

Effect of high temperature stress on ethylene biosynthesis, respiration and ripening of ‘Hayward’ kiwifruit

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Abstract

Temperatures up to 35°C have been shown to increase ethylene production and ripening of propylene-treated kiwifruit (Stavroulakis, G., Sfakiotakis, E.M., 1993). We attempted to study the regulation by high stress temperature of the propylene induced ethylene biosynthesis and ripening in ‘Hayward’ kiwifruit. ‘Hayward’ kiwifruit were treated with 130 µl/l propylene at temperatures from 30 to 45°C up to 120 h. Ethylene biosynthesis pathway and fruit ripening were investigated. Propylene induced normal ripening of kiwifruit at 30–34°C. Fruit failed to ripe normally at 38°C and above 40°C ripening was inhibited. Propylene induced autocatalytic ethylene production after a lag period of 24 h at 30–34°C. Ethylene production was drastically reduced at 38°C and almost nil at 40°C. The 1-aminocyclopropane-1-carboxylic acid (ACC) content was similar at 30–38°C and was very low at 40°C. The 1-aminocyclopropane-1-carboxylate synthase (ACC synthase) and 1-aminocyclopropane-1-carboxylate oxidase (ACC oxidase) activities decreased with a temperature increase above 30°C, but ACC oxidase decreased at a faster rate than ACC synthase. Fruit not treated with propylene showed no ripening response or ethylene production. However, kiwifruit respiration rate increased with temperature up to 45°C, reaching the respiration peak in 10 h. At temperatures up to 38°C, propylene treatment enhanced the respiration rate. After 48 h at 45°C, fruit showed injury symptoms and a larger decrease in CO₂. The results suggest that high temperature stress inhibits ripening by inhibiting ethylene production and sensitivity while respiration proceeds until the breakdown of tissues. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Kiwifruit; Temperature; Ethylene; Ripening; Respiration

1. Introduction

High temperatures (above 35°C) inhibit ripening of many fruits (Mitchell, 1986). The effect of high temperature, applied as heat shock, on inhibition of ethylene production has been studied in the last few years (Lurie and Klein, 1990, 1991).

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However, this technology may lead to physiological disorders (Pech et al., 1994).

Ethylene production usually exhibits a Q_{10} value of about 2 between 20 and 40°C, with further increases in temperature generally resulting in a decline in ethylene production rate (Field, 1985). Inhibition of ethylene production at temperatures up to 40°C does not appear to be associated with permanent tissue damage, since return of the tissue to a permissive lower temperature resulted in the resumption of ethylene production (Field, 1985).

Failure of fruit to ripe normally at high temperatures has been attributed to the reduction of ethylene biosynthesis at these temperatures (Eaks, 1978). The stress resulting from high temperature appears to inhibit 1-aminocyclopropane-1-carboxylate oxidase (ACC oxidase) more than 1-aminocyclopropane-1-carboxylate synthase (ACC synthase; Yu et al., 1980; Field, 1985). Apelbaum et al. (1981) proposed that high temperatures causes impairment of ethylene production by perturbing cellular membranes, resulting in inhibition of the membrane-associated ACC oxidase. This finding was supported by Yu et al. (1980) but was in contrast to Horiuchi and Imaseki (1986) and Biggs et al. (1988) who found ACC synthase more sensitive to high temperature stress than ACC oxidase. Removal of high temperature stress resulted in more rapid recovery of ACC synthase than ACC oxidase activity (Biggs et al., 1988).

Many climacteric fruit are inhibited from ripening or exhibit abnormal ripening at high temperatures. The respiration rate and ethylene production of harvested pears and avocados were suppressed at temperatures above 30–35°C and fruit suffered from heat injury (Maxie et al., 1974; Lee and Young, 1984). At temperatures above 30°C, colour development, softening, respiration rate and ethylene production of tomatoes were suppressed (Yakir et al., 1984; Inaba and Chachin, 1988). Inaba and Chachin (1989) reported maximum ethylene production in tomatoes at 25°C, a decrease thereafter and only small amounts of ethylene at 40°C. Eaks (1978) found typical climacteric patterns of respiration in avocado from 20 to 35°C, with the climacteric maximum increasing with temperature and a

respiration rate decreasing with time at 40°C. Inaba and Chachin (1989) reported that the peak respiration rate of tomato fruit was highest at 30°C, even though ethylene production was less than at 25°C.

Stavroulakis and Sfakiotakis (1993) found increased ethylene production (induced by propylene) in kiwifruit, as temperature increased from 17 to 35°C. Ripening was induced and was similar between 20 and 35°C. A systematic study of inhibition of ethylene production and ripening under heat stress has not been conducted. The purpose of this study was to investigate the effect of high temperature stress on ACC synthase and ACC oxidase activities, ACC content, ethylene and CO₂ production and ripening of 'Hayward' kiwifruit with or without exposure to propylene.

2. Material and methods

2.1. Plant material and treatments

Since kiwifruit (cv. Hayward) did not show autocatalytic ethylene production when attached to the vine during the maturation period (Sfakiotakis et al., 1997), we found no problem in harvesting them after commercial harvest time. Kiwifruit (*Actinidia deliciosa* cv. Hayward) were harvested from an orchard in Pieria-North Greece in the beginning of November, with 53 N flesh firmness and 12% soluble solids content (SSC) and immediately transferred to the postharvest laboratories at the University Farm at Thessaloniki. After selection for uniformity of size and freedom from defects, fruit were placed in 5-l jars through which a continuous, humidified, air stream with 130 µl/l propylene or air free of propylene was passed at a rate of 100 ml/min. Each set of six jars was kept in a separate water bath at a constant temperature of 30, 34, 38 or 40°C. Experiments were set up within 24 h of harvest. The experimental design was that of a two-factor experiment distributed in a completely randomised design with the temperatures as first factor, propylene treatment as second and the jars as replications. Each treatment consisted of four replications with 30 fruit per replication. Experi-

ments were repeated at least twice. Statistical analyses were made with a SAS computer program. Two-way analyses of variance (ANOVA), Least Significant Difference and Duncan's Multiple-Range Test ($P < 0.05$) for comparisons between treatments over time were conducted.

A complementary experiment with the objective to complete the study of high temperature stress effects on CO₂ production, was performed with fruit harvested at 34 N flesh firmness and 11.7% SSC. Experiments were set up as described above, but at temperatures of 38, 42 or 45°C.

2.2. Measurements

Six fruit per replicate were removed from the jars at intervals of 24 h. Measurements of ACC content, ACC synthase and ACC oxidase (*in vivo*) activities, firmness of flesh and core and SSC were carried out on these fruit. Ethylene production was measured daily. Respiration was measured three times in the first day and once per day thereafter. The initial rates of ethylene and CO₂, firmness and SSC were measured at room temperature ($\cong 20^\circ\text{C}$).

2.2.1. Ripening parameters and gas analysis

Flesh and core firmness were recorded by puncture with a Chatillon penetrometer fitted with a flat 8-mm tip. The tip was inserted after skin removal, at the fruit equator to a depth of 7 mm for flesh and 20 mm for core firmness measurements. The SSC was measured using a digital Atago refractometer in juice from the equatorial zone of the fruit. Ethylene measurements were performed by withdrawing a 1-ml-headspace gas-sample with a syringe and injecting it into a Varian 3300 gas chromatograph, equipped with a stainless steel column filled with Porapak, length 100 cm, diameter 0.32 cm, at 50°C and a flame-ionisation detector at 120°C. The carrier gas was N₂ at a flow rate of 20 ml/min. Respiration was measured as CO₂ production automatically by an infrared gas analyser connected to a computer, in the gas phase of the jars.

2.2.2. ACC content, ACC synthase and ACC oxidase activities

ACC content and ACC synthase activity were extracted and assayed as described previously (An-

tunes and Sfakiotakis, 1997). One unit of ACC synthase activity is defined as the formation of 1 nmol of ACC/2 h at 30°C. ACC oxidase activity was measured *in vivo* by infiltrating flesh disks with 1 mM ACC under vacuum as described elsewhere (Metzidakis and Sfakiotakis, 1993).

3. Results

3.1. Firmness and soluble solids content (SSC)

Flesh firmness of kiwifruit treated with propylene decreased during 72 h at 30–38°C, while at 40°C the decrease was significant only after 96 h (Table 1). Fruit at 30–34°C softened to less than 10 N in 72 h, while at 38°C, 120 h were needed to reach this firmness. Fruit at 40°C did not ripen during the experiment.

Core firmness of kiwifruit treated with propylene followed the same pattern as flesh firmness at 30 and 34°C (Table 1). However, at 38°C, fruit failed to ripen normally; the core was still hard when flesh had softened to eating-ripeness. The 40°C treatment reduced core softening in comparison with the other temperatures.

The SSC increased significantly during 72 h when fruit were treated with propylene at all temperatures (Table 1). Although values were always lower at 40°C than in the other treatments, differences were not significant.

There were no changes in flesh and core firmness and SSC in kiwifruit not treated with propylene during the experimental time at any temperature (Table 1).

3.2. Ethylene production

Autocatalysis of ethylene production was induced by propylene after kiwifruit reached a threshold level of 0.1–0.3 $\mu\text{l}/\text{kg}$ per hour ethylene production with a lag period of 24 h at 30 and 34°C, and 48 h at 38°C (Fig. 1(Aa)). A temperature of 38°C significantly reduced ethylene production induced by propylene (Fig. 1(A)). After 120 h exposure to propylene, fruit ethylene production was 40 $\mu\text{l}/\text{kg}$ per hour at 38°C, while it was 320 and 380 $\mu\text{l}/\text{kg}$ per hour at 30 and 34°C, respectively. Ethylene was drastically inhibited at 40°C, being less than

2 $\mu\text{l/kg}$ per hour (Fig. 1(Aa)). Kiwifruit not treated with propylene had very low ethylene production and did not become autocatalytic during the experiment (Fig. 1(B)).

3.3. ACC content

The ACC concentrations in kiwifruit treated with propylene increased after 48 h at 30, 34 and 38°C with no differences between treatments (Fig. 2(A)). At 40°C, fruit produced only small amounts of ACC with no increase during the experiment. Kiwifruit in air free of propylene showed only trace amounts of ACC at all temperatures (Fig. 2(B)).

3.4. ACC synthase activity

ACC synthase activity increased after 48 h at all temperatures when fruit were treated with propylene (Fig. 3(A)). Activity was higher at 30°C and decreased as temperature increased. At 40°C, activity was very low compared with the other temper-

atures. ACC synthase activity increased significantly from 48 to 72 h at 30, 34 and 38°C and remained almost constant thereafter. At 40°C, the increase in ACC synthase activity was constant until 96 h, after which it decreased. In air free of propylene, kiwifruit ACC synthase activity was very low in all temperatures (Fig. 3(B)).

3.5. ACC oxidase activity

ACC oxidase activity was almost nil at harvest but increased with no lag period when fruit were treated with propylene in temperatures from 30 to 38°C (Fig. 4(A)). Activity was higher at 30°C followed by 34, 38 and 40°C. At 30 and 34°C, ACC oxidase activity had the highest increase between 48 and 96 h and decreased significantly thereafter. At 38°C, fruit had a constant increase in ACC oxidase activity, but its values were significantly lower than at 34°C except after 120 h. ACC oxidase activity of kiwifruit at 40°C did not increase during the experiment.

Table 1

The effect of temperature (30, 34, 38 and 40°C) on firmness and SSC of harvested 'Hayward' kiwifruit kept in a continuous, humidified, air stream with 130 $\mu\text{l/l}$ propylene (Prop) or air free of propylene (Air)

Hours	Temperature (°C)	Flesh firmness (N)		Core firmness (N)		SSC (%)	
		Prop	Air	Prop	Air	Prop	Air
0	Ambient	53	53	128	128	12.0	12.0
48	30	25	51	74	113	13.9	12.0
	34	30	58	84	124	13.2	12.3
	38	39	53	99	125	13.0	12.8
	40	33	51	108	124	13.1	11.6
72	30	8	48	11	112	15.4	12.7
	34	8	58	11	127	15.6	12.0
	38	13	52	55	120	15.5	12.9
	40	28	48	93	110	14.4	13.1
96	30	6	45	8	115	14.7	12.9
	34	6	54	9	134	15.6	12.4
	38	10	53	41	124	15.0	12.4
	40	25	48	88	101	14.5	13.0
120	30	5	45	6	102	14.7	13.4
	34	5	51	7	115	15.4	12.2
	38	8	49	37	119	15.3	12.6
	40	23	47	88	104	14.3	13.3
LSD ($P < 0.05$)		13.25	15.34	18.05	17.03	1.11	1.14

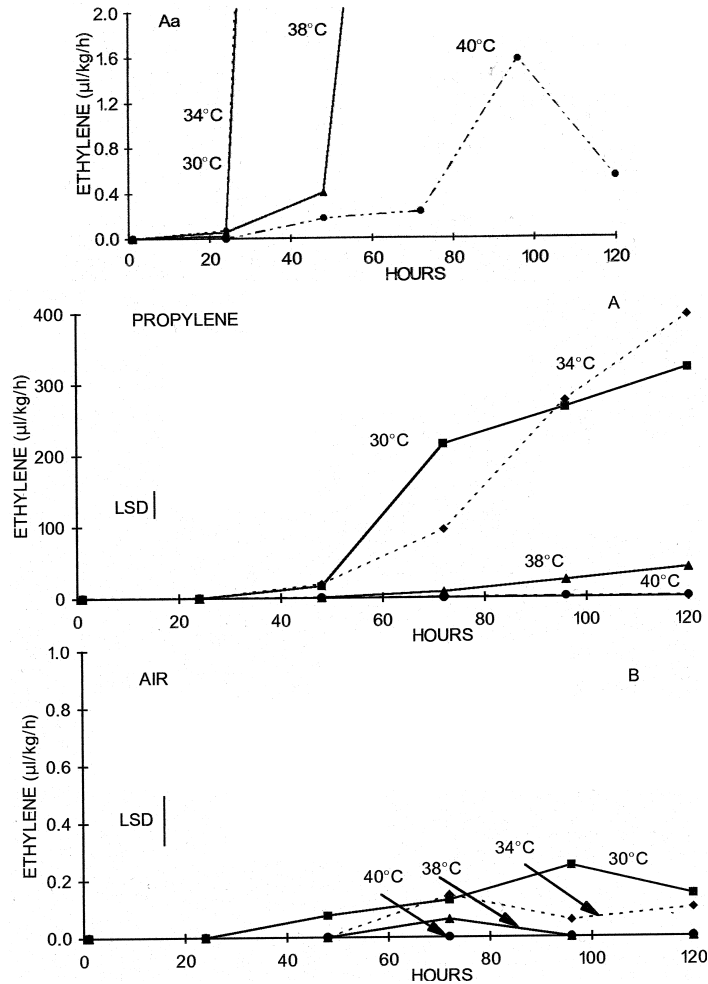


Fig. 1. Ethylene production of harvested 'Hayward' kiwifruit kept in a continuous, humidified, air stream with 130 µl/l propylene (A, Aa) or air free of propylene (B) at 30, 34, 38 and 40°C. LSD at $P < 0.05$.

Kiwifruit not treated with propylene had very low values of ACC oxidase activity during the experiment (Fig. 4(B)).

3.6. CO_2 production

The respiration peak increased with temperature presenting the lowest values at 30°C and the highest at 40°C in fruit treated or not with propylene (Fig. 5). Peak respiration of fruit treated with propylene occurred after 10 h at all temperatures with no difference between treatments except between 30 and 40°C (Fig. 5(A)). Thereafter, CO_2 production

decreased to values of about 3 µmol/kg per hour through 55 h, after which it remained constant at all temperatures.

Respiration rate of fruit not treated with propylene reached a simultaneous peak after 4–10 h at 30–38°C and after 10 h at 40°C (Fig. 5(B)). Peak values were significantly higher at 40°C followed by 38, 34 and 30°C. There was no significant difference between peak respiration rates at 30 and 34°C. Carbon dioxide production significantly decreased thereafter to values of about 2 µmol/kg per hour through 30 h and then remained constant. After 30 h, there were no differences between treatments ex-

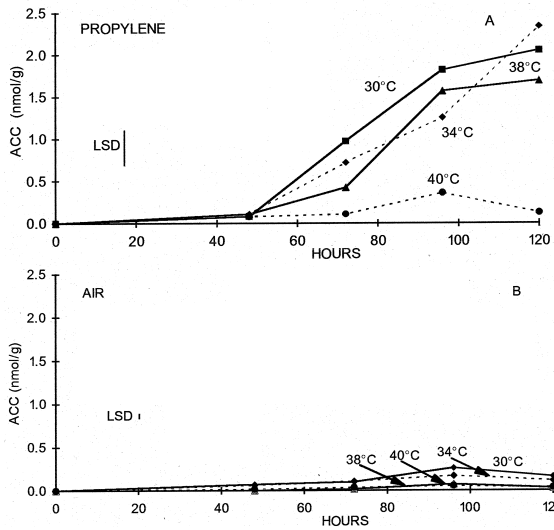


Fig. 2. ACC content of harvested 'Hayward' kiwifruit kept in a continuous, humidified, air stream with 130 μ l/l propylene (A) or air free of propylene (B) at 30, 34, 38 and 40°C. LSD at $P = 0.05$.

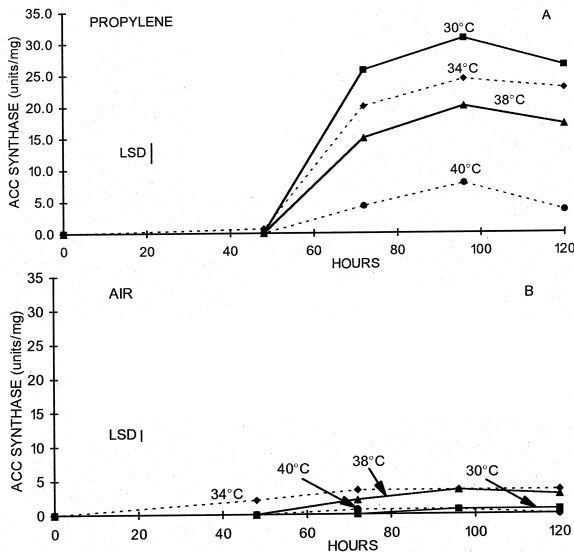


Fig. 3. ACC synthase activity of harvested 'Hayward' kiwifruit kept in a continuous, humidified, air stream with 130 μ l/l propylene (A) or air free of propylene (B) at 30, 34, 38 and 40°C. 1 unit/mg = 1 pmol ACC/mg protein per 2 h. LSD at $P < 0.05$.

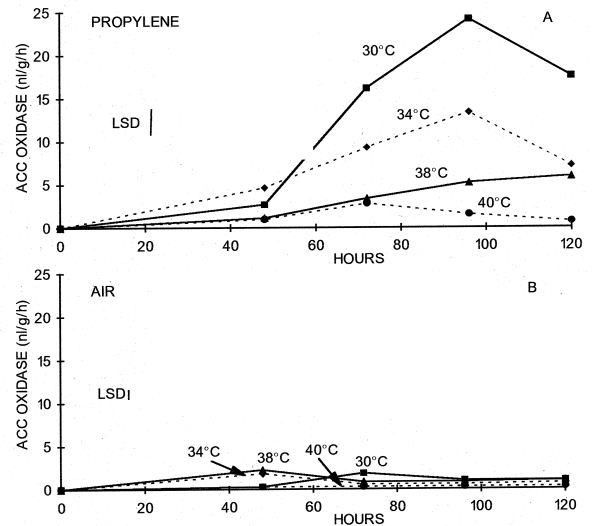


Fig. 4. ACC oxidase activity of harvested 'Hayward' kiwifruit kept in a continuous, humidified, air stream with 130 μ l/l propylene (A) or air free of propylene (B) at 30, 34, 38 and 40°C. LSD at $P < 0.05$.

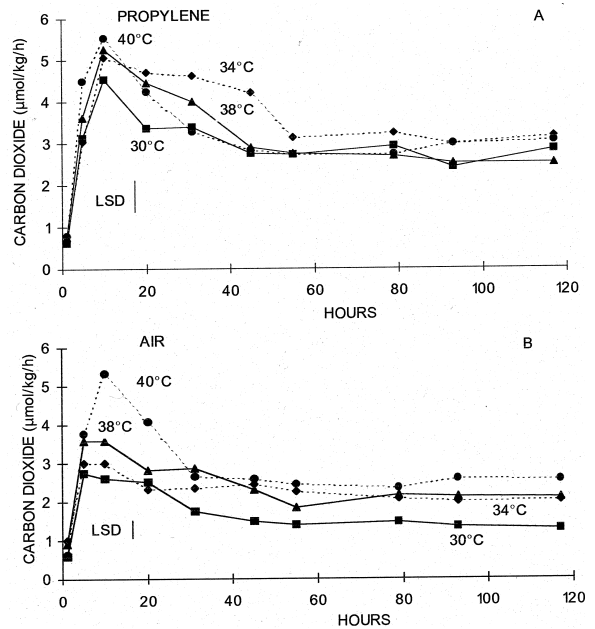


Fig. 5. CO₂ production of harvested 'Hayward' kiwifruit kept in a continuous, humidified, air stream with 130 μ l/l propylene (A) or air free of propylene (B) at 30, 34, 38 and 40°C. LSD at $P < 0.05$.

cept at 30°C, which had significantly lower values than the other treatments.

Generally CO₂ production was less in fruit not treated with propylene than in fruit treated with propylene (Fig. 5). However, differences decreased as temperature increased.

Respiration rate increased at temperatures up to 45°C reaching a peak after 10 h (Fig. 6). At 38 and 42°C, CO₂ production decreased slightly between 10 and 24 h and then remained constant. Respiration was always higher at 42 than at 38°C. At 45°C, fruit respiration rate was significantly higher than the other treatments for the first 10 h, but it decreased sharply and after 48 h was lower than for fruit at the other temperatures. After 72 h at 45°C, fruit showed a respiration rate lower than in the beginning of the experiment. There were no differences between fruit treated or not with propylene. Fruit did not produce ethylene during the experiment (data not shown).

During the first 24 h, fruit at 45°C had similar flesh colour to that in other treatments, but after this there was increased flesh yellowing coincident with the decrease in fruit respiration. Temperatures of 42 and 45°C inhibited normal fruit ripening independently of whether it was treated with propylene or not. Kiwifruit were cooked after 72 h at 45°C (data not shown).

4. Discussion

Kiwifruit cv. 'Hayward' behaves as a climacteric fruit by starting autocatalysis of ethylene produc-

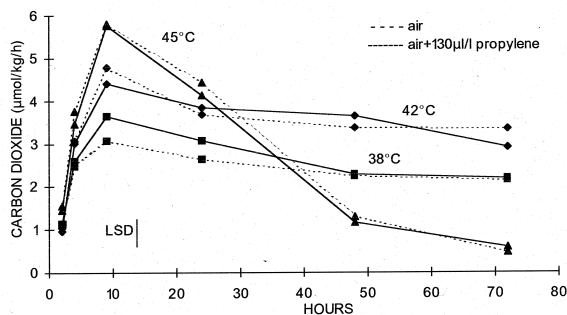


Fig. 6. CO₂ production of harvested 'Hayward' kiwifruit kept in a continuous, humidified, air stream with 130 µl/l propylene or air free of propylene at 38, 42 and 45°C. LSD at $P < 0.05$.

tion, the respiration climacteric and ripening approximately 19 days after harvest when placed at 20°C in air free of propylene (Arpaia et al., 1994; Antunes et al., 2000). The application of propylene at increasing temperatures up to 34°C advanced ethylene production and ripening. However, the application of propylene changed the climacteric pattern: the rise in respiration rate and ripening-associated changes started after 4–10 h, while the ethylene burst initiated late in the ripening process, after a lag period of 68–79 h at 20°C, and 24 h at 30–34°C, just preceding fruit senescence (Stavroulakis and Sfakiotakis, 1993; Antunes and Sfakiotakis, 1997), making kiwifruit different from most climacteric fruit (Whittaker et al., 1997; Antunes et al., 2000). The increase in ethylene production was accompanied by an increase in ACC content and ACC synthase and ACC oxidase activities. The temporal separation of ethylene sensitivity and climacteric ethylene production confirms that kiwifruit senses ethylene prior to its autocatalysis (Stavroulakis and Sfakiotakis, 1993; Whittaker et al., 1997; Antunes et al., 2000).

High temperature stress (> 38°C) decreased ripening rate and ethylene production in kiwifruit, while respiration was increased. Similar results were observed for avocado (Eaks, 1978), tomato (Yakir et al., 1984; Inaba and Chachin, 1988) and apple (Lurie and Klein, 1990). However, the upper temperature limits for both these processes vary from species to species. In kiwifruit, high temperature stress affected firmness more than SSC as reported for apples (Lurie and Klein, 1990). 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 due not only to the reduction of ethylene biosynthesis at these temperatures (Eaks, 1978), but also to the decreased sensitivity of the fruit to propylene application (Maxie et al., 1974). Alternatively, the inhibition of synthesis or activity of cell-wall degrading enzymes may have prevented softening (Lurie and Klein, 1990).

Carbon dioxide production was increased by propylene at 30–34°C. This is similar to the behaviour at lower temperatures (Antunes et al.,

2000) and seems to be a response to the stress induced by exogenous propylene (Tucker, 1993). 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. Maxie et al. (1974) found that pears in an ethylene-free atmosphere showed an initial increase in respiration rate with temperatures up to 40°C and a decrease at 50°C. However, when ethylene was applied, respiration increased with temperature up to 50°C. These authors suggested that failure of pears to ripen at 40°C when exposed to ethylene is an example of preferential stimulation of respiration by this gas without affecting other biochemical events associated with ripening. This same effect may occur in kiwifruit.

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. This result, together with those for tomatoes and apples (Inaba and Chachin, 1989; Lurie and Klein, 1991) indicates that respiration rate of some fruit is not directly controlled by endogenous ethylene concentration (Inaba and Chachin, 1989). It seems that from the beginning of storage, respiration increases with temperature as a response to stress, until a temperature is reached that inhibits physiological processes. At 45°C, respiration rate of kiwifruit was highest indicating that severe stress was occurring at this temperature, finally resulting in a severe tissue injury and a decreased respiration rate after 48 h exposure. This implies that the stress effect accumulates, altering the physiological processes of the fruit gradually with increased time of exposure. Similar results occur for tomatoes, pears and avocados at temperatures from 30 to 40°C (Lee and Young, 1984; Yakir et al., 1984; Inaba and Chachin, 1989).

Biggs et al. (1988) reported a reduction in ACC synthase and ACC oxidase activities in tomatoes at high temperatures. However, the decline in ACC synthase activity with increased temperature was faster than the decline in ACC oxidase activity. Since ACC oxidase activity in kiwifruit decreased at a faster rate than ACC synthase when

fruit temperatures were above 30°C, it is likely that ACC oxidase in kiwifruit is more affected by high temperatures than ACC synthase, as reported for apple tissue and auxin-treated mungbean hypocotyls (Yu et al., 1980). This explains the accumulation of ACC at 38°C when ethylene production was very low. The decline in ACC oxidase activity found in kiwifruit after long exposure to high temperature was also observed in tomato (Biggs et al., 1988).

Lurie and Klein (1991) reported that heat treatment differentially affects processes that normally increase simultaneously during fruit ripening, inhibiting those processes that require *de novo* protein synthesis and enhancing those that do not. It is known that ethylene production requires continuous protein synthesis (Grierson et al., 1986), possibly making ethylene production one of the most sensitive indicators of heat stress (Lurie and Klein, 1990). Tucker and Grierson (1982) showed that cell wall-degrading enzymes undergo synthesis at the onset of ripening. This may explain the suppression of ethylene production and ripening of kiwifruit at high temperatures while respiration was still increasing. According to Lurie and Klein (1990), we suppose that the turnover of the enzymes involved in respiration may be such that heat treatments up to 42°C did not appreciably affect their activity in kiwifruit up to 72 h. High CO₂ production at 45°C may be a response to high stress that gradually accumulates resulting in heat injury after 48 h exposure and a consequent decrease in respiration.

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