Differential effects of low-temperature inhibition on the propylene induced autocatalysis of ethylene production, respiration and ripening of ‘Hayward’ kiwifruit

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SUMMARY
Previous studies (Stavroulakis and Sfaktiotsakis, 1993) have shown an inhibition of propylene-induced ethylene production in kiwifruit below a critical temperature range of 11–14.8°C. The aim of this research was to identify the biochemical basis of this inhibition in kiwifruit below 11–14.8°C. ‘Hayward’ kiwifruit were treated with increasing propylene concentrations at 10 and 20°C. Ethylene biosynthesis pathways and fruit ripening were investigated. Kiwifruit at 20°C in air started autocatalysis of ethylene production and ripened after 19 d with a concomitant increase in respiration. Ethylene production and the respiration rise appeared earlier with increased propylene concentrations. Ripening proceeded immediately after propylene treatment, while ethylene autocatalysis needed a lag period of 24–72 h. The latter event was attributed to the delay found in the induction of 1-aminocyclopropane-1-carboxylic acid synthase (ACC synthase) activity and consequently to the delayed increase of 1-aminoacyclopentane-1-carboxylic acid (ACC) content. In contrast propylene treatment induced 1-aminocyclopropane-1-carboxylic acid oxidase (ACC oxidase) activity with no lag period. Moreover, transcription of ACC synthase and ACC oxidase genes was active only in ethylene-producing kiwifruit at 20°C. In contrast, treatment at 10°C with propylene strongly inhibited ethylene production, which was attributed to the low activities of both ACC synthase and ACC oxidase as well as the low initial ACC level. Interestingly, fruit treated with propylene at 10°C appeared to be able to transcribe the ACC oxidase but not the ACC synthase gene. However, propylene induced ripening of that fruit almost as rapidly as in the propylene-treated fruit at 20°C. Respiration rate was increased together with propylene concentration. It is concluded that kiwifruit stored at 20°C behaves as a typical climacteric fruit, while at 10°C behaves like a non-climacteric fruit. We propose that the main reasons for the inhibition of the propylene induced (autocatalytic) ethylene production in kiwifruit at low temperature (<30°C), are primarily the suppression of the propylene-induced ACC synthase gene expression and the possible post-transcriptional modification of ACC oxidase.

Climacteric fruit are characterized by an increased rate of respiration at an early stage in the ripening process, associated with a similar pattern of increased ethylene production. Non-climacteric fruit show no increase in respiration and ethylene during ripening (Biale and Yang, 1981). 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, this effect being proportional to the concentration of applied ethylene (Tucker and Grierson, 1987). 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 like climacteric fruit.

Kiwifruit has been classified as a climacteric fruit whose ripening is mediated by ethylene (McDonald and Harman, 1982; Arpaia et al., 1994). However, Arpaia et al. (1994), Stavroulakis and Sfaktiotsakis (1995) and Antunes and Sfaktiotsakis (1997) reported that autocatalysis of ethylene production in kiwifruit does not occur until the fruit is fully ripe, making it different from most climacteric fruit where ethylene production and ripening are coincident. Arpaia et al. (1994) reported that kiwifruit placed at 20°C after harvest take 17 ± 7 d to ripen. Sfaktiotsakis et al., (1989) found autocatalytic ethylene production and ripening at 20°C after external application of 130 µl l⁻¹ of propylene. The same authors reported that propylene caused slower ripening of the fruit at 10°C, although it was not able to induce autocatalytic ethylene production. Stavroulakis and Sfaktiotsakis (1993) reported a critical temperature of 11–14.8°C below which ethylene production induced by propylene does not occur in kiwifruit, the limiting factor being ACC availability rather than ACC oxidase.

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activity. The enzyme ACC synthase, is generally regarded as the rate
limiting step in ethylene biosynthesis (Yip et al., 1992). Although ACC
oxidase is expressed constitutively in most tissues, its synthesis
increases during ripening in tomato (Picton et al., 1993). ACC
synthase is encoded by multigene families in all
species examined, and differential regulation of the
individual genes has been reported (Huang et al., 1991;
Olson et al., 1991). Multiple ACC oxidase genes have
been isolated from both tomato and petunia, and these
also are differentially regulated (Tang et al., 1994; Barry
et al., 1996).

The objective of this study was to find whether
kiwifruit behaves as a climacteric or non-climacteric
fruit and to identify the biochemical basis of inhibition of
the propylene-induced ethylene production in kiwifruit,
below the above-mentioned critical temperature range
(11–14.8°C).

MATERIALS AND METHODS

Kiwifruit (cv. Hayward) were harvested from an
orchard in Pieria, North Greece. After selection for
uniformity of size and freedom from defects, 30 fruit
were used the same day for analysis and the remaining
were put in 51 jars through which a continuous,
humidified, air stream was passed at a rate of 100 ml
min⁻¹. Treatments consisted of air free of propylene
(control), air + 100 μl litre⁻¹, air + 130 μl litre⁻¹, air + 400 μl litre⁻¹
and air + 1000 μl litre⁻¹ propylene (130 μl litre⁻¹ propylene is
equivalent to 1 μl litre⁻¹ ethylene). Jars were kept in
separate water baths at a constant temperature of 10 and
20°C. Each treatment consisted of four replications. At
regular intervals, six fruit per replication were removed
from the jars for ethylene biosynthesis pathway evalu-
ation, respiration and fruit ripening. Experiments
were repeated at least twice.

Firmness and soluble solids content (SSC)

Firmness was 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 firmness measurements. The
SSC (% Brix) were measured by a digital Atago
refractometer in juice from the equatorial zone of the
fruit.

Gas analysis

Ethylene was measured by withdrawing a 1 ml head-
space 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-ionization
detector at 120°C. The carrier gas was N₂ at a flow rate
of 20 ml min⁻¹. Respiration was measured as CO₂
production automatically by an infrared gas analyser
connected to a computer, in the gas phase of the jars.

ACC content, ACC synthase and ACC oxidase

ACC content and ACC synthase activity were extracted
and assayed as described previously (Antunes
and Sfakiotakis, 1997). One unit of ACC synthase
activity is defined as the formation of 1 nmol of ACC
per 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 (Mizidakis and Sfakio-
takis, 1993).

RNA extraction and Northern blot hybridization

Total RNA was isolated from flesh tissue without
seeds based on the method of Slater et al. (1985).

The ACC synthase probe was a 311 bp cDNA
(KWACC1) from ethylene-treated kiwifruit (Ikoma
et al., 1995), a gift from Dr Ioshino from the Fruit Tree
Research Station, Okitsu-Japan. The ACC oxidase
probe used was a 1230 bp cDNA clone (pME1) from
a climacteric melon fruit (Balague et al., 1993). The
insert used was from 378 to 1079 bp. Both KWACC1
and pME1 cDNA inserts were labelled using a nick-
translation kit (Amersham) in the presence of (α-32P)
dCTP, as described by the manufacturer and used as
probes.

Total RNA (10 μg) was fractionated on a formalde-
hyde-agarose gel before blotting onto a Hybond-N
membrane (Amersham) (Sambrook et al., 1989). The
membrane was then baked at 80°C for 2 h to fix the
RNA. Prehybridization and hybridization were per-
formed with the Church buffer (1 M NaHPO₄/NaH₂PO₄, pH 7.0) (Church
and Gilbert, 1984) at 52°C for ACC synthase and 55°C for ACC
oxidase. Prehy-
bridization took 30 min and hybridization overnight.
The blots were washed three times with a solution of 0.15 M
NaCl + 15 mM sodium citrate NaOH pH 7.0, 0.1% SDS,
for 20 min at the hybridization temperature. After
drying, the blots were exposed to X-ray films with an
intensifying screen at -80°C.
The respiration rate of kiwifruit at 20°C increased earlier in fruit treated with 1000 μl l⁻¹ propylene followed by 400 μl l⁻¹ and 100 μl l⁻¹ (Figure 1B). Peaks were achieved in 55 h for all propylene treatments. Carbon dioxide production increased with increased propylene concentration until 120 h of exposure. After that, values were similar in all propylene treatments, coinciding with the increase in ethylene production (Figure 1). Fruit kept continuously in air free of propylene did not significantly change their respiration rate during the 260 h of the experiment at either 10 or 20°C (Figures 1B and 2B).

Propylene concentration did not induce autocatalysis of ethylene production at 10°C (Figure 2A). At 10°C, the respiration rate of kiwifruit increased significantly with increase in propylene concentration, showed a wide peak and remained almost constant after 200 h of exposure (Figure 2B). Respiration of fruit in 400 μl l⁻¹ propylene was always lower than fruit of 1000 μl l⁻¹ treatment with significant differences between 120 and 200 h of exposure. Fruit in 100 μl l⁻¹ propylene had significantly lower CO₂ production than that exposed to the other propylene treatments.

Kiwifruit treated with 130 μl l⁻¹ propylene at 20°C, followed a typical climacteric pattern for ethylene production (Table 1). The ACC content and ACC synthase activity of kiwifruit were almost nil at harvest, but increased significantly after 120 h in fruit treated with 130 μl l⁻¹ propylene at 20°C (Table 1). Peak values were achieved after 240 h and decreased significantly thereafter. In fruit treated with propylene at 20°C, ACC oxidase activity was almost nil at harvest, started to increase significantly after 48 h, reached a peak after 240 h and decreased sharply thereafter (Table 1). Fruit treated with propylene at 10°C and fruit in air free of propylene at 10 and 20°C showed no significant increase in ethylene production, ACC content, ACC synthase and ACC oxidase activities during the experiment (Table 1).

Kiwifruit kept at 20°C in air started autocatalysis of ethylene production and ripened after 19 d with a concomitant increase in respiration. Propylene treatment for 24 h (130 μl l⁻¹) at 20°C were enough to stimulate autocatalysis of ethylene production with a lag

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### Table 1

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<th>Temperature (°C)</th>
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<th>Prop</th>
<th>Air</th>
<th>ACC (nmol/g)</th>
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<th>Air</th>
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LSD (P<0.05) 18.7  n.s.  3.8  n.s.  3.5  n.s.

n.s. = not significant at P<0.05.
1 unit/mg = 1 pmol ACC/mg protein/2 hours
Prop = 130 μl/l propylene.
Air = Air free of propylene.
Low temperature and kiwifruit ripening

<table>
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<th>Temperature (°C)</th>
<th>Propylene (µl/l)</th>
<th>Firmness (kg)</th>
<th>SSC (% Brix)</th>
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LSD (P<0.05) 0.9 1.0

The period of 68 h. When propylene was removed, respiration decreased significantly, but increased again with the commencement of autocatalysis of ethylene production (data not shown).

After 192 h of exposure to propylene, it was found that ACC synthase and ACC oxidase gene transcription occurred in ethylene producing kiwifruit at 20°C (Figure 3). Kiwifruit treated with propylene at 10°C did not show transcription of ACC synthase gene up to 192 h, but did so for ACC oxidase. The expression of ACC oxidase was stronger at 20 than at 10°C. Fruit not treated with propylene did not show transcription of ACC synthase or ACC oxidase genes at any temperature, like just harvested fruit.

The changes in firmness and soluble solids content (SSC) of fruit kept in air free of propylene at 10 and 20°C were not significant in terms of ripening (Table II). After 260 h, fruit firmness significantly decreased and SSC increased when treated with propylene, showing similar values in all propylene treatments. Firmness decrease and SSC increase were significantly greater at 20°C than at 10°C.

DISCUSSION

Kiwifruit has been classified as a climacteric fruit (Arpaia et al., 1994). All climacteric fruit are characterized by transient increases in both ethylene synthesis and respiration at an early stage of ripening (Tucker and Grierson, 1987). The present research confirms that kiwifruit cv. Hayward behaves as a climacteric fruit by starting autocatalysis of ethylene production, respiration climacteric and ripening in approximately 19 d after harvest when placed at 20°C in air free of propylene. If we consider the respiration rise as an indicator of the commencement of ripening (Yang et al., 1986), we may conclude that kiwifruit belongs to that group of climacteric fruit which shows the respiration rise coincidentally to the rise in ethylene production (Tucker, 1993).

The application of external ethylene to a climacteric fruit, providing it is mature enough, will advance the onset of the climacteric, this effect being proportional to the concentration of applied ethylene (Tucker and Grierson, 1987). We observed that the application of increasing propylene concentrations to kiwifruit at 20°C advanced the respiration climacteric and the autocatalysis of ethylene production in the same way as for other climacteric fruit. 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 68–79 h, just preceding fruit senescence (Antunes and Sfakiotakis, 1997), making kiwifruit different from most climacteric fruit as reported by Wittaker et al. (1997). In this respect, kiwifruit differs from avocado and tomato, for instance, which are characterized by a surge in ethylene production, respiration and ripening upon exposure of mature fruit to external ethylene (Metzidakis and Sfakiotakis, 1989; Abeles et al., 1992). The temporal separation of ethylene sensitivity and climacteric ethylene production in kiwifruit suggests that both ripening and ethylene autocatalysis are regulated by two independent mechanisms (Stavroulakis and Sfakiotakis, 1993). 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 started. The burst in CO₂ production immediately after propylene application seems to be a response to stress induced by exogenous propylene and the second increase a response to the endogenous ethylene production (Tucker, 1993).

A temperature of 10°C slowed down a little the ripening but inhibited drastically autocatalysis of ethylene production as shown previously (Stavroulakis and Sfakiotakis, 1993). However, propylene treatment induced an immediate rise in CO₂ production, being the respiration rate dependent on the concentration of the applied propylene. Removal of propylene at 10°C decreased the respiration rate of kiwifruit which, recovered upon re-exposure to propylene. This
behaviour is characteristic of a non-climacteric fruit (Tucker and Grierson, 1987; Tucker, 1993). Treating kiwifruit with propylene at 10°C advanced ripening as in non-climacteric fruit (Tucker and Grierson, 1987). Kiwifruit at 10°C, in which propylene was removed for some periods, did not completely ripen since ripening was caused only by external propylene. At 20°C, fruit were equally ripe when continuously in propylene or when propylene was applied for only 24 h because both induced internal autocatalysis of ethylene production.

In the present work, transcripts of ACC synthase and ACC oxidase genes were found after 12 h of propylene (130 μl l⁻¹) treatment at 20°C, corresponding to the climacteric rise of ethylene production. Similar results were obtained by Ikoma et al. (1995) for ACC synthase and by Whittaker et al. (1997) for ACC synthase and ACC oxidase in kiwifruit. In addition, the latter found ACC synthase gene transcription to increase with climacteric ethylene production in ripe fruit, while ACC oxidase transcripts were induced earlier, immediately after treatment with exogenous ethylene, reaching a maximum before the ethylene burst. This may explain why ACC oxidase activity starts immediately after propylene treatment, while ACC synthase needs a lag period before starting its activity. Based on these findings, we confirm that ACC synthase is responsible for the atypical behaviour of kiwifruit at room temperature (ca. 20°C) which needs a lag period of 68-72 h prior to autocatalysis of ethylene production as postulated by Stavrakakis and Sfakiotakis (1995), Antunes and Sfakiotakis (1997) and Whittaker et al. (1997).

Ikoma et al. (1995) found transcription of KWACC1 (an ACC synthase gene induced by ethylene in kiwifruit) after 48 h of exposure to ethylene with increasing levels of expression until 144 h. Whittaker et al. (1997) support the concept that ACC synthase has a controlling role in ethylene biosynthesis early in the climacteric. Later in the post-climacteric, ACC synthase transcript levels remain high, suggesting that ACC oxidase activity is impaired late in ripening as in other fruit (Abeles et al., 1992). In the present work, it was found that late in the climacteric, the decline in ethylene production was due to decreased ACC synthase and ACC oxidase activities. However, it is still possible that ACC oxidase is impaired before ACC synthase since there was some accumulation of ACC in the post-climacteric. Mature unripe kiwifruit not treated with propylene did not show transcription of ACC synthase or ACC oxidase for up to 12 h at 10 or 20°C. Thus, in kiwifruit, as for ACC synthase (Theologis, 1992; Woodson et al., 1992; Gaudiere and Vendrell, 1993), ACC oxidase is not a constitutive enzyme as presumed by Yang and Hoffman (1984), but is induced by ethylene treatment or other stimuli as in a range of other tissues (Woodson et al., 1992; Tang et al., 1994).

Kiwifruit has been classified as an unique climacteric fruit which at low temperature lacks the ability for autocatalysis of ethylene production (induced by propylene) the limiting factor being ACC availability rather than ACC oxidase activity (Stavrakakis and Sfakiotakis, 1995). The present research showed that inhibition of ethylene production at 10°C was associated with low activities of ACC synthase and ACC oxidase. An interesting observation was the fact that we found no transcription of ACC synthase gene in kiwifruit treated with propylene at 10°C, while there was transcription of ACC oxidase. It seems that temperature is crucial in controlling the ethylene induced ACC synthase gene and, as a consequence, the biosynthesis of endogenous ethylene in kiwifruit, making it different from the other climacteric fruit. However, it was found that kiwifruit infected with Botrytis cinerea produced ethylene and showed increased levels of ethylene at 0 and 10°C (Niklus et al., 1993), suggesting that the gene for wound induced ACC synthase is not affected by low temperature. It was found that ACC synthase and ACC oxidase are encoded by highly divergent multigene families differentially expressed in response to different stimuli (Theologis, 1992; Botella et al., 1995). Ikoma et al. (1995) isolated two ACC synthase genes from kiwifruit: KWACC1 which was expressed after wounding and ethylene treatment and, KWACC2 which was expressed only after wounding. More research is needed to clarify this point.

The present study suggests that kiwifruit stored at room temperature behaves as a typical climacteric fruit in reference to respiration and ethylene production, while at a low temperature such as 10°C it behaves like a non-climacteric fruit. Our results suggest that temperature as low as 10°C inhibits the expression of the ACC synthase gene that is induced by propylene, and this was the main reason for the non-climacteric pattern of kiwifruit at this temperature. For ACC oxidase, 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. This behaviour of kiwifruit with respect to respiration and ethylene production offers certain advantages in handling operations. After harvest, keeping the fruit at low temperatures ensures no accumulation of ethylene production in storage rooms, thus the post-harvest life of the fruit is prolonged, providing there are no diseased fruit or other sources of ethylene nearby.

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