than those at higher temperatures, but after 17 days, fruit at 0°C had less capacity to produce ethylene than the ones kept at 15°C [8*]. It seems that prolonged storage damages ACCO [2, 37;, 39, 40].

Kiwifruit, like cucumber [37] and unlike apples [23], did not produce ethylene and did not increase the activity of ACCS or ACCO during a chilling period up to 17 days [8*].

Wounding stress

It is known that wounding of fruit tissues can advance senescence of horticultural produce. Physical damage induces physical disorders and causes tissue disruption as enzymes and substrates become mixed [41]. In addition, it induces an increase in ethylene and CO_2 production [42, 43]. As kiwifruit being highly sensitive to ethylene [9], even slight wounding of the fruit can have drastic impact on the fruit storage potential.

Kiwifruit do not produce ethylene at temperatures ≤10ºC if the fruits are healthy [2**], but does produce it at low temperatures when wounded [1*]. Sfakiotakis *et al.* [44] found that wounded kiwifruit stored at 5ºC produce ethylene up to 0.35 mL/kg/h, which is enough to induce ripening of the healthy unwounded fruit at storage temperatures.

Arpaia *et al.* [7] reported that impact of kiwifruit during handling causes higher damage as fruit firmness decreases. The same authors also noted that impact and vibration bruising stimulated respiration and ethylene production rates in kiwifruit of less than 6 kgf firmness. Injuries to kiwifruit are typically from impacts, cuts and punctures, and abrasion [1*]. Mechanical injuries can occur during handling from harvest to storage or marketing and they should be avoided.

Kiwifruit *Botrytis* infection

Kiwifruit is very sensitive to *Botrytis cinerea* which can cause serious commercial losses. *Botrytis* causes direct losses in infected fruit, but more severe is the induction of ethylene production which causes ethylene to accumulate in the storage room and accelerates the ripening and senescence of kiwifruit [1*].

Qadir *et al.* [45] showed that *B. cinerea* needs methionine to produce ethylene *in vitro*. The same authors report high ethylene production even in kiwifruit infected with small amounts of *B. cinerea* mycelia. Moreover, as with wounded kiwifruit tissue, kiwifruit infected with *B. cinerea* produced significant amounts of ethylene at low temperatures (31–77 μL/kg/h at 0–10ºC, respectively) [46*]. Ethylene levels in the *Botrytis* infected kiwifruits increased as temperature increased.

Stavroulakis and Sfakiotakis [18*] and Antunes *et al.* [2**] reported that healthy kiwifruit did not produce ethylene at ≤ 10ºC due to lack of ACC and ACCS activity. Niklis *et al.*

[26] found *B. cinerea*-infected kiwifruit to produce considerable amounts of ethylene and ACC closely associated with mycelia growth at such temperatures, while healthy fruit did not produce ethylene. Since kiwifruit is very sensitive to ethylene, the presence of fruits infected with *Botrytis* may cause severe consequences in the storage of the healthy fruits and such fruit should be discarded before entering the storage room.

Controlled atmosphere storage

Kiwifruit can be air-stored (conventional storage [CS]) for 4–6 months at 0ºC in an atmosphere free of ethylene [15, 40, 47]. Controlled atmosphere (CA) storage in 2% O_2 + 5% CO_2 has been proven to increase storage life of kiwifruit beyond normal air-storage, provided ethylene is not present [1, 40, 47]. Also, 1% O_2 + 1% CO_2 treatments were effective in prolonging storage life of kiwifruit with few changes in quality parameters, while 0.7% O_2 + 0.7% CO_2 for more than 120 days resulted in development of flesh breakdown, making this treatment unsuitable for long-term storage of kiwifruit [40, 48].

Kiwifruit in CS at 0ºC softened faster during the first 2 months and slower thereafter [40, 49]. Antunes *et al.* [40**] reported that CA storage plays an important role in decreasing the initial rate of softening in kiwifruit. The better maintenance of quality of kiwifruit under CA or ultra low oxygen (ULO) may also be related to the reduction in the expression of genes involved in fruit ripening caused by low oxygen conditions [50].

Arpaia *et al.* [47] and Antunes *et al.* [40**] reported that kiwifruit stored in air or 2% O_2 + 5% CO_2 became eating-ripe and produced ethylene during a 1-week shelf-life. As shown previously, fruit from cold storage started to produce ethylene upon re-warming with no lag period [8, 40]. This was due to the induction of ACCS by chilling temperatures, since ACCO does not need a lag period to start its activity upon re-warming.

Kiwifruit stored in 1% O_2 + 1% CO_2 did not ripen upon removal from storage, unless treated with propylene and were not able to induce autocatalysis of ethylene even when treated with propylene [40**]. Stavroulakis and Sfakiotakis [17*] postulated that reduction of oxygen concentration (<10%) inhibited the effectiveness of propylene on autocatalytic ethylene production in kiwifruit through a reduction in ACC concentration. In contrast, although ethylene production was inhibited in pears kept under very low oxygen, it resumed upon removal to air [51]. It seems that prolonged storage at oxygen levels of ≤ 1% inhibits the system that produces, upon re-warming, ethylene induced by chilling in kiwifruit [40**]. The same authors reported that low ACCO activity was the main factor for the lack of ability of ULO-stored fruit to produce ethylene upon re-warming, rather than ACCS activity, since there was accumulation of ACC at low temperature, as reported for other fruits [23, 52].

Hyodo *et al.* [53] and Antunes and Sfakiotakis [40**] found some ACC accumulation in kiwifruit during storage in CS, while ACCO did not show any activity until fruit were re-warmed. Since there was no ACCS activity or ACC at low temperatures until 17 days of storage [8*], but they were observed after 60 days, Antunes and Sfakiotakis [40**] suggested that as the chilling period advances, the ACCS gene induced by chilling is completing the process of transcription, translation and protein synthesis. Hence, ACCS activity is present at chilling temperatures in kiwifruit, although at a slower rate than at warm temperatures.

The ACCO activity is not present in kiwifruit at low temperatures probably due to post-transcriptional inhibition as for apples [23, 52]. However, upon re-warming, only kiwifruits previously stored in CS and CA showed ACCO activity and ethylene production [40**]. Kiwifruit previously stored in ULO were not able to produce ethylene mainly due to low ACCO activity rather than reduced ACC production or ACCS activity [40**].

Arpaia *et al.* [7] reported that even after 180 days storage in CS at 0ºC, kiwifruit exhibited the characteristic increase in respiration and ethylene in the same way as control fruit kept at 20ºC after harvest. Antunes and Sfakiotakis [40**] observed that for CA- and CS-stored kiwifruit, as storage time increases the capacity to produce ethylene during shelf-life decreases, mostly in the first 60 days. Andersen [39] reported that prolonged chilling can reduce ethylene production upon re-warming by damaging ACCO. After 180 days storage at 0ºC, ethylene production during the shelf-life at 20ºC was very low with a maximum of 7 μL/kg/h, due to decreased ACCS and ACCO activities [40**].

Benefits of ethylene

Although much effort is devoted to avoiding exposure of kiwifruit to ethylene during prolonged storage, ethylene treatment may be desirable during harvest and early storage to accelerate kiwifruit ripening in order to capitalise on marketing opportunities [47]. Mature unripe kiwifruit can be marketed earlier if treated with ethylene [1, 54]. Because application of exogenous ethylene requires special facilities, short chilling treatments might be an alternative. We suggest storing kiwifruit for around 12 days at temperatures from 0 to 10ºC [8*]. The 15ºC or 17 days storage, although it induces autocatalytic ethylene production, it is not useful since the time required for fruit to ripen is very close to that of fruit at room temperature.

Conclusions

Some practical implications from these studies are that ripening can be advanced by applying ethylene to mature unripe kiwifruit or subjecting these fruit to chilling for short periods. In addition, due to the non-climacteric behaviour of kiwifruit at ≤10ºC, their storage can be extended for up to 6 months at low temperature, providing that sources of ethylene are re-

moved from the storage chambers. When low temperature is combined with CA, storage can be further extended with fewer changes in quality parameters.

The atypical behaviour of kiwifruit in relation to ethylene sensitivity, and ethylene production at different temperatures and atmosphere composition makes this fruit a good system for studying the ethylene biosynthetic pathway, and its regulation and action on fruit ripening and senescence. Although some efforts have been made to clarify this behaviour at the physiological level, the means by which the genes of the enzymes of ethylene biosynthesis pathway are regulated in kiwifruit need further research.

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*Marginal importance
** Essential reading

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