New Zealand Journal of Crop and Horticultural Science

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/tnzc20

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To cite this article: Yujie Han, Julian Heyes, Marcin Glowacz, Sue Nicholson, Peter Jeffery & Andrew East (2024) The responses of 'Hayward' kiwifruit to ethylene during regular and controlled atmosphere storage, New Zealand Journal of Crop and Horticultural Science, 52:3, 265-279, DOI: 10.1080/01140671.2024.2348136

To link to this article: https://doi.org/10.1080/01140671.2024.2348136

Published online: 08 May 2024.

NEW ZEALAND JOURNAL OF CROP AND HORTICULTURAL SCIENCE
2024, VOL. 52, NO. 3, 265–279
https://doi.org/10.1080/01140671.2024.2348136

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The responses of 'Hayward' kiwifruit to ethylene during regular and controlled atmosphere storage

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ABSTRACT

Maintaining kiwifruit firmness is key to global supply chain. Controlled atmosphere (CA) technology can maintain kiwifruit quality. However, there is a risk of ethylene (C_2H_4) accumulation in CA that may accelerate kiwifruit softening. The objectives of this study were to determine the impact of ethylene on kiwifruit quality in CA. 'Hayward' kiwifruit were stored in air and CA (5% CO_2 + 2% O_2) at 0°C, 95% RH for 13 weeks. Ethylene at concentrations of 10, 100, 1000 nL·L^{-1} was added after 3 weeks of storage. The responses of kiwifruit to ethylene were dose-dependent in both air and CA storage. Ethylene-induced kiwifruit softening was delayed and slowed by CA. However, white-core inclusions (WCI) disorder was observed after 8 weeks of exposure to 100 and 1000 nL·L^{-1} ethylene in CA. The lowest concentrations of ethylene ($\leq$ 10 nL·L^{-1}) in CA did not influence kiwifruit quality. This work demonstrates that kiwifruit sensitivity to ethylene is lower in CA than that in air, but excessive softening and WCI may negatively impact kiwifruit quality when exposed to a high ethylene concentration in CA for extended periods. Hence, ethylene monitoring and management may be less critical in kiwifruit stored in CA but are required.

ARTICLE HISTORY
Received 31 October 2023
Accepted 10 April 2024

HANDLING EDITOR
Mo Li

KEYWORDS
Firmness; white core inclusions; C_2H_4; modified atmospheres; *Actinidia*

Introduction

Kiwifruit (*Actinidia* spp.) is a key horticultural product in New Zealand. More than 90% of the kiwifruit produced in New Zealand are exported to distant destinations, such as Asia and Europe (Aitken and Warrington 2021). With significant variation amongst cultivars, kiwifruit is harvested from March to June in New Zealand. Kiwifruit are generally harvested when physiologically mature but unripe, and some cultivars may be stored up to six months to achieve year-round supply to the market between the two hemispheres (NZKGI 2020). The long storage requirement may be challenging to regular cool storage.

Controlled atmosphere (CA) is a technology that replaces the air (79% N_2, 21% O_2 and 0.05% CO_2) in the storage space with reduced O_2 and elevated CO_2 to extend the storage

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life of fresh products (Saltveit 2020). CA has been applied to kiwifruit for extending storage and relieving pressure on packhouses since the 1980s (McDonald and Harman 1982; Arpaia et al. 1987). The effects of CA on kiwifruit include reducing the respiration rate (Li et al. 2015), slowing down ripening and softening (Li et al. 2017), alleviating disorders (Burdon et al. 2022), suppressing ethylene production and reducing ethylene sensitivity (Arpaia et al. 1986; Antunes and Sfakiotakis 2002).

Kiwifruit firmness change during ripening is generally described by a four-phase softening model (Atkinson et al. 2011). Phase 1 is characterised as an initial stable phase where minimal softening occurs. This phase usually occurs in the first few days after harvest but may also happen on vine when the fruit is not harvested until late in the season. Phase 2 refers to a rapid softening soon afterwards, when most of the softening occurs. Phase 3 starts when the flesh firmness reaches approximately 10 N (i.e. eating firmness). This is normally when the fruit becomes edible with soft texture, low acidity and high sugar content. Additionally, autocatalytic ethylene production also starts at this stage. Following this relatively long slow softening phase, kiwifruit become overripe, too soft to eat and lose optimal flavour; this is identified as Phase 4. The storage life of kiwifruit is normally terminated when the fruit enters Phase 4, but the storage life may also be terminated by physiological disorders (e.g. chilling injury), postharvest diseases development, or damage related to physical injury.

Ethylene (C_2H_4) is a plant hormone that accelerates fruit ripening. Kiwifruit is extremely sensitive to ethylene; levels as low as 10 $nL{\cdot}L^{-1}$ can trigger excessive ripening in kiwifruit during regular cool storage (Jabbar and East 2016). Additionally, kiwifruit that have been exposed to ethylene are also more likely to get chilling injury (CI) (Jabbar and East 2016; Liu et al. 2021). The symptoms of kiwifruit CI are grainy tissue developing underneath the skin, and water soaking of tissue at higher severity. The symptoms generally start from the blossom end, and later develop throughout the whole fruit. Kiwifruit with CI are normally softer (Gwanpua et al. 2018). Another physiological disorder, white core inclusion (WCI), has been observed on CA-stored kiwifruit with ethylene at concentrations of 50 $nL{\cdot}L^{-1}$ and above, with the symptoms of white granules appearing in the core tissue (Arpaia et al. 1982; Arpaia et al. 1985). Healthy, firm kiwifruit produces ethylene at a minimal level, whilst the ethylene production rate of soft, injured, or rotten kiwifruit are much higher (Qadir 1994; Feng et al. 2003; Polychroniadou et al. 2022; Kim et al. 2023; Yang et al. 2023). In addition to the ethylene produced by fruit, ethylene contamination in the supply chain may come from pathogens and internal combustion engine fumes (Qadir et al. 1997; Blanke 2014).

In a regular cool storage facility, fruit is stored in cooled air in a non-gas-tight environment. However, CA storage is established in a gas-tight cool room, with N_2 supply and CO_2 and O_2 removal facilities. Due to the sealed nature required to establish CA, ethylene accumulation in CA facilities may be more problematic than in regular storage. Jabbar and East (2016) previously showed that high ethylene concentrations over long exposure durations contribute to kiwifruit softening and chilling injury development in regular cool storage. However, the impact of the same range of ethylene contamination has not been reported in CA conditions.

In the kiwifruit supply chain, harvested fruit can be passed over a sorting line prior to packing and storage. In this case, the soft, injured and rotten fruit are removed during sorting. Hence, defective fruit, which are more likely to produce ethylene, are less

likely to be stored. Arpaia et al. (1986) reported the effects of higher concentrations of ethylene applied in the initial phase of CA storage, however, the effects of delayed ethylene exposure in CA storage has not been studied. Hence, further study of ethylene effects in scenarios that mimic contemporary industrial CA conditions is needed. The objective for this work is to quantitively determine the effects of delayed ethylene exposure time and concentration on kiwifruit in CA conditions.

Materials and methods

Kiwifruit (*A. chinensis* var. *deliciosa* 'Hayward') was harvested at commercial maturity from three orchards as replicates, and couriered to Massey University, Palmerston North, after commercial grading and packing (NZKGI 2021). The average fruit size was 'count 36' (95–108 g). Fruit temperature was 10–15 °C upon arrival. Upon arrival, sets of 15 fruit from each orchard were randomised into mesh bags, and 12 bags from the same orchard were allocated to each 60 L plastic barrel. The initial fruit quality was determined by assessing a 60-fruit sample from each orchard upon fruit delivery (Table 1).

A flow-through system utilising the 60 L plastic barrels as storage chambers was established in a temperature-controlled room at 0°C. The flow rate was maintained at 300 $mL{\cdot}min^{-1}$ to remove excess CO_2 and ethylene produced by the fruit. The fruit was cooled to 0°C within 24 h after the barrels were sealed. For the initial 3 weeks, only air or CA (5% CO_2, 2% O_2, balance N_2) (Burdon et al. 2002; Li et al. 2017) were supplied to the barrels. Compressed dry air was supplied for the air treatments. The CA was created by mixing compressed dry air, N_2 and CO_2 (food grade, BOC Gas, Palmerston North, New Zealand) using a set of needle valves. Ethylene was added to the flow-through system after a three-week delay to imitate the development of ethylene production by soft, injured, or rotten fruit that gradually develops during storage. Ethylene from calibration standards: 9.6 ± 0.4 $\mu L{\cdot}L^{-1}$ and 92 ± 4 $\mu L{\cdot}L^{-1}$ C_2H_4 in air, (BOC Gas, Palmerston North, New Zealand) was mixed to concentrations of 10, 100, 1000 $nL{\cdot}L^{-1}$ and added into the system using mass flow controllers (GSC-A9TA-BB21, Vögtlin Instruments GmbH, Muttenz, Switzerland) after 3 weeks of storage, which created 8 treatments:

(1) Air (21% O_2, < 0.1% CO_2)
(2) Air + 10 $nL{\cdot}L^{-1}$ C_2H_4
(3) Air + 100 $nL{\cdot}L^{-1}$ C_2H_4
(4) Air + 1000 $nL{\cdot}L^{-1}$ C_2H_4
(5) CA (2% O_2, 5% CO_2)
(6) CA + 10 $nL{\cdot}L^{-1}$ C_2H_4
(7) CA + 100 $nL{\cdot}L^{-1}$ C_2H_4
(8) CA + 1000 $nL{\cdot}L^{-1}$ C_2H_4

Table 1. Initial quality of 'Hayward' kiwifruit from three orchards.

Orchard	Firmness (N)	SSC (%)	DM (%)
No. 1	51.2	14.03	18.75
No. 2	68.2	12.12	18.80
No. 3	56.8	12.57	17.52

*Data represents means of 60 fruit.

A total of 24 barrels were set up with the 8 treatments and 3 replicates, each replicate being a different orchard. Fruit from different orchards were allocated in different barrels. The mixed gas passed through a 1 L glass jar containing 500 mL 21.1% glycerol solution immediately before the barrels to maintain approximately 95% relative humidity (RH). The gas composition and flow rate in the barrel out-flow were monitored weekly using a multi-gas sampling data logger (CM-1000, CO_2 Meter, Ormond Beach, USA), an ethylene analyser (MacView®, EMS, Sint-Annaland, The Netherlands) and a flow meter (G6691A, Agilent, Santa Clara, USA).

A sample of 60 fruit was taken from each orchard at harvest; and a sample of 30 fruit was drawn from each barrel after 3, 5, 7, 9, 11 and 13 weeks of storage. The fruit were arranged into 30-cell trays and held at 20°C overnight before quality assessment.

Dry matter content (DM) was measured only at harvest. A slice of fruit (3 mm) was taken from the equator and dried in a petri dish using a food dehydrator (ULTRA FD1000, Ezidri, Tauranga, New Zealand) at 65°C for 24 h. Dry matter content (% DM) $= \frac{DW}{FW} \times 100\%$, where: DW is the dry weight of fruit slice after dehydrating (g) and FW is the fresh weight of fruit slice before dehydrating (g). The FW and DW were measured using an electronic balance (TW423L, Shimadzu, Tokyo, Japan).

The flesh firmness was determined using a penetrometer (Willowbank Electronics Ltd., Napier, New Zealand) with a 7.9 mm diameter probe inserted to a depth of 8 mm at the speed of 8 mm·s^{-1} at two points (90° apart) at the fruit equator. A 1 mm slice of skin was removed from the penetration point prior to measuring. The average peak force of the two points was recorded as the fruit firmness.

Soluble solids content (SSC) was determined by squeezing out approximately 0.3 mL of juice from the cut surface of the blossom half of the fruit and measuring using a refractometer (PR-32α, Atago, Saitama, Japan).

Core firmness was determined by removing 5 mm flesh from the flat side of the fruit and penetrating the centre of the cut surface using a penetrometer (Willowbank Electronics Ltd., Napier, New Zealand) with a 6 mm probe at the depth of 25 mm. The peak force was recorded as core firmness. Core firmness was only measured after 13 weeks of storage.

Disorders were assessed visually on the cut surfaces at the equator and 1.5 cm from the blossom end. Fruit with graininess and water soaking in the flesh tissue were recorded as CI, while fruit with white flecks in the core tissue were recorded as WCI (Figure 4C, D). Iodine-starch test was performed to indicate starch distribution with a few drops of iodide-potassium iodide solution (0.5% iodine and 2% potassium iodide dissolved in water) being applied to the cut surface, and the colour change being assessed in a few minutes. The incidence was calculated based on the percentage of fruit with each disorder in the sample.

Data were described by means and standard error of means (SEM). Statistical separation of treatment means was by analysis of variance (ANOVA). Multiple comparisons used Fisher's protected least significant difference (LSD) test at $P = 0.05$. Analysis was conducted using R version 4.0.3 (R Core Team, Vienna, Austria). Graphs were created using the package ggplot2.

Results

The average flesh firmness declined rapidly in the initial 3 weeks for both air- and CA-stored fruit, and there was no statistically-significant difference between the two storage

atmospheres ($P > 0.05$) (Figure 1). Air-stored fruit became softer than fruit stored in CA from Week 5, irrespective of the ethylene concentrations. The ethylene effects started to merge from Week 5, when Air + 1000 nL·L^{-1} C_2H_4 became the softest, followed by Air + 100 nL·L^{-1} C_2H_4, Air + 10 nL·L^{-1} C_2H_4 and Air + 0 nL·L^{-1} C_2H_4. This ranking continued to the end of the experiment. The firmness changes of CA-stored fruit followed a different pattern compared to the air-stored group. All the CA-stored fruit were firmer than air-stored fruit from Week 5 until Week 13. The differences between ethylene concentrations did not emerge until Week 11, when the firmness of fruit in CA + 100 nL·L^{-1} C_2H_4 was lower than fruit in CA + 10 nL·L^{-1} C_2H_4 and CA + 0 nL·L^{-1} C_2H_4, and that in CA + 1000 nL·L^{-1} C_2H_4 was the lowest. It is worth noting that the firmness of fruit in CA + 0 nL·L^{-1} C_2H_4 and CA + 10 nL·L^{-1} C_2H_4 remained high from Week 3 to the end of the experiment, with no rapid softening through this period. Whereas fruit in CA + 100 nL·L^{-1} C_2H_4 experienced a brief softening between Week 9 and Week 11, returning to a plateau thereafter. The fruit in CA + 1000 nL·L^{-1} C_2H_4 exhibited a slow softening phase from Week 3 to Week 9 and entered a fast-softening phase after Week 9. At the end of the experiment (Week 13), all the CA-stored fruit were still firmer than the eating firmness (Figure 1).

Although the average firmness has scientific significance, the firmness distribution is important to the industry due to high fruit-to-fruit variation. Most of the fruit started to fall below 10 N in Air + 100 nL·L^{-1} C_2H_4 and Air + 1000 nL·L^{-1} C_2H_4 at Week 7, followed by that in Air + 10 nL·L^{-1} C_2H_4 at Week 11 (Figure 2). The 3rd quartile of fruit

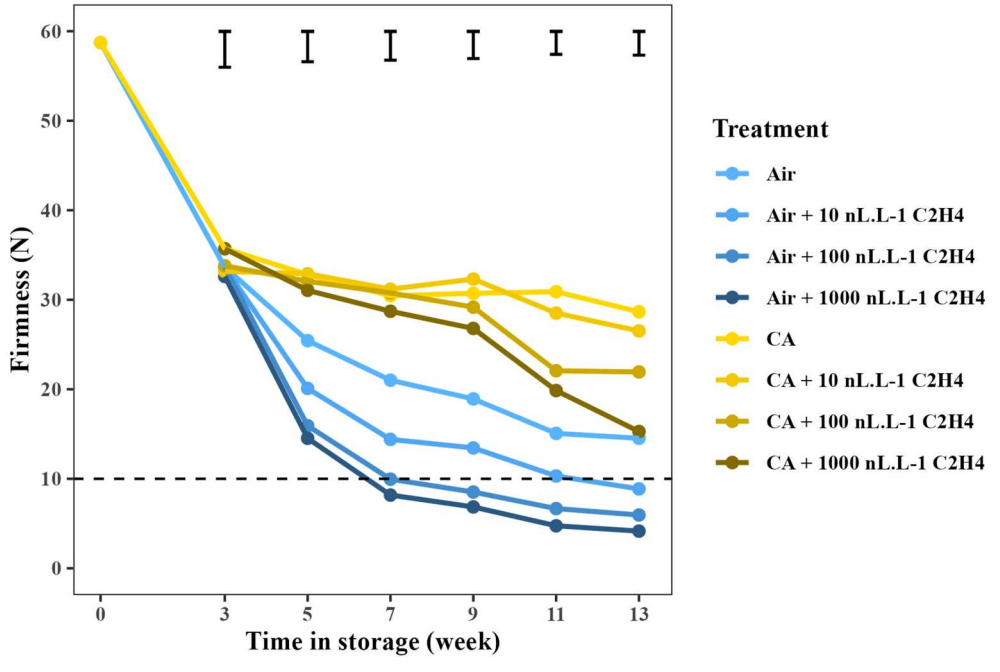

Figure 1. Firmness of 'Hayward' kiwifruit stored in CA (2% O_2 + 5% CO_2) and air at 0°C 95% RH with additional ethylene at the concentration of 0, 10, 100 and 1000 nL·L^{-1} from Week 3 to Week 13. Each data point represents a mean of 3 replicates. Error bars represent $LSD_{0.05}$. The dash line indicates the 10 N threshold.

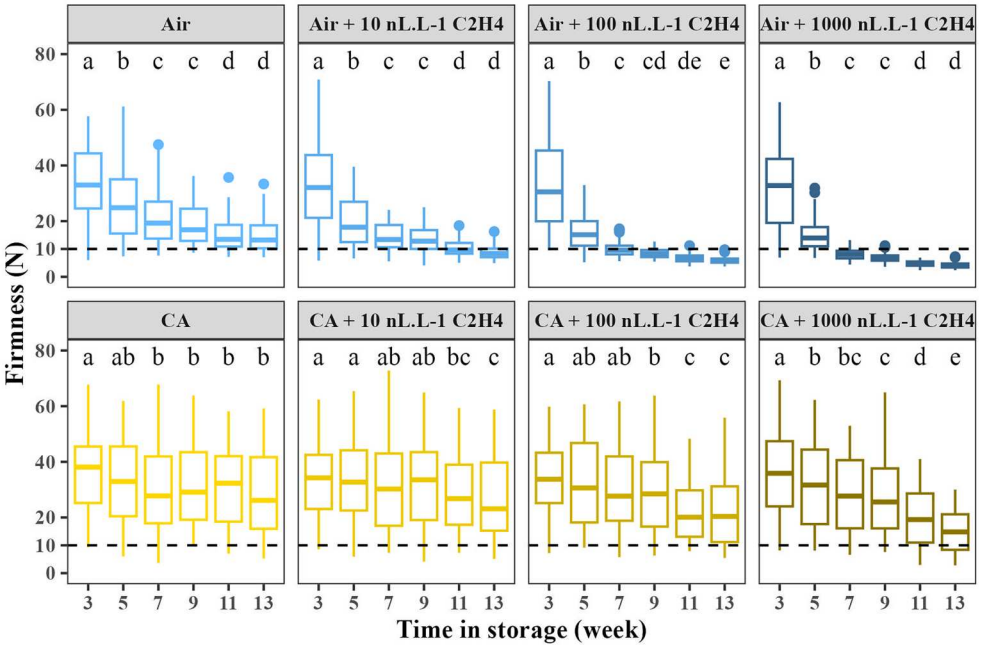

Figure 2. Firmness distribution of 'Hayward' kiwifruit in responses to ethylene at the concentration of 0, 10, 100 and 1000 nL·L^{-1}, in CA (2% O_2 + 5% CO_2) and air storage at 0°C. n = 90. Values share a same letter are not significant different at $P < 0.05$ within the same treatment. The dash line indicates the 10 N threshold.

in ethylene-free air sat above 10 N throughout the storage period. Contrastingly, all fruit in CA storage stayed above 10 N, except for CA + 1000 nL·L^{-1} C_2H_4 at Week 13 when the softer fruit started to fall below this threshold.

The fruit-to-fruit variation was similar amongst the treatments at the early stage of cool storage, but gradually decreased as fruit became softer. The firmness ranges decreased dramatically in the air-stored fruit, especially with high ethylene concentrations. This suggested the softer fruit in these populations had entered the slow softening phase near 10 N, while the firmer fruit in these populations experienced a rapid softening phase and subsequently reached a similar low firmness within a short time. In contrast, the firmness ranges of CA-stored fruit did not change much throughout the storage period, suggesting that the whole population in these atmospheres stayed in a very slow softening phase at relatively high firmness (Figure 2).

The average soluble solids content (SSC) at harvest was 12.9%. After 3 weeks of storage, SSC of fruit in air slightly increased, whilst SSC in CA remained at a low level. The air-stored fruit saw a rapid SSC increase before Week 7 and that slowed down in the subsequent 6 weeks. Whereas SSC only increased rapidly in CA-stored fruit between Week 3 and Week 5. Whereafter a gradual increase in SSC was maintained. During the 13 weeks of storage, the SSC of CA fruit were lower than those in air ($P < 0.05$), irrespective of C_2H_4 concentration (Figure 3). The effect of C_2H_4 on SSC evolution was concentration dependent in air-stored fruit. The SSC of fruit in air with C_2H_4 rose faster than that in ethylene-free air, while higher SSC was associated with higher ethylene

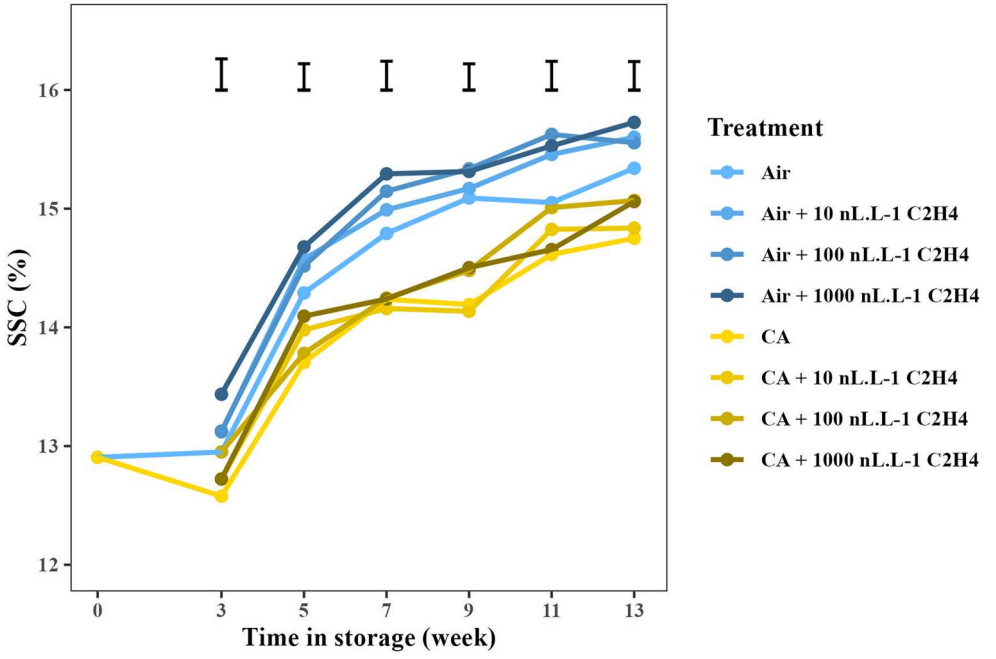

Figure 3. Soluble solids content (SSC) of 'Hayward' kiwifruit stored in CA (2% O_2 + 5% CO_2) and air at 0°C 95% RH with additional ethylene at the concentration of 0, 10, 100 and 1000 nL·L^{-1} from Week 3 to Week 13. Each data point represents mean of 3 replicates. Error bars represent $LSD_{0.05}$.

concentration. Conversely, there was no statistical difference between SSC of fruit in CA with different C_2H_4 concentrations.

Chilling injury was observed on one fruit of the whole batch, with the symptom of graininess in the outer pericarp right under the skin (Figure 4A, B). White core inclusion (WCI) was observed in CA + 100 nL·L^{-1} C_2H_4 and CA + 1000 nL·L^{-1} C_2H_4 at Week 11 and Week 13, with a higher incidence in 1000 nL·L^{-1} C_2H_4 (Figure 5). The observed symptoms of WCI were small white dots in the core tissue of fruit (Figure 4C, D). After dyeing with potassium iodide solution, the white dots turned black, indicating these dots were starch grain clusters (Figure 4E). Hard core disorder occurs when the firmness of kiwifruit core tissue remains high while the pericarp is at eating firmness. Hence the core firmness was only measured at Week 13 when the flesh firmness starts to fall below 10 N. For the fruit with flesh firmness below 10 N, the core firmness barely remains above 30 N (Figure 6), suggesting very low risk of hard-core issue under the current atmospheres. Figure 6 also illustrates that the softening pattern differs between the core and flesh tissue of kiwifruit. For firm fruit, both core and flesh softening, but the core tissue softens more slowly. Then, in the range 5–10 N for the flesh, there is a period of rapid core softening compared to flesh softening. Finally, both core and flesh are soft. In the current experiment, the CA fruit barely enter the final phase. On the other hand, in both CA and air, high C_2H_4 concentration dramatically reduced core firmness at the same flesh firmness, suggesting C_2H_4 has greater effect on core firmness compared to flesh firmness (Figure 6).

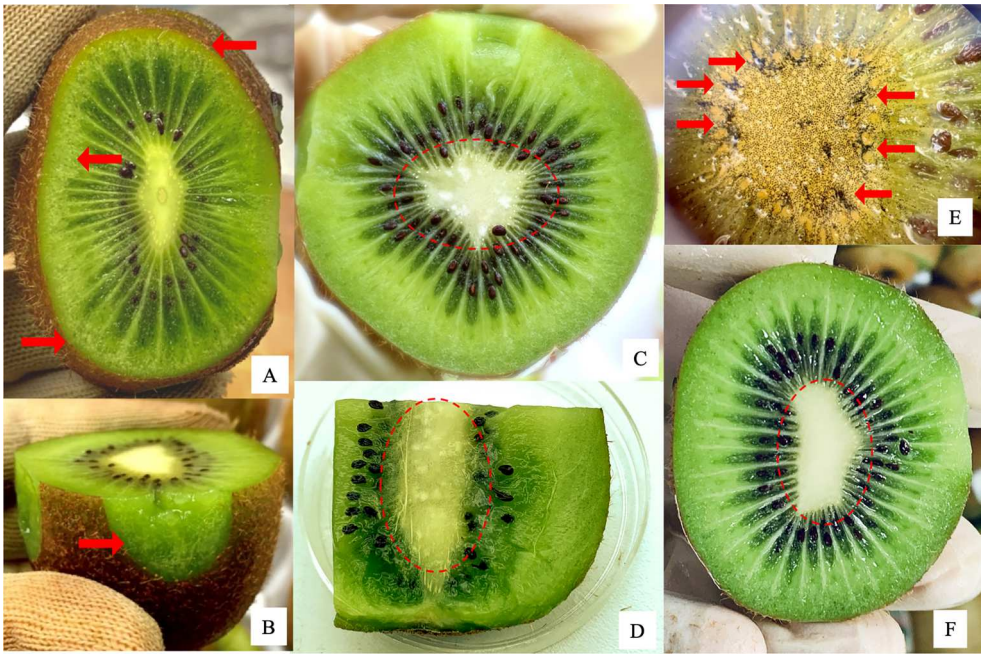

Figure 4. Symptoms of disorders on 'Hayward' kiwifruit. **A, B**: chilling injury (CI). **C, D**: white core inclusion (WCI). E: WCI dyed with potassium iodide solution in the transection of kiwifruit core tissue. The image scale is indicated by the kiwifruit seeds. The arrows point to starch clusters dyed in black. F: Healthy fruit.

Discussion

Kiwifruit softening normally follows the 4-phase model (Atkinson et al. 2011). Phase 1 (slow softening) was not observed in this experiment, either because the fruit has been held in the packhouse for a few days for sorting and packing before being delivered to the lab, or because it was already complete by the first assessment during storage at 3 weeks after harvest. Phase 2 rapid softening and Phase 3 slow softening at eating firmness were observed in air-stored fruit. In the CA-stored fruit, after the initial 3 weeks of rapid softening, there was a long non-softening period before another relatively rapid softening for 100 and 1000 $nL{\cdot}L^{-1}$ C_2H_4, but there was no second rapid softening for 0 and 10 $nL{\cdot}L^{-1}$ C_2H_4. The final over-ripe phase was not observed in this experiment. 'Hayward' has an excellent storage performance and is able to stay relatively firm in regular cool storage, which is not seen in most of the other kiwifruit cultivars (Kumar-ihami et al. 2020; Jin et al. 2021; Liu et al. 2021; Kim et al. 2023). During the first few months of 'Hayward' storage, an additional room-temperature shelf-life period is required to reach the eating firmness. This temperature-elevated period was not a part of the present work due to the size of the experiment. However, this may be addressed in a future study evaluating the impact of ethylene and CA on the eating experience.

The effect of ethylene in regular cool storage has been documented. With C_2H_4 at the concentration of 10–1000 $nL{\cdot}L^{-1}$ in air storage from the beginning of cool storage, higher ethylene concentration leads to a faster rapid softening phase within the initial 2–4 weeks,

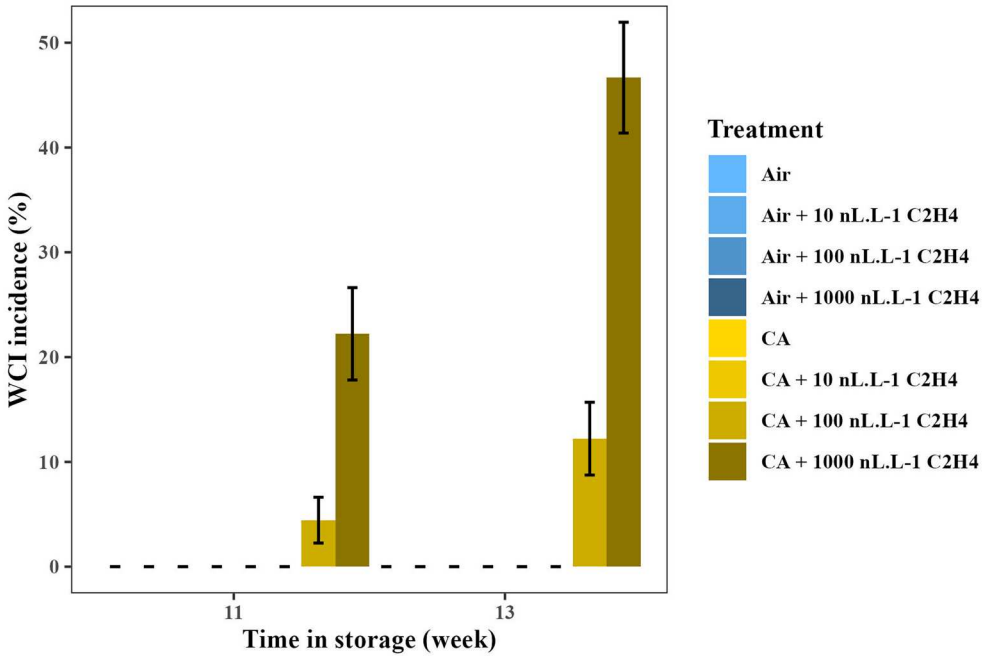

Figure 5. Incidence of white core inclusions (WCI) in 'Hayward' kiwifruit stored in air and CA (2% O_2 + 5% CO_2) storage with ethylene at the concentration of 0, 10, 100 and 1000 nL·L^{-1} at 0°C 95% RH. Each bar represents mean ± standard error of mean, n = 3. WCI was observed only in CA with 100 and 1000 nL·L^{-1} ethylene, and was not observed before Week 11.

and the fruit firmness plateauing at a lower value afterwards (Jabbar and East 2016). In the current study, ethylene was not applied to the flow-through system until 3 weeks after harvest, but the softening patterns were quite similar to what Jabbar and East (2016) had observed. After the initial rapid softening in the first 3 weeks of storage, kiwifruit stored in air without the addition of ethylene gradually entered a slower softening phase and reached the plateau at approximately 15 N; while with additional ethylene, the rapid softening continued for a further 2–4 weeks and reached a lower firmness (below 10 N), with faster softening to lower firmness in higher ethylene concentrations.

In CA storage, the responses of kiwifruit to ethylene were delayed and the sensitivity to ethylene concentration was also reduced. In air, an addition of 10 nL·L^{-1} C_2H_4 has accelerated kiwifruit softening within 2 weeks. Conversely, the same ethylene concentration in CA did not impact fruit firmness for the entire 10 weeks of ethylene treatment. However, higher ethylene concentrations (100 and 1000 nL·L^{-1}) were able to induce advanced softening of kiwifruit, although the effect did not show until 8 weeks after the initiation of the ethylene treatment started. Excessive softening only occurred in CA + 100 and 1000 nL·L^{-1} C_2H_4, suggesting 'Hayward' kiwifruit was not sensitive to the lower 10 nL·L^{-1} C_2H_4 in CA storage for the time frame measured in this study. Moreover, the firmness decrease during the relatively rapid softening phase was still slower than that in any of the air storage conditions. Similar results of firmness changes have been reported in a previous study, which applied 50, 100, 500, 1000 and 5000 nL·L^{-1} ethylene to CA-stored 'Hayward' kiwifruit (Arpaia et al. 1986). In the work of Arpaia

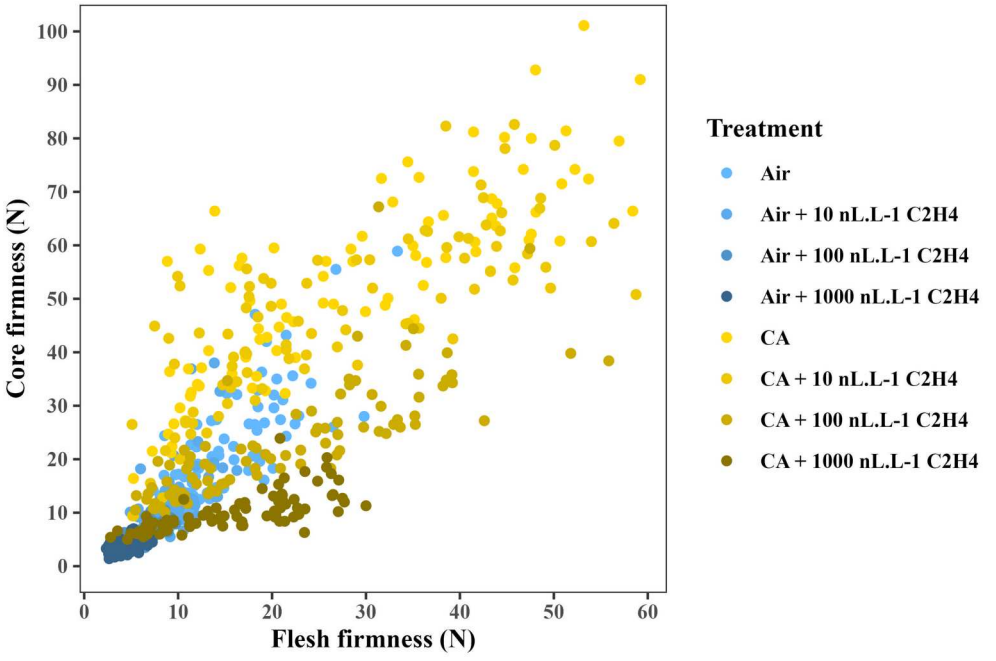

Figure 6. Correlation between core firmness and flesh firmness of 'Hayward' kiwifruit after 13 weeks of storage in air and CA (2% O_2 + 5% CO_2) with ethylene at the concentration of 0, 10, 100 and 1000 $nL{\cdot}L^{-1}$ at 0°C. Each data point represents a fruit.

et al. (1986), CA-stored 'Hayward' kiwifruit did not respond to 50 $nL{\cdot}L^{-1}$ C_2H_4 until 16 weeks in storage, while the timeframe of responses to 100 and 1000 $nL{\cdot}L^{-1}$ C_2H_4 were similar to the present study.

The mode of action for CA reducing ethylene sensitivity has been discussed in the past. The ethylene receptor requires O_2 for ethylene molecule to attach (Burg and Burg 1967, 1969), which is reduced in the low O_2 concentration in CA. It is also suggested that CO_2 binds to the ethylene binding site, thus ethylene cannot effectively bind to the receptors (Yang 1987; Ahammed and Li 2022). However, contrary to C_2H_4, the CO_2 binding is reversible and may occur on a different binding site (Tian et al. 1994). Other evidence indicated that the mode of action of CO_2 on ethylene sensitivity suppression differs from that of 1-MCP (de Wild et al. 2005).

Kiwifruit is stored up to 6 months in the commercial supply chain to fulfill year-round supply between the two hemispheres. While the current experiment only lasted for 13 weeks, previous studies have illustrated that the average firmness of 'Hayward' kiwifruit did not fall below 10 N after stored in CA with up to 1000 $nL{\cdot}L^{-1}$ C_2H_4 for 24 weeks (Arpaia et al. 1982; Arpaia et al. 1986). However, conclusions about ethylene risk in storage cannot be drawn solely based on average firmness. With the existence of high fruit-to-fruit variation, exporting decisions are made according to the firmness of the softest proportion of fruit in a batch. When a certain percentage of kiwifruit falls below the threshold, the whole batch is no longer suitable for exporting. The percentage and firmness threshold vary between cultivars. In the present work, more than 25% of fruit fell below 10 N in CA + 1000 $nL{\cdot}L^{-1}$ C_2H_4, which likely indicates that this batch

of fruit would fail the commercial inspection, and exposure to 1000 $nL \cdot L^{-1}$ C_2H_4 in CA is likely to be problematic.

SSC is commonly used as an at-harvest maturity index in the kiwifruit industry (Burdon et al. 2016). Fruit SSC of 6.2% has been used as the minimum harvest requirement. Kiwifruit harvested with SSC below 6.2% have poor storage performance and are more susceptible to CI (Burdon et al. 2007; Burdon et al. 2016). In the present study, 12.9% SSC indicated relatively high maturity at harvest. The final SSC is generally defined by at-harvest dry matter (Crisosto et al. 2012). At harvest, kiwifruit is high in starch but relatively low in SSC. SSC increases as fruit ripens due to starch degradation. Higher SSC at eating firmness means higher sweetness, which is preferred by consumers (Burdon et al. 2004). 'Hayward' kiwifruit with ≥ 14% SSC at eating firmness are regarded as acceptable (Harker et al. 2009). CA-stored fruit were not fully ripe by week 13. However, the SSC at week 13 was above 14% for both air and CA-stored fruit, thus meeting the sweetness criteria. Lower SSC has been reported in CA-stored kiwifruit compared to air-stored fruit, which agrees with the current result. However, lower SSC is also accompanied by higher firmness (Cornacchia et al. 2008; Xia et al. 2016). The CA effect on SSC evolution represents a delay in the increase of SSC caused by delayed fruit ripening, rather than reduced SSC at eating ripeness. However, SSC does not always increase during prolonged kiwifruit ripening. The reduction of SSC at the end of storage has been observed in previous studies (Pranamornkith et al. 2012; Narae et al. 2019). As starch converts to soluble sugar during ripening, sugar is also consumed by respiration. When starch is conserved by CA suppressing respiration rate, a higher SSC may be achieved at eating firmness. As most CA-stored fruit did not reach eating firmness, further investigations are required to confirm if ethylene in CA changes the kiwifruit SSC at eating firmness.

WCI disorder was first identified in the 1980s in high CO_2 storage with C_2H_4 (Arpaia et al. 1982; Arpaia et al. 1985, 1986). They suggested that it was caused by the interaction between high CO_2 and C_2H_4. The timing of WCI symptoms observed in combination of starch cluster observations suggests that the starch at these localised spots did not undergo normal degradation into soluble sugars, but remained in the form of starch grains after the starch in the surrounding tissue has degraded. This might be related to patches of cell death caused by anaerobic respiration in a high C_2H_4 environment that disturbed the starch degradation enzyme activity. However, it remains unknown why it occurs only in the core tissue but not in the pericarp. On the other hand, with the symptoms only appearing in the core tissue, the eating experience is not likely to be affected. Hence, WCI should not affect the commercial value of kiwifruit despite it being labelled as a physiological disorder.

The softening pattern of the core tissue of kiwifruit differs from the pericarp. Fruit pericarp softening follows an exponential pattern, but the firmness change of the core tissue is closer to linear (Li et al. 2017; Chai et al. 2023). To achieve a pleasant eating experience, the pericarp and core tissue should reach the eating firmness in a similar time frame. Hard core disorder occurs when the flesh firmness of kiwifruit reaches the eating window (< 10 N) while core firmness remains high (> 30 N) giving an unpleasant texture when the consumer bites or scoops into a kiwifruit. Hard core disorder has been observed in kiwifruit after CA storage as well as in 1-MCP treated kiwifruit (Harman and McDonald 1989; Zoffoli et al. 2016). However, more recent studies have identified hard

core as a maturity issue rather than a physiological disorder induced by the post-harvest treatment (Gong et al. 2020). In the current study, core firmness was measured at the last assessment (Week 13) when the CA-stored fruit were entering the eating window. The result shows that there is only a small number of fruits with core firmness above 30 N when the flesh firmness fell below 10 N, suggesting the risk of hard-core disorder is relatively low. At the same time, the correlation between core firmness and flesh firmness suggested that the core firmness of CA-stored kiwifruit in high C_2H_4 concentrations reduced faster than the flesh firmness, indicating ethylene in CA has a greater impact on inducing core softening than outer pericarp softening.

Conclusions

Responses of 'Hayward' kiwifruit to C_2H_4 at the concentrations of 0, 10, 100 and 1000 $nL{\cdot}L^{-1}$ have been examined in both air and optimal CA (2% O_2 + 5% CO_2) during storage over 13 weeks at 0°C 95% RH. CA-treated fruit retained higher firmness in extended storage after the initial three weeks of softening. C_2H_4 accelerated fruit softening in air storage, and the C_2H_4 effect on firmness was dose-dependent. CA reduced kiwifruit response to C_2H_4 by increasing the minimum C_2H_4 concentration that accelerated softening, delayed C_2H_4 triggering softening and reduced the rate of C_2H_4 induced softening. CA delayed kiwifruit SSC increase and offset the C_2H_4 effect on accelerating SSC increase. WCI was induced by 100 $nL{\cdot}L^{-1}$ or higher concentration of C_2H_4 in CA after 11 weeks of storage, and the incidence of WCI was dose-dependent. Hard core disorder and CI were not problematic in this experiment. A low concentration of C_2H_4 ($\leq$ 10 $nL{\cdot}L^{-1}$) present in CA storage did not alter kiwifruit quality, however excessive softening and WCI may negatively impact kiwifruit quality when exposed to a high concentration of C_2H_4 in CA for extended storage time. Therefore, ethylene monitoring and management may be less critical in kiwifruit stored in CA but is still required for prolonged storage.

Acknowledgements

The authors are grateful to Anthony Pangborn (Agriculture Risk Management Ltd) for fruit sourcing. We would also like to acknowledge the help of Micaela Reyes and Josephine Longuet-Higgins on fruit quality assessment.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This project was fully funded by Zespri International (FP20171).

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