Understanding Kiwifruit Postharvest Physiology and Quality Changes in Tropical Retail Market Conditions

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Abstract

Kiwifruit is New Zealand's major horticulture crop. A challenge that exists for the New Zealand kiwifruit industry in emerging tropical markets is maintaining fruit quality during marketing. In Asia and the Middle East, high ambient temperatures (> 30 °C) are often prevalent. The domination of traditional fruit marketing practices in these regions results in fruit exposure to these conditions. Understanding of fruit postharvest responses to high ambient temperatures is limited.

In this thesis, a supply chain survey was conducted in India and Singapore, where kiwifruit at edible ripeness were found to be exposed to temperatures > 30 °C and ethylene concentrations as high as 150 nL L^{-1} during retail. Back in the laboratory, kiwifruit were exposed to simulated tropical conditions, where 12 h of exposure to 40 °C resulted in significant changes in fruit physiology as evidenced by rapid respiratory decline. The findings from this initial study indicated that 40 °C exposure may have a lethal impact on kiwifruit whilst 33 °C may not.

The role of ethylene in influencing kiwifruit physiology under tropical conditions was investigated by treating kiwifruit with 1-MCP to prevent ethylene responses. Consequently, 1-MCP treated fruit exposed to 33 °C retained firmness both in the presence or absence of exogenous ethylene whilst untreated fruit softened rapidly, indicating that the possible ethylene exposure in tropical conditions advances kiwifruit softening.

A further study aimed to identify exposure temperature and time combinations that trigger detrimental outcomes for kiwifruit including after a period returned to coolstorage. Like previous, kiwifruit at 40 °C exhibited rapid respiratory decline, while at 33-38 °C, no such response was evident. This confirmed that 40 °C exposure for

12 h could have a lethal impact on kiwifruit physiology. Fruit that were exposed to high temperatures (33-40 °C) beyond 24 h and later coolstored developed internal breakdown symptoms indicating that irrecoverable degradative processes are induced.

A plausible mechanism as a result of heat exposure is the occurrence of anaerobic respiratory metabolism. At 33-40 °C, Respiratory Quotient (RQ) in kiwifruit remained ≥ 1 reaching 3 at 40 °C whilst at 20 °C, RQ remained close to 1. Contrastingly, ethanol accumulation increased at high temperatures but minimal ethanol content changes occurred at 20 °C. At some high temperatures, ethanol content increased with time but no symptoms of heat injury were evident, suggesting that heat injury may not be exclusively caused by the accumulation of anaerobic metabolites. The increase in ethanol content measured in kiwifruit at high temperatures indicates the potential risk of off-flavour development at retail conditions in tropical markets.

Overall, this research contributes to kiwifruit quality maintenance in tropical markets by elucidating safe exposure durations for kiwifruit and identifying a postharvest treatment of 1-MCP as a potential quality maintenance tool. Future research requirements include identifying molecular mechanisms that control physiological changes in kiwifruit at high temperatures, identifying causes for the differential responses observed between ‘Hayward’ and ‘SunGold™’ and investigating the efficacy of 1-MCP at wider ranges of high temperature conditions.

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Dedicated to Science and Scientists

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AAT	alcohol acyltransferase
ACC	1-aminocyclopropane-1-carboxylic acid
acetyl-CoA	acetyl coenzyme A
ACO	1-aminocyclopropane-1-carboxylic acid oxidase
ACP	anaerobic compensation point
ACS	1-aminocyclopropane-1-carboxylate synthase
ADH	alcohol dehydrogenase
ALDH	aldehyde dehydrogenase
AM	ante meridiem
ANOVA	analysis of variance
AOS	active oxygen species
ATP	adenosine triphosphate
C_2HNO_2	cyanoformic acid
CA	controlled atmosphere
CAS	cyanoalanine synthase
Ccs	colour assessed after high temperature exposure plus cool storage
Ce	colour assessed after high temperature exposure
C-end	cytoplasmic end
CO_2	carbon dioxide
Co-Q	coenzyme-Q
CTR-1	constitutive triple response-1
Cyt-C	cytochrome-C
d	day (s)

DACP	diazocyclopentadiene
DM	dry matter
DMCP	dimethyl cyclopropane
DNA	deoxyribonucleic acid
EAN	European Article Numbering
ECPI	Export consignment product inspection
EDI	Electronic Data Interchange
EIN-2	ethylene insensitive-2
EIN-3	ethylene insensitive-3
Eq	equation
ERFs	ethylene responsive factors
ETC	electron transport chain
ETD	ethylene detector
ETP-1	ethylene targeting protein-1
ETR-1	ethylene receptor-1
F6P	fructose 6-phosphate
$FADH_2$	flavin adenine dinucleotide
FBP	fructose 1,6-biphosphate
Fcs	firmness assessed after high temperature exposure plus cool storage
Fe	firmness assessed after high temperature exposure
g	gram (s)
g/L	gram/Litre (s)
GL	grower line

GLM	general linear model
GPT	glutamate pyruvate transaminase
h	hour (s)
HSD	honest significant difference
IEC	internal ethylene concentration
ISO	international organisation for standardisation
IT	international tray
KELA	Kiwifruit Export Licensing Authority
kg	kilogram (s)
kgf	kilogram force
KMLA	Kiwifruit Marketing Licencing Authority
LDH	lactate dehydrogenase
LOL	lower oxygen limit
LSD	least significant difference
Ltd	limited
M2	modular double
MB	modular bulk
min	minute (s)
mL	millilitre
ML	modular loose
mm	millimetre (s)
MTA	methylthioadenosine
N	newton

n	number
NAD	nicotinamide adenine dinucleotide
$NADH_2$	adenine dinucleotide
NADP	nicotinamide adenine dinucleotide phosphate
NBD	Norbornadiene
nL	nanolitre (s)
nm	Nanometre
nmol	nano-mole
NZ	New Zealand
NZKA	New Zealand Kiwifruit Authority
NZKMB	New Zealand Kiwifruit Marketing Board
O_2	oxygen
OAA	oxaloacetic acid
P1	Plateau
PCD	programmed cell death
PDC	pyruvate decarboxylase
PFK	phosphofructokinase enzyme
PG	polygalacturonase
PPO	polyphenol oxidase activity
Psa	*Pseudomonas syringae*
Q_{10}	temperature co-efficient
QC	quality control
RAN-1	response to antagonist-1

r_{CO2}	carbon dioxide production rate
RH	relative humidity (%)
ROS	reactive oxygen species
rPET	recycled polyethylene terephthalate
rpm	rotations per minute
RQ	respiratory quotient
s	second (s)
SCI	spectral component included
SDH	succinate dehydrogenase
SEM	scanning electron microscope
SFS	softness fruit sensor
SSC	soluble solids content
TCA	tricarboxylic acid cycle
TSS	total soluble solids
U K	United Kingdom
U S A	United States of America
WVPD	water vapour pressure deficit
%	percent
°C	degree celsius
µL	micro litre (s)
1-MCP	1-methylcyclopropene

Chapter 1: Introduction

The rising health consciousness amongst individuals across the globe has resulted in increased fruit and vegetable consumption (Artés et al., 2009; Yahia et al., 2017; Jideani et al., 2021). This increase in demand has resulted in increased production, sales and an opportunity for export-oriented countries like New Zealand in entering new markets. However, as fruits and vegetables are perishable, a key challenge exists in preserving the freshness and quality until they reach consumers and are consumed. An efficient postharvest handling procedure is necessary to ensure safe and good quality products reach consumers (Wills and Golding, 2016).

New Zealand horticulture produce reaches diversified (in terms of climatic conditions and supply chain) international markets of which tropical markets (especially in Asia and Middle East regions) are major emerging markets due to increase in demand for several products. The prevalence of ambient high temperatures in these tropical regions poses a potential risk for storage and delivery of high-quality fresh produce to international consumers with variability in supply chain conditions (due to dominance of traditional marketing channels) adding up to the problem.

Kiwifruit is the leading horticulture export crop for New Zealand. Orchardist Jim MacLoughlin initially came up with the concept of exporting New Zealand grown kiwifruit to overseas market (England) in 1952 (Berry, 1997; Kilgour et al., 2007; Milne, 2014). Ever since the first shipment, the New Zealand kiwifruit industry has undergone a tremendous transformation and currently New Zealand grown kiwifruit are marketed by Zespri®, a New Zealand kiwifruit growers co-operative to over 50 countries globally (Aitken and Warrington, 2020).

The prevalent issues in emerging international tropical markets which could affect New Zealand kiwifruit sales have previously been elucidated by Bellavi Jayashiva (2012). A key take-home message from this previous study was that kiwifruit reach final retail conditions nearly at ‘over-ripe’ state due to the handling and storage practices followed in off-shore markets. New Zealand exported kiwifruit reaching international consumers have potential to be of inferior quality, which may be of serious concern to the reputation of the New Zealand kiwifruit industry in international markets. More studies are required to ascertain the influence of tropical market conditions on kiwifruit postharvest physiology and quality, which could lead to the development of strategies to reduce quality losses and facilitate superior quality kiwifruit delivery to international consumers.

Figure 1.1: New Zealand kiwifruit marketed under ambient conditions at a cart vendor stall in Hyderabad, India (an emerging market).

Information regarding fruit responses to high temperatures during the postharvest supply chain is scarce in scientific literature. Usually, scientific experiments in postharvest research consider 18-22 °C as ambient conditions for shelflife estimation (Punter et al., 2018). These conditions may not fairly represent that ambient condition of tropical markets where the average mean day temperature during most periods of the year remains above 20 °C and often exceeds 40 °C during summer. It is also possible that fresh produce in tropical traditional markets are exposed to ambient ethylene concentrations which may be of additional risk for product quality maintenance.

Keeping these facts in mind, the objectives of this doctoral research are formulated as follows:

- Survey the supply chain practices in tropical emerging markets and identify the prevalent quality detrimental factors for fresh produce in these markets.
- Develop an understanding of the influence of potential tropical market conditions on kiwifruit physiology and quality.
- Elucidating the role of ethylene (if any) in influencing kiwifruit physiology and quality in tropical market conditions.
- Identifying tolerable durations of exposure to high temperature for kiwifruit that do not result in damage before return to cool storage.
- Investigating if high temperature exposure activates anaerobic respiratory metabolism in kiwifruit and consequently identifying whether a relationship exists between anaerobic metabolites (if any) and unique high temperature disorder symptoms.

1.1 Thesis overview

The experiments of this study were conducted at the Postharvest Laboratory, Massey University, Palmerston North, New Zealand while the kiwifruit supply chain survey was conducted in India and Singapore. The prominent New Zealand kiwifruit cultivars ‘Hayward’ and ‘SunGold™’, of *Actinidia deliciosa* and *Actinidia chinensis* species respectively are the cultivars of interest in this project.

Chapter 2 provides background information on the New Zealand kiwifruit industry, illustrates the fundamental knowledge of postharvest fruit ripening mechanism and kiwifruit-specific postharvest metabolism. Further, the existing knowledge on fruit responses to elevated temperatures is elucidated. This chapter finally concludes by highlighting the key knowledge gaps in the existing literature which are considered research opportunities for this project.

The supply chain practices and potential retail sale conditions (by obtaining real conditions data) for kiwifruit under traditional marketing systems in tropical markets (India and Singapore) are elucidated (by a survey) in Chapter 3.

The influence of simulated tropical traditional market conditions on postharvest ripening mechanisms of kiwifruit (at edible ripeness) is demonstrated in Chapter 4.

The consequences of ethylene exposure on kiwifruit (at edible ripeness) physiology and quality under simulated tropical traditional market conditions is illustrated in Chapter 5.

Chapter 6 identifies a time-temperature interaction that induces irrecoverable physiological damage in kiwifruit after long-term storage. Additionally, this chapter elucidates the tolerable durations of exposure for kiwifruit to high temperatures before return to cool storage.

Chapter 7 investigates the influence of heat stress in inducing anaerobic respiratory metabolism in eating ripe ‘Hayward’ kiwifruit and identifies whether a relationship exists between anaerobic metabolites and high temperature induced disorder.

The final discussion (Chapter 8) addresses the overall findings of experimental chapters and their contributions to the existing understanding of kiwifruit responses to high temperatures. Further, this end chapter suggests future research opportunities based on compelling findings.

Chapter 2: Literature review

2.1 The New Zealand kiwifruit industry

2.1.1 History of kiwifruit introduction, industry development and status

Kiwifruit, originally known as ‘yang tao’ or ‘mihoutao’ meaning ‘monkey peach’ in its native land China (Yan, 1981; Ferguson, 1983; Huang and Ferguson, 2007; Ferguson, 2013) was first introduced into New Zealand in 1904 (Jie and Thorp, 1986; Ferguson, 2004). Isabel Fraser, a missionary, carried a few seeds of green fleshed kiwifruit while returning to New Zealand from Yichang, a city in the western province of China (Ferguson, 1983). All the current commercially grown kiwifruit cultivars can be related to those seeds (Ferguson, 1983; Ferguson, 1999). The earliest kiwifruit plants in New Zealand are thought to be cultivated in 1905 by Alexander Allison in Wanganui (Aitken et al., 2005) with the first fruiting from these plants recorded in 1910 (Ferguson, 2004).

The world-dominating (in terms of cultivated area and production) green fleshed cultivar ‘Hayward’ is named after famous New Zealand horticulturist Hayward Wright, who identified this cultivar through natural selection from a group of seedlings in 1925 (Currie, 1997; Ferguson, 1999). The commercial kiwifruit cultivation in New Zealand dates to the 1930s with the establishment of orchards in the regions of Wanganui and Bay of Plenty (Berry, 1997). Although minimal preference was given to ‘Hayward’ at the beginning and most of the initial planting and export consisted of other cultivars such as ‘Bruno’, ‘Gracie’ and ‘Monty’ (Berry, 1997), ‘Hayward’ subsequently became the most preferred cultivar in both local and international markets due to its attractive shape and size, better taste and longer storage life (Ferguson, 1999). This not only resulted in the exponential increase in ‘Hayward’ cultivation expanding to almost

98.5% by 1980 but ‘Hayward’ also became the sole preferred cultivar for export by 1975 (Ferguson, 1999).

The increase in production volume created a fear of glut among the kiwifruit growers resulting in the exploration of options such as postharvest storage as well as the concept of export (Berry, 1997). A trial shipment of kiwifruit (then known as ‘Chinese gooseberry’) sent to England in 1952 was the first ever New Zealand grown kiwifruit exported (Berry, 1997; Kilgour et al., 2007; Milne, 2014). Subsequently, New Zealand kiwifruit entered other foreign markets such as Australia and the United States of America (USA) in 1952 and 1959, respectively (Milne, 2014). While still being marketed as ‘Chinese gooseberry’ during its initial period of export, it was renamed as kiwifruit in the 1970s by its then exporter Turners and Growers Ltd. to avoid import duties in the USA (Milne, 2014).

As reported by Berry (1997), good export earnings during the years 1962-1964 led to cultivation expansion with the export volume first surpassing local consumption in 1972. With widespread kiwifruit cultivation, production, and flourishing international trade, the idea of establishing a marketing board arose among the growers leading to the formation of the Kiwifruit Export Licensing Authority (KELA) in 1972. Later in 1977, with additional objectives such as industry development, export expansion, licensing and quality standards, the New Zealand Kiwifruit Marketing Licencing Authority (KMLA) was formed which subsequently became New Zealand Kiwifruit Authority (NZKA) in 1980. Until 1988, New Zealand kiwifruit was exported through multiple exporters but with the passing of the bill for the establishment of the New Zealand Kiwifruit Marketing Board (NZKMB), a single desk marketing system (except for New Zealand and Australian markets) came into existence from 1989 onwards. NZKMB was later renamed Zespri® International Limited in 1997.

The gold-fleshed kiwifruit cultivar ‘Hort16A’ was developed in 1991 with the prediction of monoculture issues as well as to extend the fruit category and was first exported to international markets in 1999 (Martin, 2008). The serious outbreak of bacterial canker disease in 2010 caused by *Pseudomonas syringae* pv. *actinidiae* (commonly known as Psa) (Vanneste, 2012; Tanner, 2015) affected most of the ‘Hort16A’ plantations resulting in its replacement with improved Psa tolerant cultivar ‘Zesy002’ from 2012 onwards (Donati et al., 2014).

Currently, kiwifruit is New Zealand’s major horticulture crop and recently contributed to a value of almost 69.1% to fresh fruit exports and 38.3% to total horticulture exports (Aitken and Warrington, 2020). New Zealand also stands as the largest exporter of kiwifruit (by value and volume) in the world (Workman, 2021) with sales extending to over 50 countries. The present commercial production comprises of green flesh cultivars ‘Hayward’ and ‘Zesh004’ (marketed as Green™ and Sweet Green™), gold-fleshed cultivar ‘Zesy002’ (marketed as SunGold™) and the newly introduced red-fleshed cultivar ‘Zes008’ (marketed as RubyRed™). Despite significant challenges, the New Zealand kiwifruit industry continues to thrive and aims to reach a sales value of NZ $4.5 B by 2025 (Fox, 2020).

2.1.2 A brief understanding of New Zealand kiwifruit supply chain operations

The New Zealand kiwifruit export industry is operated by Zespri® International Ltd, a grower owned marketing co-operative. Zespri® is involved in international export and marketing, research and development and provides logistical services. Zespri® follows a conscientious quality monitoring process known as the ‘Zespri System’ from production through to marketing which has enabled the delivery of consistent high quality kiwifruit at international markets.

The initial process begins with the production systems wherein growers periodically monitor their crop and maintain a record consisting of all the packages of practices followed such as nutrient application and pesticide sprays. The information gathered is later submitted to Zespri®. After fruit are physiologically mature, individual assessors from Zespri® visit the orchard and collect kiwifruit samples from different parts of the orchard for quality measurements. Kiwifruit are assessed for dry matter content, soluble solids, colour and maturity (detailed in section 2.2.2.1). After quality testing, clearance is given for harvesting. Harvesting is done manually by seasonal labours and backpackers and care is taken to avoid physical damage during harvest (Fearne, 2020). After harvest, fruit is collected in wooden bins and later the fruit filled bins are labelled and transported by a truck to the packhouse (Hume et al., 2011).

Packhouse operations (Figure 2.1) include decision-making processes that need to balance continuous supply in combination with assuring quality fruit (Jabbar, 2014). On arrival at the packhouse, the fruit bins are transferred to a covered area and stored under ambient conditions for 2-3 days to remove field heat and facilitate curing (Bautista-Banos et al., 1997; Doleh, 2018; East et al., 2018). Curing is essential for kiwifruit as it contributes to the healing of stem scar which on one hand reduces fruit susceptibility to *Botrytis* rot and on the other minimises mechanical damage by reducing fruit water loss (Pennycook and Manning, 1992; Bautista-Banos, 1995; Bautista-Banos et al., 1997; Doleh, 2018). Since temperature and relative humidity remain uncontrolled during curing, different fruit batches may be subjected to different curing conditions (Bautista-Banos et al., 1997; Jabbar, 2014).

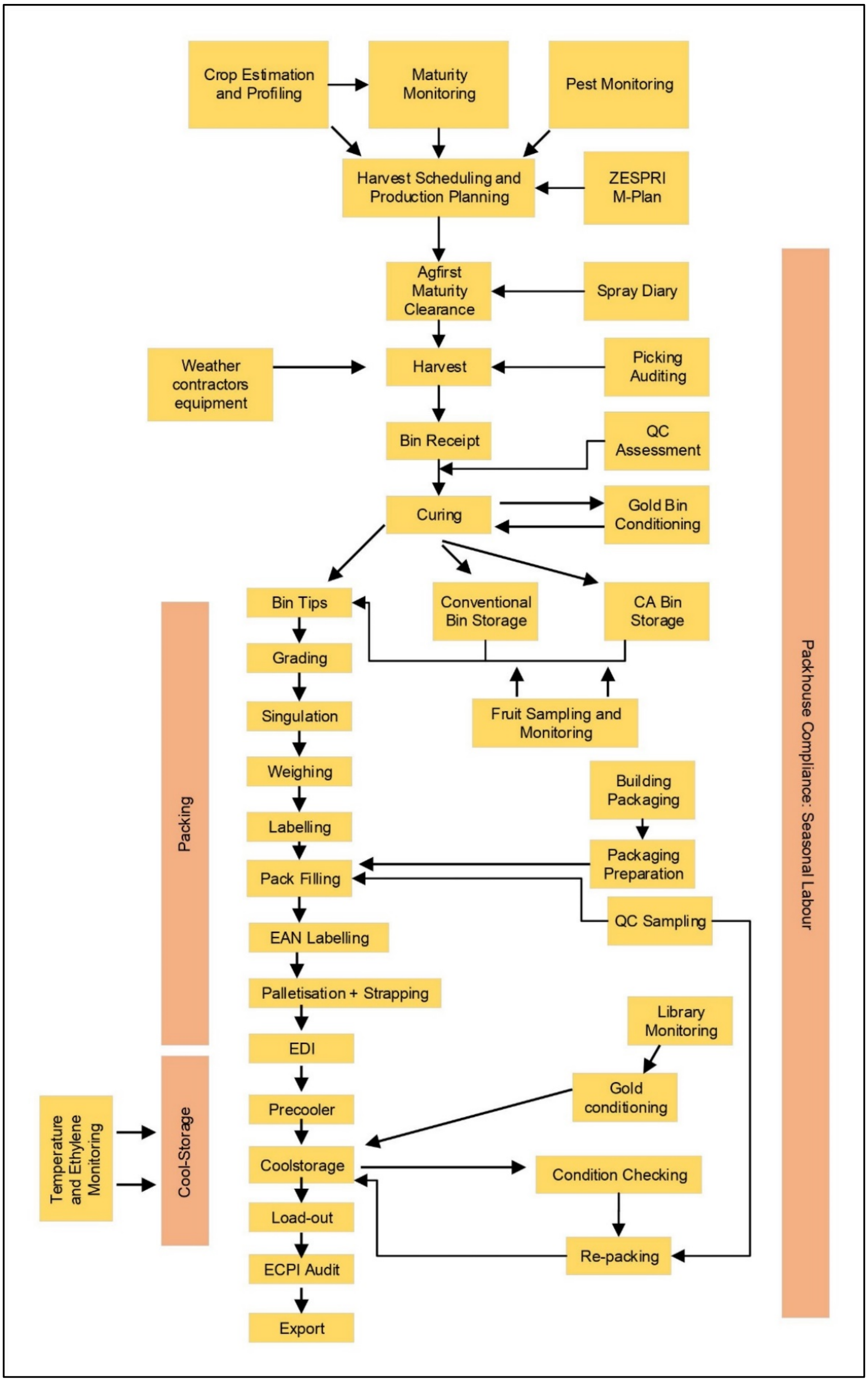


Figure 2.1: Depiction of kiwifruit supply chain operations and factors (pre and postharvest) considered for decision-making processes in New Zealand (representation from Baker et al., 2018).

Curing is subsequently followed by fruit grading (according to size) and packaging. Each fruit is checked through highly mechanised automated grading machinery before packing into boxes. Class I fruit are exported while Class II fruit are sold within New Zealand (Hume et al., 2011). The packaging types used are International tray (IT trays), Modular loose (ML) box, Modular bulk (MB) box, Modular double (M2) box and Plateau box (P1). Fruit from each grower is packed separately to provide feedback to the growers and ensure traceability that assists with food safety assurance and quality management. The packed fruit boxes are then stacked into pallets for storage or transportation. Each box and pallet are labelled with a specific bar code and can be tracked down at any time from the point it leaves the packhouse until it reaches the consumer (Gautam et al., 2017). This track and trace system assist in knowing the fruit status along the supply chain as well as for having consumer feedback on a grower.

During storage, fruit from each grower are regularly assessed for quality (firmness, rots and disorders). This quality check practice is termed condition checking (Benge and Kay, 2003). Condition checking is essential to keep an eye on the storage performance of an individual grower and manage efficient inventory flow (Mills, 2004; Adams et al., 2010; Jabbar, 2014). In addition, inventory decisions may also consider other factors of a grower such as past year storage performance, pre-harvest and at-harvest information (Adams et al., 2010; Tanner et al., 2012; Jabbar, 2014).

Fruit samples for condition checking are drawn from an operational fruit library, a storage facility wherein different growers are stored under the same conditions to obtain a good representative sample and compare storage performances (Benge and Kay, 2003; Jabbar, 2014). A sample population of 300 fruit (based upon ISO quality control standards) is chosen to evaluate if a batch or lot of a grower qualifies for export or not (Jabbar, 2014). The export standards are fixed mainly based on the firmness threshold. The average firmness of a batch or lot to qualify for export is ≥ 1.2 kg_f and each fruit within a batch or lot must measure firmness above 1 kg_f (Jabbar, 2014). However, there is a 1.3% acceptable fraction limit of soft fruit (< 1 kg_f) within a fruit lot which for example denotes that in a lot of 300 fruit, the presence of ≤ 8 soft fruit could still result in export acceptance while ≥ 9 soft fruit results in export rejection (Jabbar, 2014). For the rejected batch, repackaging is followed to remove soft and rotten fruit.

Once the order is received, fruit is allocated to the specific order based on the requirement of the consumer in that specific market. Before fruit leaves the packhouse, fruit are again assessed for quality. Fruit assigned for overseas markets is transported in the container (40%) and reefer (60%) vessels. Fruit destined for containerised shipping are loaded onto the containers at the packhouse while for reefer shipping, fruit pallets are transported to the ports and directly loaded into the reefer vessels. Before being loaded, fruit are subjected to export consignment product inspection (ECPI) by the fruit inspectors. Fruit are checked for various quality aspects such as firmness, blemishes, and rots. Since the loading point varies between containerised and reefer shipping, ECPI checks happen at the packhouse and port for fruit intended for containerised and reefer shipping, respectively (P. Biswas, personal communication, January 19, 2022). ECPI checks may also happen beforehand during fruit packing or during storage at packhouses (P. Biswas, personal communication, January 19, 2022).

Until fruit reaches the port of departure, the ownership of the fruit is still held by the growers and is transferred to Zespri® before shipping (Fearne, 2020). Reefer ships are charted by Zespri® which benefits in various ways such as controlling shipping routes, delivery timings, higher volume fruit delivery and fruit conditioning (by a combination of ethylene and temperature control treatments) in transit (Fearne, 2020). Monitoring of temperature and storage conditions is followed during shipping.

The distribution of fruit in some offshore markets such as in Europe, Korea, Japan and China is controlled by Zespri®. These markets are known as supplier accountability markets. Once fruit reach supplier accountability markets, a quality check (on 200 fruit per grower) is done by Zespri® (within 14 days of delivery) and the ordered fruit is distributed to the importers (P. Biswas, personal communication, January 19, 2022). The remaining stock in supplier accountability markets are under control of Zespri® which ensures better control over the distribution and marketing of available fruits (Fearne, 2020). These remaining stock fruits are held at Zespri® contracted cool stores located either at port or outskirts depending on the markets (P. Jeffery, personal communication, January 20, 2022). Most of the fruit shipped in reefer vessels are to supplier accountability markets. On the other hand, markets such as India, Singapore, Taiwan, South Africa and Dubai are considered as non-supplier accountability markets in which the importers take complete control over fruit once received at the port.

2.2 Fruit postharvest physiology and quality

2.2.1 Fruit ripening – a fundamental understanding

2.2.1.1 The differentiation between climacteric and non-climacteric fruit groups

The life stage of fruit can be grouped into growth, maturation, and senescence (Biale, 1950; Biale, 1964). During growth, cell division and cell enlargement occurs resulting in the final fruit size attainment (Biale, 1964). Maturation initiates before the cessation of growth and the mechanisms involved are crop and cultivar dependent

(Wills and Golding, 2016). Ripening (an intermediate phase following maturation and preceding senescence) is a genetically fixed multiplex mechanism influencing changes in physiological and biochemical properties of the fruit, which are prerequisite for improving the organoleptic nature (Gillaspy et al., 1993; Gapper et al., 2013; Forlani et al., 2019; Fuentes et al., 2019). Senescence is an aging process resulting in final cell death (Sacher, 1973; Gapper et al., 2013).

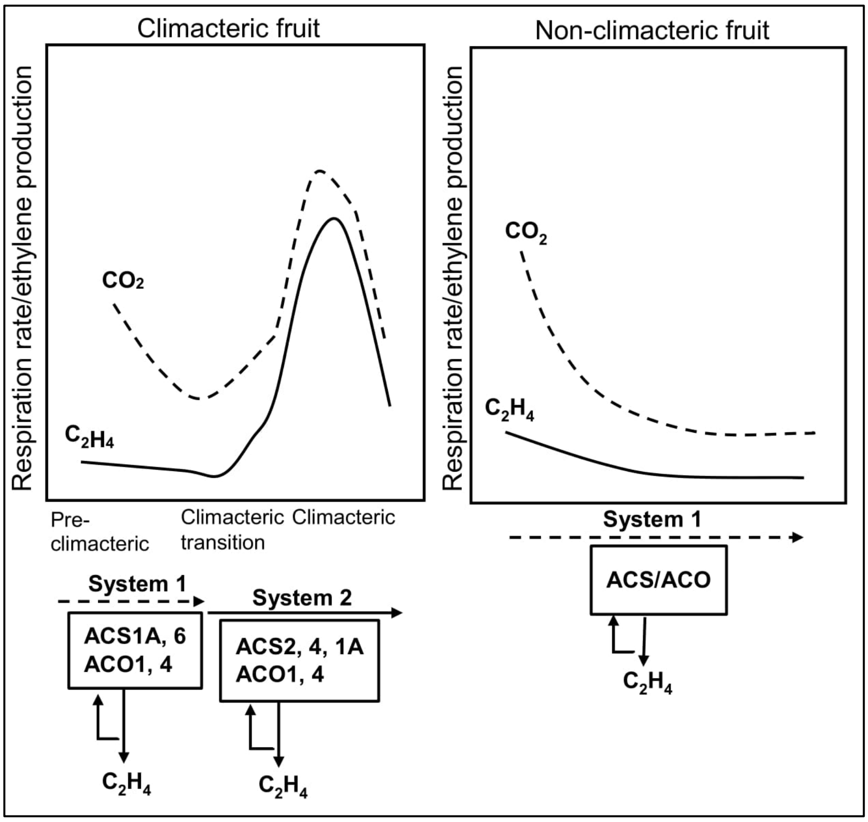


Figure 2.2: Changes in respiration and ethylene production along different developmental stages in climacteric (tomato) and non-climacteric (mandarin) fruits. 'System 1' ethylene synthesis is active in immature climacteric fruits and throughout life stages in non-climacteric fruits. 'System 2' is active in mature climacteric fruits. Specific enzyme groups active during 'System 1' and 'System 2' ethylene synthesis in both fruit categories are indicated (representation from Alos et al., 2018).

Fruits, based on their ripening pattern are classified into ‘climacteric’ and ‘non-climacteric’ groups (Figure 2.2) (Kidd and West, 1930; Biale, 1964; McMurchie et al., 1972; Cherian et al., 2014; Alos et al., 2018; Figueroa et al., 2021; Kou et al., 2021). Climacteric fruits exhibit an upsurge in respiration and ethylene production at the climacteric phase (during ripening) and these mechanisms subsequently decline and stop during the senescent phase (Atkinson et al., 2011; Fukano and Tachiki, 2021).

Giovannoni et al. (2017) based on the climacteric model fruit tomato suggests that respiratory rise initially precedes with a concomitant increase in ethylene production leading to increased production of proteins and ripening related enzymes which are involved in events such as softening, chlorophyll degradation, conversion of starch to sugar, decline in acidity and synthesis of aromatic volatiles. These changes are naturally destined to serve as attractive features for seed dispersal organisms (Janson, 1983; Fukano and Tachiki, 2021). Non-climacteric fruit exhibit lower respiratory activity and ethylene production throughout their life stages (Figure 2.2) (Giovannoni, 2004; Van de Poel et al., 2012).

Earlier suggestions for the observed distinctiveness in the respiratory nature between climacteric and non-climacteric fruits was due to the differences in energy requirements between these two fruit groups (Richmond and Biale, 1966; Pratt and Goeschl, 1969). Since ripening in climacteric fruits occurred after harvest, respiratory rise was essential to supply energy required for ripening related events while respiratory rise was non-essential for non-climacteric fruits as they ripen pre-harvest. However, this theory was put into question based on observations in strawberry (a non-climacteric fruit) in which rapid softening (on plant) occurred in the absence of respiratory rise (Knee et al., 1977). This may also closely imply with kiwifruit (a climacteric fruit) in which respiratory climacteric is not directly linked with substrate availability used for energy generation (MacRae et al., 1992) and occurs only after fruit has significantly ripened (Ritenour et al., 1999; Atkinson et al., 2011; Mitalo et al., 2019a). Further, apples and kiwifruit suppressed in ethylene synthesis exhibited respiratory rise only upon exposure to exogenous ethylene (Defilippi et al., 2005; Atkinson et al., 2011). All these findings lead to a conclusion that respiratory increase in climacteric fruits may be one of many ripening related changes induced by ethylene.

An additional distinctiveness between climacteric and non-climacteric fruits is based upon the responsiveness towards exogenous ethylene (Alós et al., 2018). This characteristic feature has helped classify some climacteric fruits (e.g. kiwifruit) which ripen significantly without increased ethylene synthesis (Whittaker et al., 1997; Asiche et al., 2018). While both climacteric and non-climacteric fruits consist of a common system of ethylene synthesis known as 'System 1' in which fruit synthesise minute concentrations of ethylene and remain unresponsive or partially responsive to exogenous ethylene (McMurchie et al., 1972; Chen et al., 2018), the presence of an additional 'System 2' in climacteric fruits (after maturation) makes them highly sensitive and responsive to exogenous ethylene (McMurchie et al., 1972; Giovannoni et al., 2017).

In climacteric fruits, under 'System 1', ethylene exposure activates an autoinhibitory domain towards ethylene synthesis while in 'System 2', a positive feedback loop of ethylene autocatalysis is activated (Alexander and Grierson, 2002; Van de Poel et al., 2012; Hewitt and Dhingra, 2020). Although ethylene may not induce ripening in immature fruits, it still can accelerate the onset of maturity in these fruits (Yang, 1987) and correspondingly fastens ripening initiation in mature climacteric fruits (Biale, 1964; Bufler, 1986). Evidence in non-climacteric fruits suggests exogenous ethylene could influence some ripening mechanisms such as a decline of acidity in grapes (Weaver and Montgomery, 1974), chlorophyll degradation in mandarins (Alos et al., 2014), respiratory rise in cherries (Gong et al., 2002). However, ethylene responsiveness in non-climacteric fruits ranges from very low to low levels with the only exception of citrus groups which possess moderate sensitivity towards ethylene (Alós et al., 2018).

2.2.1.2 An insight into fruit respiration, ethylene production and ethylene perception mechanisms

2.2.1.2.1 Respiration

Respiration is a key catabolic process that serves as the sole source of energy for fruits during the postharvest stage (Solomos, 1983). During respiration, carbohydrates which are generally stored in the form of starch, organic acids, proteins, lipids and fats (Taiz et al., 2015) are utilised for the generation of energy required for several cellular maintenance processes (Biale, 1950; Romani, 1984; DeEll et al., 2003; Colombié et al., 2017; Pott et al., 2020). Since these reserved food substrates cannot be replenished at the postharvest stage, it is of prime importance to keep the respiration rate as low as possible to delay substrates exhaustion and obtain maximum storage life (Tano et al., 2005). Minimising respiration remains to be the basic concept of postharvest storage techniques and the rate of respiration is considered as a potential indicator of fresh produce storage life (Robinson et al., 1975; Tano et al., 2005; Colombié et al., 2017). Respiration can either be aerobic or anaerobic in contingent on the surrounding atmospheric conditions (mainly gases) at which the fruits are stored.

2.2.1.2.1.1 Aerobic respiration

Under conditions of normal levels of oxygen and carbon dioxide, aerobic respiration occurs and the general equation for aerobic respiration is presented below:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + 36\ ATP \qquad Eq\ 2.1$$

Aerobic respiration involves three steps: glycolysis, Kreb's cycle (tricarboxylic acid cycle) and oxidative phosphorylation (Fonseca et al., 2002; Boeckx et al., 2019). Glycolysis is an anaerobic process common in both aerobic and anaerobic respiration occurring at the cytoplasm and plastids of the cell (Plaxton, 1996). It is an energy investment step wherein glucose is phosphorylated through a series of reactions leading to the formation of two molecules of pyruvic acid, 2 molecules of adenosine triphosphate (ATP) and two molecules of nicotinamide adenine dinucleotide ($NADH_2$) (Plaxton, 1996; Bessemans, 2018). The formed latter two compounds (ATP and $NADH_2$) are the energy carrying molecules.

Pyruvic acid proceeds to the mitochondria wherein Kreb's cycle occurs (Givan, 1999). An important step in glycolysis with relation to fruit climacteric respiratory peak is the conversion of fructose 6-phosphate (F6P) into fructose 1,6-biphosphate (FBP) by phosphofructokinase enzyme (PFK). The respiratory peak in kiwifruit (MacRae et al., 1992) and banana (Ball et al., 1991) is accompanied by an increase in glycolytic flux which is thought to be due to an increase in the activity of PFK enzyme and rapid conversion of F6P to FBP.

Before initiation of the Kreb's cycle, pyruvic acid which is a three carbon compound undergoes oxidative decarboxylation to form a two carbon compound known as acetyl coenzyme A (acetyl-CoA) (Murphy and Stumpf, 1981; Wendokoon et al., 2004). Acetyl- CoA later binds to the oxaloacetic acid to form citrate and subsequently through a step by step process citrate gets converted into *cis*-aconitase, isocitrate, α-ketoglutarate, succinate, fumarate, malate to finally form oxaloacetic acid (OAA) (Kornberg, 1987; Jacoby et al., 2012; Etienne et al., 2015). The formed OAA is reutilised for the normal continuation of the cycle and generation of energy carrying molecules (Perotti et al., 2010). A total of six $NADH_2$, two $FADH_2$ and one ATP molecule are formed at the end of Kreb's cycle.

The final step oxidative phosphorylation consists of electron transport chain (ETC) and chemiosmosis which occur at the inner membrane of the mitochondria (Alberts et al., 2002; Makino, 2013). ETC involves four different proteins complexes (complexes I-IV) along with components coenzyme-Q (Co-Q) and cytochrome-C (Cyt-C) (Fernie et al., 2004; Millar et al., 2011; Jacoby et al., 2012). The $NADH_2$ and $FADH_2$ molecules formed during glycolysis and Kreb's cycle donate electrons which travel through the ETC protein complexes and components resulting in the generation of protons. These protons move from the mitochondrial matrix to the intercellular membrane resulting in the proton gradient between the mitochondrial matrix and the intermembrane space. At the final step of ETC, electrons are accepted from complex-IV by oxygen and later oxygen in combination with protons forms two molecules of water (Yonetani and Ray, 1965). Next during chemiosmosis, the protons present at the mitochondrial matrix are utilised by ATP synthase to finally generate 36 ATP molecules (Mitchell, 1966; Giacomello et al., 2020).

2.2.1.2.1.2 Anaerobic metabolism

Anaerobic respiration is an alternative pathway of energy synthesis under conditions of critical oxygen concentrations (Bessemans, 2018; Boeckx et al., 2019). Fruits switch from aerobic to anaerobic respiration as the surrounding oxygen concentrations deplete below the critical oxygen borderline termed as “anaerobic compensation point” (ACP) (Hertog et al., 2004; Franck et al., 2007; Thewes et al., 2017). Additionally, fruits are often prone to anaerobiosis even under conditions of normal oxygen levels due to their bulky compositional nature which restricts oxygen transport within the internal atmosphere (Rajapakse et al., 1990; Hertog et al., 2004; Ho et al., 2006; Ho et al., 2008; Biais et al., 2010; Valle-Guadarrama et al., 2013; Mellidou et al., 2014; Paul and Pandey, 2014; Cukrov, 2018).

In anaerobic respiration, unlike aerobic respiration, there is termination of Kreb’s cycle and electron transport chain resulting in the accumulation of glycolysis end products pyruvate and $NADH_2$ (Ke et al., 1995). Pyruvate is utilised by enzyme pyruvate decarboxylase (PDC) to form acetaldehyde which is subsequently converted to ethanol by alcohol dehydrogenase (ADH) and finally to ethyl acetate by the enzyme alcohol acyl transferase (AAT) (Botondi et al., 2012; Boeckx et al., 2019). These overall anaerobic reactions finally result in the generation of just two ATP molecules which are inefficient to provide enough energy required for the cellular maintenance processes but facilitate cell survival as far as the carbohydrate substrates are available (Ke et al., 1995; Bailey-Serres et al., 2012).

An additional lactate pathway of fermentation (a major anaerobiosis pathway in animal cell) in fruits also exists during which pyruvate is directly converted into lactate by lactate dehydrogenase (LDH) enzyme (Ke et al., 1995). However, the concentrations of lactate produced are negligible in comparison to that of ethanol in fruits (Peppelenbos and Oosterhaven, 1998).

Increased activity of PDC and ADH enzymes along with a rise in ethanol production under conditions of lower oxygen concentrations have been reported in kiwifruit (Botondi et al., 2012), apples (Boeckx et al., 2019), avocados (Kanellis et al., 1991), pears (Ke et al., 1994) and strawberries (Blanch et al., 2015). Increased accumulation of anaerobic metabolites results in off-flavours (Cohen et al., 1990; Richardson and Kosittrakun,1995; Thomai and Sfakiotakis, 1997; Wright et al., 2015) as well as internal disorders in apples (Richardson and Kosittrakun,1995), pears (Deuchande et al., 2017) and avocados (Yahia and Carrillo-López, 1993). Not to be forgotten is the fact that fruit synthesise minute concentrations of ethanol and acetaldehyde prominently as part of the ripening process and the active role of these metabolites in aromatic volatile production is well established (reviewed in Podd and Van Staden, 1998; Pesis, 2005). In addition, the accumulation of ethanol increases as fruit becomes overripe and reaches senescence (Gustafson, 1934; López et al., 1999; Ali et al., 2021).

2.2.1.2.1.3 Respiratory Quotient (RQ)

Respiratory Quotient (RQ) is a good indicator of oxygen deficiency within the fruit internal atmosphere (Hertog et al., 2004; Bessemans, 2018; Boeckx et al., 2019). RQ is defined as the ratio of CO_2 produced to the O_2 consumed by fruit tissue (Fonseca et al., 2002). Under aerobic conditions, the RQ value ranges between 0.5-1.3 depending on the substrates utilised for respiration process (Kader, 2003; Hertog et al., 2004; Bessemans, 2018). Under aerobic conditions, RQ may vary between different fruits (Kubo et al., 1996). For example, an RQ value of 0.5 and 1 was obtained under aerobic conditions for kiwifruit (Hertog et al., 2004) and lemons (Biale and Young, 1947), respectively. Under conditions of critical oxygen levels, RQ increases above 1 and steeply rises when oxygen level further falls below the lower oxygen limit (LOL) (Prange et al., 2005; Wright et al., 2015). This significant rise in RQ is termed as respiratory quotient breakpoint (RQB) (Beaudry, 1993; Gran and Beaudry,1993; Hertog et al., 2004).

RQ is determined using the following equation:

$$\mathrm{RQ} = \frac{\Delta C_{CO2}}{\Delta C_{O2}} \qquad \text{Eq. 2.2}$$

Where RQ = Respiratory Quotient
ΔC_{CO2} = estimated change in CO_2 production over time
ΔC_{O2} = estimated change in O_2 consumption over time

2.2.1.2.2 Ethylene

2.2.1.2.2.1 Ethylene biosynthesis pathway

Ethylene's significant role in climacteric fruit ripening makes it to be the most important and widely studied phytohormone in postharvest research (recently reviewed in Liu et al., 2020). Additionally, ethylene's function in regulating plant growth as well as stress response remains to be of key interest among plant physiologists. The ethylene biosynthesis pathway is a three-step process starting with the conversion of methionine (a sulphur containing amino acid) to S-adenosylmethionine (AdoMet) by enzyme S-adenosylmethionine synthase (Lieberman and Mapson, 1964). The resultant AdoMet is transmuted to 1-aminocyclopropane-1-carboxylic acid (ACC) and 5-deoxy-5 methylthioadenosine (MTA) by enzyme 1-aminocyclopropane-1-carboxylate synthase (ACS) (Adams and Yang, 1979).

MTA which is produced as a by-product in the AdoMet to ACC conversion step is restored into methionine (Miyazaki and Yang, 1987). This salvage pathway termed as ‘Yang cycle’ was first demonstrated by Baur and Yang (1972) with these authors concluding that MTA restoration into methionine is essential for abundant ethylene production in plants. In the final step, enzyme 1-aminocyclopropane-1-carboxylic acid oxidase (ACO) oxidises ACC to N-hydroxy-ACC, which then gets fragmented into ethylene (C_2H_4) and cyanoformic acid (C_2HNO_2) (Houben and Van de Poel, 2019). The cyanoformic acid formed further gets converted to carbon dioxide and hydrogen cyanide (Yang and Hoffman, 1984). To prevent toxicity, build up due to cyanide accumulation within plants, β-cyanoalanine synthase (β-CAS) enzyme detoxifies hydrogen cyanide into β-cyanoalanine (Argueso et al., 2007; Van de Poel et al., 2012).

2.2.1.2.2.2 Ethylene sensing and signal transduction mechanisms

Ethylene is perceived by the receptors at the N-terminal (Malley et al., 2005). These receptors are present on the endoplasmic reticulum and the lumen of endoplasmic reticulum serves as the reception site of these receptors (Binder, 2008). The receptors require copper ion as a cofactor to be fully functional and response to antagonist-1 (RAN-1) transporter acts as copper ion provider to the receptors (Rodriguez et al., 1999). These receptors function as negative regulators of the pathway, which means the absence of ethylene will initiate and drive the pathway whereas in the presence of ethylene the pathway is terminated (Hua and Meyerowitz, 1998; Ju and Chang, 2015).

In the absence of ethylene, auto-phosphorylation occurs on the histidine kinase residue which in turn phosphorylates the constitutive triple response-1 (CTR-1) kinase domain and activation of CTR-1 signals the ethylene insensitive-2 (EIN-2) and phosphorylates its cytoplasmic end (C-end) (Moussatche and Klee, 2004). The phosphorylation of C-end in turn activates ethylene targeting protein-1 (ETP-1) (Qiao et al., 2009). These ETP-1 proteins are f-box proteins having the ability to cause ubiquitination (inactivation) of proteins and protein turnover within the cell (Gagne et al., 2004). Therefore, EIN-2 molecule is ubiquitinated at the C-end by ETP-1 protein and sent into the 26-S proteasomal complex where it is degraded (Christians et al., 2009). This EIN2 is an essential molecule for stabilising the ethylene insensitive-3 (EIN-3) transcription factor by detaching it from the proteasomal complex but gets degraded in the absence of ethylene. Similarly, EIN-3 which is responsible for the transcription of the ethylene signalling genes at the nucleus gets degraded by proteasomal complexes in the absence of EIN-2. Therefore, in the absence of EIN-3 no transcription happens leading to ethylene insensitivity.

In the presence of ethylene, the receptor is turned off and de-phosphorylation occurs in ETR-1 which in turn releases CTR-1. EIN-2 is dephosphorylated in the presence of ethylene and this de-phosphorylation mediates the cleavage of C-end which gets translocated into the nucleus and saves EIN-3 from degradation. The saved EIN-3 attaches to ethylene responsive factors genes (ERFs) and drives the transcription process resulting in ethylene sensitivity.

In the climacteric model fruit tomatoes, six receptor genes have been identified (Wilkinson et al., 1995) while in apples and kiwifruit, the presence of five receptor genes has been confirmed (Tatsuki et al., 2007; Yin et al., 2008). Interestingly, these receptor genes possess varying natures of expression during ethylene production as well as upon ethylene perception and some may be specific to either ‘System 1’ or ‘System 2’ ethylene production and some being active under both these systems. For example, in tomatoes, the receptor gene *LeETR4* is expressed upon ethylene exposure during developmental stages while *LeETR8* expression is confined to ‘System 2’ ethylene production (Kevany et al., 2007).

Similarly, in kiwifruit, of the five receptor genes identified, *AdERS1a*, *AdETR2*, and *AdETR3* were concomitantly expressed at both climacteric phase as well as upon ethylene exposure but conversely, *AdERS1b* remained inactive (Yin et al., 2008). An additional response of negative regulation was noted in *AdETR1* receptor gene which led to an overall conclusion that this receptor gene inhibits ethylene sensing by the continuation of ethylene signal transduction upon ethylene perception (Yin et al., 2008).

2.2.2 Kiwifruit maturity and postharvest metabolism

2.2.2.1 Maturity indicators and important quality attributes

Kiwifruit is harvested after attaining physiological maturity (Macrae et al., 1989; Goldberg et al., 2021) which is indicated through measures of harvest index (Burdon et al., 2014a; Burdon et al., 2016). Fruit maturation in ‘SunGold™’ happens earlier than ‘Hayward’ and this may subsequently result in an earlier harvest (Burdon et al., 2021). For ‘Hayward’, maturity is judged based on soluble solids content (SSC), with 6.2° Brix (in New Zealand) being considered as minimum maturity standard for harvest (Burdon, 2015; Burdon, 2018). Fruit harvested with higher SSC (7-10° Brix) possess better storage potential and hence harvest may be delayed for fruit (both ‘Hayward’ and ‘SunGold™’) intended for long-term storage (Harman and Hopkirk,1982; Burdon, 2018). SSC may vary between fruit of a cultivar as well as at different internal regions of an individual fruit with increased content detected in the distal rather than at the proximal or stem end (Hopkirk et al., 1986). Therefore, a composite juice sample obtained from both proximal and distal ends is necessary for a precise SSC measurement of an individual kiwifruit (Hopkirk et al., 1986).

Flesh colour is considered as an important maturity indicator for yellow fleshed kiwifruit cultivars and the proposed time for harvest is when flesh hue is ≤ 103 ° (Burdon et al., 2021). Harvest at this stage ensures commercial acceptability (Burdon et al., 2021). While the optimal harvest periods have been well established for both ‘Hayward’ and ‘SunGold™’ cultivars, the stage of maturity at harvest may still vary in the commercial production to meet varying supply windows (Burdon, 2018; Burdon et al., 2021). This may result in fruit being harvested either earlier or later from the standard established harvest period after attaining physiological maturity. Different harvest strategies in the New Zealand kiwifruit industry are termed ‘Kiwistart’ and ‘MainPack’, distinguishing the fruit harvested earlier or later in a harvest season respectively (Hertog et al., 2016).

In addition to SSC and flesh colour, firmness is an important criterion signifying kiwifruit maturity at harvest (Harman, 1981; Burdon et al., 2017). Firmness in kiwifruit is generally determined by a puncture test on the outer fruit pericarp after slicing the fruit skin (Watkins and Harman, 1981). Kiwifruit at harvest are very firm with firmness ranging approximately 60-90 N (Beever, 1990) depending on fruit maturity at harvest. As no visible ripening changes are evident in kiwifruit (Stec et al., 1989), most of the supply chain requirements such as handling, storage and export depend on firm fruit that are not susceptible to physical damage (Ilina et al., 2010; Burdon et al., 2017; Gong et al., 2020). Regardless of being harvested very firm, kiwifruit is perceived to be best for consumption only when firmness declines to 5-10% of harvested firmness, between 4-13 N (Lallu et al., 1989; Stec et al., 1989; Crisosto and Crisosto, 2001).

Dry matter content largely determines kiwifruit taste profile and influences consumer acceptability (Harker et al., 2009; Jaeger et al., 2011). Dry matter represents the total stored carbohydrates in a fruit and is a combination of both soluble and insoluble solids (Burdon et al., 2004; Harker et al., 2009; Goldberg et al., 2021). By determining the fruit dry matter content at harvest, the possible soluble sugar content in ripe fruit (rSSC) and the final eating quality can be determined (Scott et al., 1986; Crisosto and Crisosto, 2001; Burdon et al., 2004; Harker et al., 2009).

At-harvest dry matter content in 'Hayward' and 'SunGold™' may range between 12 to 20% (Beever, 1990; Burdon et al., 2004). The variability in dry matter content between fruit is influenced by environmental factors and orchard management practices (Burdon et al., 2004; Lievre et al., 2021). Hayward fruit containing an at-harvest dry matter of 15-20% may develop best quality with rSSC of 12-16% (Burdon et al., 2004; Harker et al., 2009). Similarly, yellow-fleshed kiwifruit cultivars harvested at above 16% dry matter are perceived best for consumption with a rSSC of 14% and above (Harker et al., 2009).

2.2.2.2 Postharvest metabolism

Kiwifruit are categorised as climacteric (Pratt and Reid, 1974; Antunes et al., 2000) exhibiting an atypical ripening pattern since most of the ripening events occur independently of significant ethylene production (Kim, 1999; Antunes et al., 2000; Mworia et al., 2012; Mitalo et al., 2019a; Fullerton et al., 2020). The ripening phases in kiwifruit are distinctively characterised by a quadratic softening pattern comprising of initial slow, a rapid, a final slow and over-soft phase (Figure 2.3) (MacRae and Redgeell, 1992; Atkinson et al., 2011). The occurrence of the initial slow softening phase may be shortened or absent with advancement in fruit maturity at harvest (Burdon et al., 2017).

Softening transition from initial slow to rapid phase may be more apparent in 'SunGold™' than in 'Hayward' (Burdon et al., 2017). The cellular level manifestations occurring at different phases of kiwifruit softening include changes in pectin (by solubilisation and depolymerisation), decline in cell wall strength (by weakening of xyloglucan and loss of galactose) and loss of middle lamella (marks the complete collapse of cell wall strength) (Arpaia et al., 1987; Hallett et al., 1992; Redgwell and Percy, 1992; Schroder and Atkinson, 2006; Atkinson et al., 2011; Fullerton et al., 2020).

Figure 2.3: Four different softening phases evident in kiwifruit. At initial slow (phase 1) and rapid softening (Phase 2), fruit may not produce significant ethylene but are highly sensitive and responsive to ethylene exposure. At phase 3, respiratory climacteric and ethylene autocatalysis initiates and fruit reach edible ripeness. At phase 4, fruit lose commercial value due to over-softness and off-flavours (representation from Atkinson et al., 2011).

The climacteric peaks of respiration and ethylene production are observed at phase 3 of softening when firmness declines below 10 N (Figure 2.4) (Stec et al., 1989;

Ritenour et al., 1999; Schroder and Atkinson, 2006). Volatiles produced during the climacteric phase include aldehyde, esters (mainly butonates) and alcohols, with the concentration of the latter two volatiles further increasing at the overripe state (Young and Paterson, 1985; Paterson et al., 1991; Wang et al., 2011).

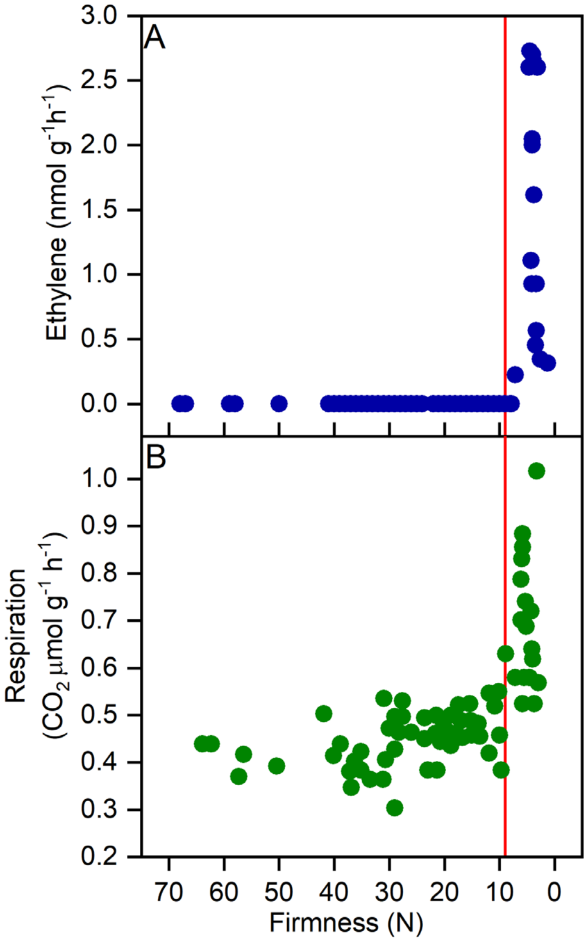


Figure 2.4: The pattern of ethylene production (A) and respiration (B) along with firmness changes in 'Hayward' kiwifruit at 20 °C (representation from Ritenour et al., 1999).

2.2.2.2.1 Factors influencing kiwifruit postharvest ripening mechanisms

Temperature, relative humidity and ethylene exposure mainly influence kiwifruit ripening at the postharvest stage while storage handling practices are also of crucial importance in determining the ripening rate. Kiwifruit are stored at 0 °C for 4-6 months (Burdon and Lallu, 2011; Burdon et al., 2017). While it is true that fruit temperature after harvest as well as during storage should be reduced to achieve maximum storage life, kiwifruit remains at risk of developing chilling injury if subjected to rapid cooling immediately after harvest or if refrigerated for longer periods (Burdon and Lallu, 2011; Burdon et al., 2017; Burdon et al., 2021; Gwanpua et al., 2022) or if stored below the recommended storage temperatures (Lallu, 1997; Gwanpua et al., 2018b). The susceptibility or tolerance to chilling injury in kiwifruit is influenced by several pre-harvest and at-harvest factors (Burdon et al., 2014c; Zhao, 2017; Alavi et al., 2021).

Previous investigations have elucidated kiwifruit ripening (considering softening as the key ripening indicator) during refrigerated storage (Kim, 1999; Burdon et al., 2014a; Gong et al., 2020; Goldberg et al., 2021), at ambient temperatures either after harvest (Jabbar et al ., 2014; Asiche et al., 2015; Asiche et al., 2017; Mitalo et al., 2019a; Tilahun et al., 2020) or after a period of storage (Manolopoulou and Papadopoulou, 1998; Koukounaras and Sfakiotakis, 2007; Yin et al., 2009; Zhao, 2017). Exposure to higher storage temperatures accelerates softening, increases ethylene sensitivity and advances ethylene production.

Interestingly, low temperature ripening acceleration is evident in kiwifruit resulting in increased ripening at a range of lower temperatures than at higher temperatures (Mworia et al., 2012). For example, in early harvested ‘Hayward’ kiwifruit, storage at 10 °C increased softening than at 12-16 °C (Burdon et al., 2017). The molecular level mechanisms involved in low temperature modulated softening have been elucidated in investigations of Mworia et al. (2012) and Mitalo et al. (2018) in ‘Sanuki Gold’ and ‘Rainbow Red’ kiwifruit, respectively.

Under ambient conditions, climacteric respiration and ethylene production may be evident within 1 to 3 weeks of storage depending on several pre-harvest and postharvest factors. For example, Ilina et al. (2010) observed 10 days differences in ethylene peak in 'Hayward' kiwifruit grown in two different regions harvested at the same maturity and stored at 20 °C. Refrigerated storage may result in the early onset of climacteric phase in kiwifruit at 20 °C (Koukounaras and Sfakiotakis, 2007; Ilina et al., 2010) with the advancement towards climacteric phase becoming more rapid with increasing storage duration (Hyodo et al., 1987).

Kiwifruit during postharvest stage are highly susceptible to ethylene (Pratt and Reid, 1974; Wills et al., 2001; Atkinson et al., 2011; Defilippi et al., 2011). The presence of ethylene as low as 0.005-0.01 μL L^{-1} concentrations in the storage environment accelerates onset as well as the rate of ripening restricting long-term storage (Kim, 1999; Antunes, 2007; Pranamornkith et al., 2012; Jabbar and East, 2016). A wide range of studies have focused on understanding the role of ethylene (or its analogue propylene) on kiwifruit ripening at refrigerated storage temperatures (Pranamornkith et al., 2012; Hertog et al., 2016; Jabbar and East, 2016; Tongonya et al., 2018), at normal ambient temperatures (Antunes et al., 2000; Antunes and Sfakiotakis, 2002; Antunes, 2007) or at temperatures over 30 °C (Antunes and Sfakiotakis, 1997; Antunes and Sfakiotakis, 2000).

The influence of ethylene on kiwifruit ripening mechanisms is observed to be dependent on ethylene concentration, exposure duration, fruit maturity and storage temperature. For example, at 20 °C, exposure of 'Hayward' kiwifruit to 1000 μL L^{-1} of propylene resulted in immediate ethylene autocatalysis (within 24 h) but was delayed to 72 h at concentrations of 400 μL L^{-1} (Antunes et al., 2000). Mworia et al. (2010) reported 'Sanuki Gold' kiwifruit harvested earlier than the commercial harvest period required a reduced duration of propylene exposure (5000 µL L^{-1}) than that of the fruit harvested at the commercial harvest period to initiate ethylene autocatalysis at 25 °C. Although these authors did not point out a specific reason for the observed delayed response to propylene with maturity advancement, it could be that increased internal basal ethylene levels may have resulted in reduced sensitivity to exogenous ethylene.

2.2.2.2.2 Kiwifruit storage-life extension by inhibiting ethylene perception

A diverse group of chemicals such as 2,5-norbornadiene (NBD), 3,3-dimethyl cyclopropane (DMCP), diazocyclopentadiene (DACP), 1-methylcylopropene (1-MCP) have been known to inhibit ethylene perception in fruits (Sisler and Serek, 1999). Of these, 1-MCP remains to be of commercial importance (especially for apples) due to its non-toxic nature, efficacy at lower concentrations, minimal residues and simple treatment technique (Regiroli and Vriends, 2007; Zhang et al., 2020). The irreversible binding nature of 1-MCP to the active ethylene receptors (greater than ethylene) regulates a negative feedback mechanism of ethylene sensing and thereby delays ripening and senescence (Sisler and Blankenship, 1996; Sisler and Serek, 1997; Watkins, 2006). The efficiency of 1-MCP is dependent on concentration, target species, maturity of the product, temperature at the time of treatment and treatment duration (Blankenship and Dole, 2003).

In kiwifruit, 1-MCP is effective in delaying ripening at storage temperatures or ambient temperatures either as an at-harvest or post-storage application strategy (Kim et al., 2001; Ilina et al., 2010; Asiche et al., 2015). However, the presence of ethylene in either coolstorage or shelflife conditions during 1-MCP treatment diminishes the effect (Kim, 1999). Further, coolstorage duration after or before 1-MCP treatment is found to influence treatment efficacy on kiwifruit with prolonged storage under both treatment strategies to cause reduced 1-MCP treatment effect (Koukounaras and Sfakiotakis, 2007; Ilina et al., 2010).

Kim et al. (2001) applied 1-MCP (0, 1, 10, 100 µL L^{-1} for 16 h at 20 °C) on 'Hayward' kiwifruit as an at-harvest treatment and stored either at 20 °C or 0 °C for 30 days. The treated 0 °C stored fruit were subsequently transferred to 20 °C for a further 30 days. It was noted that the fruit stored at 20 °C had reduced softening compared to untreated fruit with highest 1-MCP concentration resulting in the lowest firmness changes. A similar response was noted in the 0 °C stored fruit but upon transfer to 20 °C, the 1-MCP effect on softening diminished to no significant differences between concentrations. It was concluded that the synthesis of new ethylene receptors during storage at 0 °C may have resulted in no treatment effect upon transfer to 20 °C.

This was further confirmed in an additional experiment from Kim et al. (2001) which involved 1-MCP (10 µL L^{-1} for 16 h at 20°C) treatment after storage at 0 °C (0-128 d), subsequent exposure to ethylene (10 µL L^{-1} for 16 h at 20°C) and later fruit transfer to 20 °C for 8 days. After different storage durations, 1-MCP treated fruit softened similarly at 20 °C irrespective of the presence or absence of ethylene while in untreated fruit, ethylene exposure induced rapid softening faster than the control fruit. These authors concluded that 1-MCP was effective in blocking receptors synthesised during storage at 0 °C and this reduced softening (even in the presence of ethylene) at 20 °C after different storage durations at 0 °C.

Koukounaras and Sfakiotakis (2007) reported a similar response in 'Hayward' kiwifruit wherein 1-MCP (0.5 µL L^{-1} for 24 h at 0 °C) application as an at harvest treatment was effective in delaying softening during short (4 weeks) and medium-term (8 weeks) cool storage and under subsequent shelflife conditions whereas the effect diminished after long term cool storage (20 weeks) which was attributed to enough time taken for the synthesis of new ethylene receptors.

Few investigations however have found 1-MCP as an at-harvest treatment to be effective even after long-term storage. For example, Cantin et al. (2011) found 1-MCP treatment (0.5 µL L^{-1} for 24 h at 1 °C) to be effective in delaying softening in 'Hayward' kiwifruit during long-term cool storage (180 d) in the presence of exogenous ethylene (continuous exposure to 1 µL L^{-1}) and during shelflife assessment. Interestingly, these authors noted that further increasing 1-MCP concentration (1 µL L^{-1} for 12 or 24 h) did not further boost the treatment effect indicating a treatment concentration of 0.5 µL L^{-1} for 24 h was enough to achieve the best results.

A recent investigation by Gong et al. (2020) found 1-MCP treatment (650 nL L^{-1} for 24 h at 0 °C) to reduce softening rate in all three tissue zones of kiwifruit during 21 weeks of coolstorage. Further, when the fruit were exposed to ethylene (0, 10, 100 µL L^{-1} for 16 h at 20 °C) after different durations of coolstorage and later assessed for shelflife, the 1-MCP treated fruit still exhibited delayed softening confirming the persistence of 1-MCP treatment even after long-term storage.

Boquete et al. (2004) observed that the application of 1-MCP (0.5 or 5 µL L^{-1} for 16 h at 20 °C) on 'Hayward' kiwifruit after 30 days of coolstorage resulted in a lower rate of softening during subsequent shelflife assessment. These authors suggested that kiwifruit could elicit a response to 1-MCP even when applied after short-term cool storage when fruit are at pre-climacteric stage of ripeness. A further investigation conducted by Ilina et al. (2010) found 1-MCP (1 µL L^{-1} for 24 h at 0 °C) treatment delayed softening in 'Hayward' kiwifruit under shelflife conditions when applied after short, medium and after long-term cool storage. It was observed in this study that 1-MCP application after 40, 80 and 120 days of cool storage suppressed the expression of two ethylene biosynthesis genes and delayed softening resulting in the extension of eating ripe stage under shelflife conditions. It was concluded that 1-MCP could be effective in delaying softening in 'Hayward' kiwifruit even when applied at advanced stage of ripeness, but the treatment effect could diminish with the progression of the ripeness stage. Another similar investigation by Salazar et al. (2019) found 1-MCP treatment (650 nL L^{-1} for 24 h at 20 °C) after 45 days of coolstorage extended the eating window of yellow-fleshed 'Soreli' kiwifruit for about 10 days.

2.2.3 Effect of elevated temperatures and different humidity ranges combinations on fruit postharvest mechanism

The optimal temperatures which favour normal fruit ripening processes ranges between 10-30 °C varying between chilling sensitive, moderately chilling sensitive and non-chilling sensitive fruit groups (Wills and Golding, 2016). Nevertheless, most of the fruits in all these groups develop the best ripening qualities when stored at temperatures ranging 20-23 °C. As temperature exceeds the normal physiological range (>30 °C), fruit suffer moderate heat stress and temperatures over 35 °C could induce severe heat stress (Wills and Golding, 2016). Moderate heat stress could hamper the normal fruit ripening mechanisms while severe heat stress could completely cease ripening metabolism (Mitchell, 1987; Klein and Lurie, 1990).

The susceptibility or tolerance of fruit to heat stress may vary between different cultivars of a fruit species, between fruits of a single cultivar as well as in between fruits of the same tree. This difference is influenced by both pre-harvest environmental factors as well as the fruit's biological factors (Pedreschi and Lurie, 2015). Fruits that get exposed to direct sunlight or high temperature in the field may develop induced thermotolerance which later results in tolerance towards both high temperature and chilling stress at the postharvest stage (reviewed in Woolf and Ferguson, 2000). Similarly, in relation to biological factors, the stage of fruit maturity is one of the key factors which significantly influence heat stress response. In apples, fruit at post-climacteric stage were highly susceptible to heat injury than at pre-climacteric or commercial maturity stages (Fan et al., 2011).

In fruits, respiration, ethylene production and changes in firmness are the topmost ripening mechanisms monitored and studied under conditions of high temperatures. Respiration serves as a potential indicator of overall metabolic rate and storage life and is relatively easy to measure. Similarly, ethylene largely influences ripening processes while firmness is a key indicator of quality in most fruits. In addition to these mechanisms, the influence of high temperatures on fruit sugar content as well as acidity changes has been elucidated in fruit such as apples (Porritt and Lidster, 1978; Klein and Lurie, 1990; Saftner et al., 2002; Fan et al., 2011; Li et al., 2013).

In postharvest research, pre-storage exposure of fruits to acute or short-term heat stress has been of major interest as this treatment strategy enhances fruit tolerance to chilling stress and in addition, serves as a quarantine treatment to prevent the spread of various pest and diseases (reviewed in Lurie, 1998; Paull and Chen, 2000; Lurie and Pedreschi, 2014). On the other hand, understanding of the consequences of prolonged or chronic heat stress on fruit postharvest ripening mechanisms has been limited and concerns over the rise in global temperature indicate a pressing need for more investigations on this aspect.

One should realise that plant or plant products are not only affected by high temperatures at the pre-harvest stage but are much more vulnerable to heat stress at the postharvest stage as they are separated from the parent plant and possess a reduced ability of recovery. Additionally, the worldwide increase in ambient temperatures specifies the fact that postharvest shelflife investigations beyond the traditionally considered temperature ranges i.e. 20-25 °C are very crucial as well as practical under the current global climate scenarios.

Exposure of fruits to high ambient temperatures at the postharvest stage is often prevalent, especially in low- and middle-income nations wherein cool chain adoption is limited (Onwude et al., 2020). Contrarily, although not an extensive issue in developed countries, fruits may still be exposed to high temperatures within the modern supply chains wherein temperature abuse is often frequent (Nunes et al., 2009; Ktenioudaki et al., 2021).

An overall postharvest physiological knowledge on fruit responses to prolonged high temperatures is contributed through the investigations involving several fleshy fruits such as kiwifruit (Antunes and Sfakiotakis, 1997; Antunes and Sfakiotakis, 2000; Bellavi Jayashiva 2012; Zhao, 2017), apples (Johnston et al., 2001; Punter et al., 2018), pears (Hansen, 1942; Maxie et al., 1974), plums (Tsuji et al., 1984), avocados (Eaks, 1978; Lee and Young, 1984), guavas (Bron et al., 2005) and tomatoes (Biggs et al., 1988; Atta-Aly, 1992) while the majority of the molecular level understandings come from the climacteric model fruit tomatoes.

2.2.3.1 Temperature coefficient

A good starting point to understand the relationship between temperature and fruit ripening is by first elucidating the concept of temperature coefficient (Q_{10}). Q_{10} mathematically estimates the influence of temperature on the rate of metabolic reactions involved in fruit respiration or ethylene production processes (Bron et al., 2005; Ravindra and Goswami, 2008). As per Q_{10}, the rate of metabolic reactions is expected to increase approximately two-fold for every 10 °C rise in temperature. Q_{10} is estimated using the following formula:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\frac{10}{(T_2 - T_1)}} \qquad \text{Eq. 2.3}$$

Where, R_2 = respiration rate at temperature T_2

R_1 = respiration rate at temperature T_1

The final Q_{10} value estimated by Eq. 2.3 represents an increase in the rate of metabolic reactions between the compared two temperatures. For example, in guavas, a mean Q_{10} value of 3 was obtained for CO_2 production at temperatures between 1-11 °C and almost doubled to a value of 5.9 at 11-21 °C (Bron et al., 2005). Q_{10} however has its limitations as the exponential increase in Q_{10} value over 10 °C rise could be for a limited range of temperatures (reviewed in Atkin and Tjoelker, 2003). Further, the estimated Q_{10} value varies and may not exactly be 2 specifically at low temperature ranges wherein a very slight temperature rise could cause a significant rise in the fruit metabolisms resulting in higher Q_{10} values as evident in the case of bananas (Ravindra and Goswami, 2008). Similarly, at temperatures beyond the physiological optimum, the obtained Q_{10} values between two compared high-temperatures may be low due to a decline in the rate of metabolic reactions as in guavas in which Q_{10} values were 1.5 and 0.8 at temperatures 21-31 °C and 31-41 °C, respectively (Bron et al., 2005). Similarly, a Q_{10} value of 2 is observed in several fruits for ethylene production at 20-40 °C range but may decline beyond 40 °C ranges (Field, 1985).

2.2.3.2 Fruit postharvest physiological mechanisms at elevated temperatures

In some fruits, respiration rate is observed to increase with temperatures as evident in kiwifruit (Antunes and Sfakiotakis, 2000; Patterson et al., 2003) in which an increase in CO_2 production occurred even at 45 °C (Figure 2.5) (Antunes and Sfakiotakis, 2000). A contrasting respiratory rise along with increasing temperature up to 40 °C has also been observed in pears (Maxie et al., 1974) and plums (Tsuji et al., 1984). At tolerable high temperatures, it is noted that fruit respiration rate peaks during initial hours of exposure and gradually declines as the storage period progresses. Conversely, at lethal temperatures, a sharp decline from the respiratory peak may be evidence indicating permanent irrecoverable tissue damage as observed in kiwifruit at 45 °C (Figure 2.5A) (Antunes and Sfakiotakis, 2000), in pears at 35 °C (Maxie et al., 1974) and in plums at 40 °C (Tsuji et al., 1984).

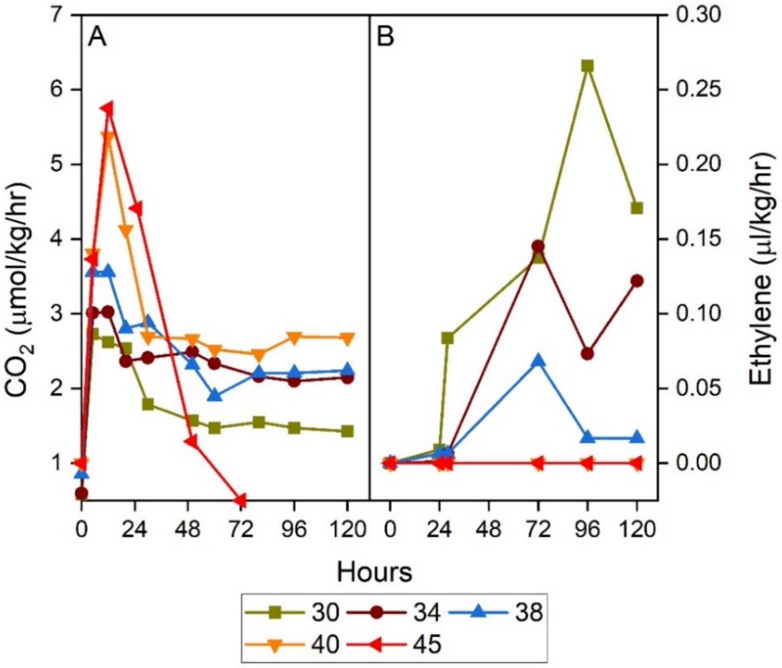


Figure 2.5: Respiration (A) and ethylene production (B) in kiwifruit stored in humidified air at 30, 34, 38, 40 and 45 °C (representation from Antunes and Sfakiotakis, 2000).

Temperature exceeding a certain range could inhibit respiration in fruits such as in avocados in which CO_2 production increased at 30-35 °C but was inhibited at 40 °C (Eaks, 1978). Unlike ethylene production, the physiological mechanisms resulting in the inhibition of fruit respiration at high temperature is less investigated but are speculated to be due to the inhibition of enzymes involved in the respiratory mechanisms. A previous investigation by Smillie (1992) suggests Kreb's cycle and more specifically CO_2 fixation by enzyme Rubisco to be the heat sensitive step in the fruit respiration process which may result in respiratory inhibition at high temperatures.

Ethylene production in fruits is observed to be more sensitive to heat stress than respiration since it declines with the rise in temperatures either above 30 or 35 °C varying between fruit species and ceases at extreme temperatures. Hansen (1942) observed that in pears, an increase in temperature from 20-40 °C led to an exponential rise in CO_2 production while ethylene production declined and ceased at 40 °C. This author initially thought that the decline in oxygen concentration within the fruit's internal atmosphere at high temperatures may have limited ethylene production at 40 °C. However, in a subsequent experiment, both increasing oxygen concentration around the fruit storage environment as well as exposing the cut fruit tissue (to increase internal oxygen diffusion) to higher oxygen concentrations at 40 °C did not result in ethylene synthesis.

Investigations of Antunes and Sfakiotakis (1997), Antunes and Sfakiotakis (2000) on kiwifruit, Biggs et al. (1988) and Atta-Aly (1992) on tomatoes have confirmed that reduced or termination of ethylene synthesis at high temperatures is due to inhibition in the activity of ethylene biosynthesis enzymes. Biggs et al. (1988) observed a sharp decline in the activity of ACS enzyme while a gradual activity decline was noted in ACO enzyme upon transfer of tomatoes (at breaker to turning maturity stage) from 25 to 35 and 40 °C.

Biggs et al. (1988) based on their observations in tomatoes theorised that the initial inhibition of ethylene production at 35 or 40 °C was due to reduced activity of ACS caused by either breakdown of ACS related proteins or suppression of ACS activity or could be the combined effect of both these factors. This subsequently at the later period of exposure reduced ACC availability for ACO restricting its function in ethylene production. Interestingly, these authors noted ethylene production in fruits held at 35 and 40 °C was reversible (at 25 °C) after an exposure duration of 7 and 2 days respectively, indicating no permanent damage to the ethylene synthesis system had occurred during 7 and 2 days storage at 35 and 40 °C, respectively.

Similarly, Antunes and Sfakiotakis (2000) reported ethylene production in kiwifruit at firm stage to decline over 30 °C and almost cease at 40 °C (Figure 2.5B). However, this inhibition in kiwifruit was found to be differentially influenced by heat stress than in tomato since ACO was much more sensitive to heat than ACS. Exposure to 130 $\mu L\ L^{-1}$ propylene (an ethylene analogue) stimulated ethylene autocatalysis at 30 and 34 °C while some ethylene production was also detected in 38 and 40 °C stored fruit. Antunes and Sfakiotakis (2000) concluded that the failure of propylene to induce ethylene autocatalysis in kiwifruit at 38 and 40 °C could be due to a decline in sensitivity of fruit towards propylene which subsequently resulted in minimal ethylene production. This conclusion was further supported by an observation that propylene significantly increased CO_2 production in fruits stored at 30 and 34 °C, while minimal and no differences existed in fruits at 38 and 40 °C, respectively.

A similar response of reduced sensitivity towards exogenous ethylene or propylene even at exposure concentrations of 1000 $\mu L\ L^{-1}$ has been reported for pears

(Maxie et al., 1974) and avocados (Eaks, 1978) at 40 °C. The exact mechanism resulting in reduced sensitivity of fruits to ethylene or propylene at temperatures over the optimal range remains unknown. There are possibilities that heat stress could either limit the expression of ethylene receptors or affect their functionality through compositional changes. Since receptors are protein complexes (Lin et al., 2009; Chen et al., 2010), a strong possibility for receptor compositional changeover due to heat stress exists.

Ethylene largely influences fruit softening under optimal ripening conditions while temperature plays a role in the initial regulation of ethylene synthesis. Johnston et al. (2001) in apples have elucidated that softening at high temperatures is regulated by ethylene synthesis. These authors observed that when fruit of apple cultivars Cox's Orange Pippin and Royal Gala were exposed to temperatures ranging 20-35 °C, internal ethylene concentration increased resulting in rapid softening. Conversely, in fruit of Pacific Rose and Granny Smith cultivars, minimal increase in internal ethylene occurred at temperatures 20-35 °C resulting in minimal firmness changes.

While the findings of Johnston et al. (2001) suggest that ethylene could control softening in climacteric fruits at higher temperatures, it also raises the question of whether a similar response could be expected in kiwifruit, as significant softening occurs independently of any increase in ethylene production (Mitalo et al., 2018; Mitalo et al., 2019b). The results from Antunes and Sfakiotakis (2000) suggest that ethylene could still regulate softening in kiwifruit at temperatures over 30 °C since minimal ethylene production in kiwifruit at 38 °C resulted in slight firmness changes while no ethylene production at 40 °C resulted in no firmness changes.

A study by Yin et al. (2012) found expression of fourteen ethylene response factor genes (*ERFs*) in firm kiwifruit from day 1 of exposure to 35 °C. Of these 14 *ERFs* genes, increased expression was observed in one specific *ERF*s gene i.e. *AdERF 14* which remained high during 4 days of exposure and upon subsequent storage at 20 °C. Although it was noted that high temperature exposure led to expression of *ERFs* genes in kiwifruit which is thought to be a stress regulated response, it is unsure whether ethylene synthesis at basal or increased levels occurred either during or after treatment since ethylene production was not measured. It could be that ethylene production may have occurred due to stress regulation during treatment at basal levels since minimal firmness changes were noted and subsequently could have increased after treatment withdrawal since firmness rapidly dropped from 75 N to almost 50 N in a span of 2 days at 20 °C.

2.2.3.3 Fruit quality attributes at elevated temperatures

Acidity and soluble solid content (SSC) in fruits are minimally influenced by high temperature exposure. In apples, high temperatures may accelerate acidity decline but may not have any influence on SSC (Porritt and Lidster, 1978; Klein and Lurie, 1990; Saftner et al., 2002; Fan et al., 2011; Li et al., 2013). In kiwifruit, Antunes and Sfakiotakis (2000) observed no significant changes in SSC in kiwifruit stored at 30-40 °C while Yin et al. (2012) noted an increase in SSC with storage time at 35 °C. In mangoes, exposure to 38 °C for 3 days resulted in slower acidity decline upon subsequent storage at 25 °C while no changes in SSC occurred (Ketsa et al., 2000). In grape fruit, acidity declined while TSS increased with increase in temperature from 46-50 °C (McGuire and Reeder, 1992). In tomatoes, neither acidity nor TSS changes were influenced by high temperature exposure (Klein and Lurie, 1992; McDonald et al., 1999). These overall mixed reports suggest a pattern of acidity and SSC changes over time under high temperature conditions may vary according to different fruit species as well as between cultivars of a fruit species.

2.2.3.4 The influence of relative humidity on fruit quality at elevated temperatures

Optimal relative humidity within the storage environment is essential to minimise weight loss and preserve freshness in fruits (Burdon and Clark, 2001; Burdon et al., 2014b; Lufu et al., 2020). For most fruits, optimal storage humidity ranges between 85-95% and is product specific (Paull, 1999). Humidity below the normal optimum promotes increased weight loss which leads to unenviable changes in fruit quality resulting in visual degradation and postharvest losses (Nunes and Emond, 2007; Paniagua et al., 2013; Xanthopoulos et al., 2017). Further, weight loss contributes to economic losses due to a reduction in fruit saleable weight (Laurin et al., 2005). Inversely, humidity above the normal optimum could also be detrimental as it causes condensation over the fruit skin which not only restricts gaseous movement but also promotes pathological infestation (Cook and Papendick, 1978; Linke and Geyer, 2013; Mahajan et al., 2016).

Weight loss in fruits majorly occurs through transpiration and to a smaller extent by respiration (Burton, 1982). Transpiration mechanism in fruits could be best described by Fick's law of diffusion which states that the rate of water vapour transport between fruit and the storage environment is directly proportional to the partial pressure gradient between the fruit surface and the surrounding air and inversely related to the fruit surface resistance (Ben-Yehoshua, 1987; Nobel, 1999). Transpiration rate in addition to environmental factors is further influenced by fruit intrinsic factors such as skin resistance (recently reviewed in Lufu et al., 2020).

The driving force for transpiration is the water vapour pressure deficit (WVPD) which represents the vapour pressure gradient between the fruit's internal environment and the surrounding air (Song et al., 2021). WVPD is a function of both temperature and relative humidity. By reducing the temperature or increasing the relative humidity, the WVPD within a storage environment is reduced (Talbot and Baird,1991; Paull, 1999). Respiratory heat could increase the internal temperature of the fresh produce resulting in higher WVPD values even within the recommended storage conditions (Mahajan et al., 2016).

A 3-10% reduction from the initial weight can render fruits unmarketable while a 1-2% weight loss could significantly reduce the marketing value in some fruits (Ben-Yehoshua, 1987). A common practice adopted in several fruit industries to reduce weight loss is by packing fruit with polyliners which serves as a barrier between fruit surface and outer environment and thus increases humidity within the microenvironment surrounding fruit (Burdon et al., 2014b). In postharvest research, the influence of low, medium and high humidity ranges on fruit physiology and quality at storage temperatures (Sharkey and Peggie, 1984; Asakura et al., 2001; Hong and Lee, 2007; Shin et al., 2008) or under ambient temperatures of 20-25 °C (Tu et al., 2000; El-Malki et al., 2016; Mukama et al., 2018) is known. Minimal information exists on the influence of different humidity ranges at temperatures over 30 °C but it is obvious that both respiration and transpiration rates remain higher at these temperatures.

Increasing relative humidity may not be a solution to reduce weight loss at higher temperatures since both respiration and diffusion (fruit internal water to the outer environment) mechanisms are promoted by high temperatures (Lufu et al., 2020). Further, since water content in fruits is initially almost closer to saturation, WVPD between fruit and storage environment always exists even at a storage environment with 90% RH. Suppose a RH closer to 100% (generally challenging to simulate in a laboratory environment) is set at high temperatures, a consistent RH maintenance is almost impossible which may again result in WVPD differences and in addition may lead to condensation issues which further affects the fruit gaseous transport at high temperatures and promotes pathogen infestation.

The best, easiest and perhaps the only way to identify whether different humidity ranges (low-medium-high) influence fruit quality at high temperatures is by monitoring fruit quality stored at one high temperature with different humidity ranges. Previously Zhao (2017) stored kiwifruit (after 14 weeks of coolstorage) at 30 °C under four different humidity ranges (35-95% RH) and measured firmness for six days. Rapid fruit softening occurred at 30 °C, but with no significant differences in firmness between fruits stored at different humidity ranges (Figure 2.6). It was concluded by this author that higher ripening rate (evident from firmness changes) may have increased elasticity and plasticity of the cell wall resulting in the absence of cell turgor pressure differences in fruit stored under different humidity conditions resulting in similar water loss and minimal firmness differences. A further conclusion was that the puncture test used may not have been able to identify firmness changes influenced by water loss. Yin et al. (2012) noted a significant increase in weight loss in kiwifruit during 4 days of exposure to 35 °C but firmness changes (assessed by puncture test) in 35 °C exposed and control fruit were almost similar. Both these reports on kiwifruit suggest that under high temperatures, the influence of relative humidity on softening may not be significant.

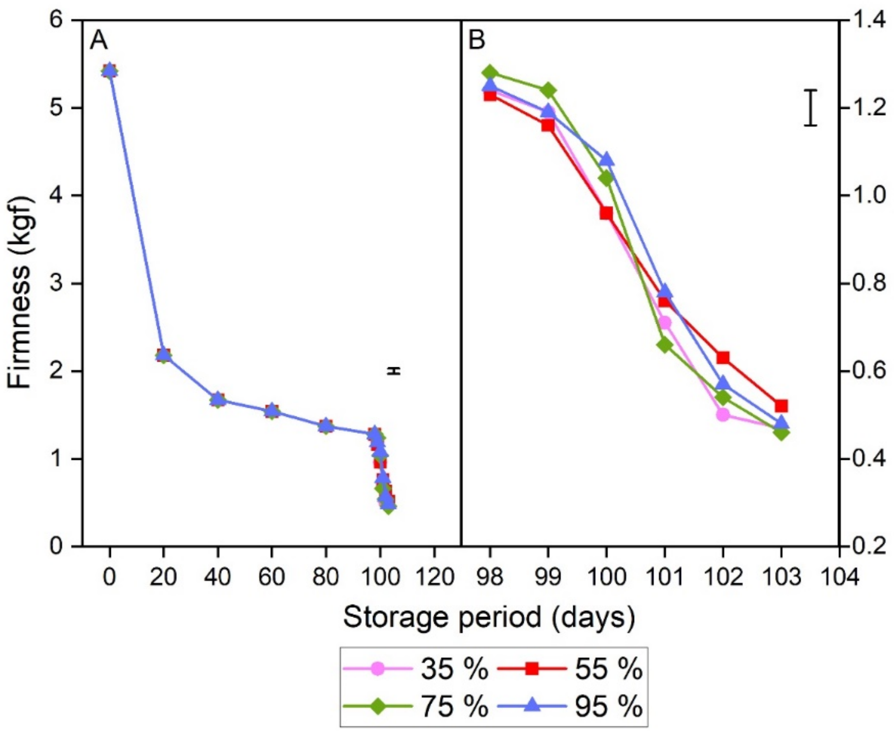


Figure 2.6: Firmness changes in kiwifruit stored at 30 °C with different humidity ranges (35, 55, 75 and 95%) after 14 weeks of cool storage (n=108). A represents firmness changes during cool storage and after exposure to 30 °C. B is an enlarged version of A presenting firmness changes only during exposure to 30 °C (representation from Zhao, 2017).

2.3 Research opportunity and overall conclusions

2.3.1 Challenges for kiwifruit quality maintenance in tropical markets – An opportunity for research

Kiwifruit handling in overseas markets can be controlled by importers and later wholesalers and retailers (Kilgour et al., 2007) where fruit are subjected to differing handling patterns. In general, off-shore distribution channels are diverse and comprise both modern and traditional retail formats (Goel, 2010; Schipmann and Qaim, 2011; Bollen et al., 2015). Although the coexistence of both these retail formats is not uncommon in most parts of the world (Goldman and Hino, 2005), modern retail dominates in developed countries, while traditional retail occurs in emerging and low-income countries (Gorton et al., 2011; Kelly et al., 2015). For example, in India, where modern retail growth has been rapid (Dholakia et al., 2018) increasing from 11 to 67 thousand stores between 2006-2016 (Atroley and Rajat, 2014), these retail sectors still contribute to less than 2% of the total fresh food sales (Sandoval and Sawant, 2019; Kotval-K, 2020). A reflection of this fact is the sales of New Zealand kiwifruit in India, which is majorly dominated (over 80%) by traditional marketing channels (M. Jain, personal communication, June 27, 2019).

Kiwifruit handled through modern retail chains flow through specialized logistical operations and as a result, may reach the consumer at a better quality. Further, the short distribution channel adopted in modern retail i.e. fruit directly transported from the importer's storage facility to supermarkets (Boselie et al., 2003; Buntong et al., 2013), minimizes risks of temperature abuse as the product flows through the supply chain. While the cool chain is an integral part of the modern retailing systems, complete elimination of temperature mismanagement or prevention of fruit losses is not possible (Cicatiello et al., 2017; Mercier et al., 2017) but is expected to be less than that of the traditional marketing systems.

In most instances, kiwifruit sold through traditional channels are exposed to open conditions due to an inefficient or complete lack of cool chain during handling, transportation and marketing (Trappey and Lai, 1997; Mashau et al., 2012). Traditional marketing channels are largely heterogeneous and comprise several informally organized formats such as wet markets, fresh markets and flea markets, which function on a daily or weekly basis (Goldman and Hino, 2005; Hernández et al., 2007; Minten and Reardon, 2008). These markets are operated by independent vendors or grocers or hawkers (Trebbin, 2014) who specialize in either specific food produce (fruit and vegetables or meat or milk) or multiple produces (Kotval-K, 2020). Vendors tenant small spaces within a market or area (e.g. roadside pavements, street corners) closely accessible to consumers and sell their produce through stationary stalls or travel around residential areas and provide doorstep sales through pushcarts or bicycles or by carrying large baskets filled with fresh produce on their heads (Minten et al., 2010; Sharma, 2016; Kotval-K, 2020).

To give a better insight into the influence of traditional retailing systems on kiwifruit quality, Bellavi Jayashiva (2012) conducted an investigation aiming to understand the supply chain in India. Kiwifruit firmness and core temperature were assessed as kiwifruit entered and exited each point of the supply chain. As an example, the obtained results for a batch of product passing from Mumbai to Delhi are shown (Figure 2.7). Fruit firmness on arrival (day 0) and exit (day 3) from the importers coolstore was consistent and ranged above 2 kg_f. A firmness decline (ranging 0.8-1 kg_f among growers) was observed on fruit arrival at a Delhi wholesale market (day 8) demonstrating that the temperature during fruit transportation (12-20 °C) significantly influenced firmness loss. Temperature data as fruit left wholesale market (11.4-19.7 °C, day 10) suggests that the fruit were held at relatively high temperatures during wholesale handling. During final retail sales (day 11-12), fruit temperature exceeded 20 °C with firmness declining close to 0.5 kg_f (a reduction of 1.5-2 kg_f from initial firmness within 12 days).

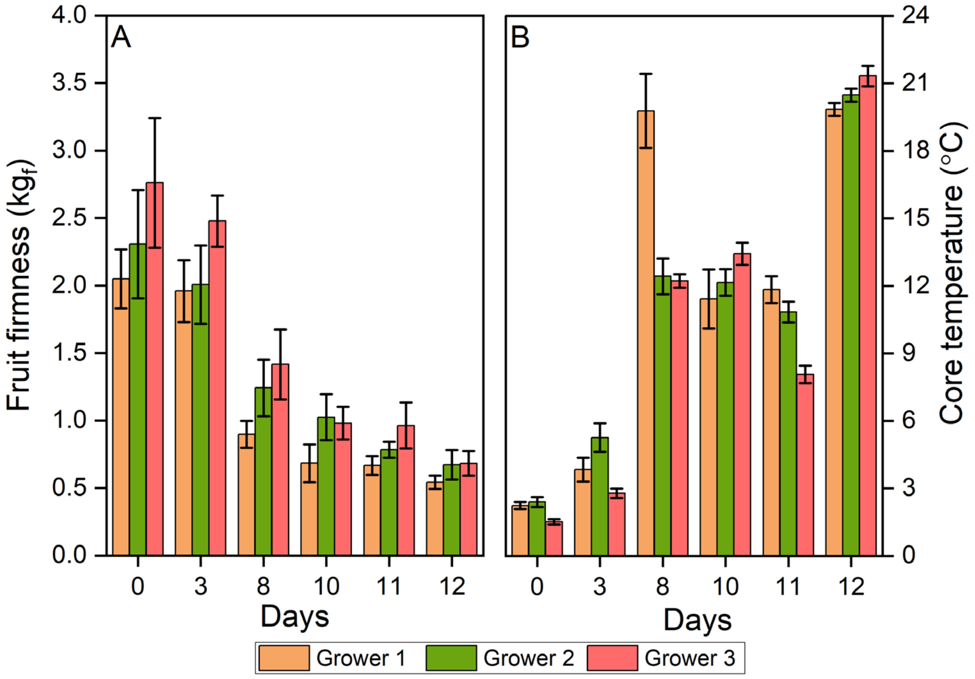


Figure 2.7: Firmness (A) and fruit core temperature (B) as 'Hayward' kiwifruit passes through different channels of the supply chain extending from Mumbai to Delhi in India. Error bars on each column represent standard deviation of 20 fruit samples (data extracted from Bellavi Jayashiva, 2012).

The results of Bellavi Jayashiva (2012) suggest that kiwifruit are delivered to overseas markets in a state of good quality but as kiwifruit exit the importers storage facility, continuous exposure to higher temperatures occurs (in regions where traditional retailing system dominates) along the supply chain. It is clear from Figure 2.7 that high temperature exposure results in fruit reaching the retailers store (day 11) in a soft state and exposure to temperatures over 20 °C at this point further advances fruit to an over-soft state even within a short duration. This poses a challenge for retailers as they may earn less (either due to quality or weight reduction) and for the New Zealand kiwifruit industry as a negative eating experience of the consumers may result in fewer fruit purchases and poor product reputation over time.

Day temperatures exceeding 30 or even over 40 °C have become very common in the current global climate scenario. It is expected that kiwifruit marketed through traditional channels may often get exposed to temperatures over 30 °C which could result in rapid quality deterioration. Antunes and Sfakiotakis (2002) have elucidated the influence of temperatures over 30 °C on firm kiwifruit but a further understanding is necessary to understand high temperature influence on soft kiwifruit (< 2 kg_f) as fruit will be ripened to this firmness for sale to enable rapid consumption after retail. This understanding may be beneficial in identifying an exposure time frame beyond which kiwifruit are considered unmarketable under traditional marketing scenarios. On the other hand, a physiological understanding may further lead to identifying strategies that may help delay ripening and reduce fruit losses under higher temperatures.

2.3.1.1 Environmental ethylene – an additional fruit quality detriment

Ethylene, despite being a natural hormone is considered an air pollutant as it is abundantly released by various anthropogenic sources into the natural environment (Abeles and Heggestad, 1973). Some of these anthropogenic sources include smoke from vehicles, factories, garbage combustion, coal combustion and cigarettes (Keller et al., 2013; Morgott, 2015). Vehicle exhausts are the prominent anthropogenic source of ethylene and due to higher vehicle numbers, increased ambient ethylene concentrations exist in urban environments than in rural environments (Jorquera and Rappengluck, 2004; Wang et al., 2013; Cui et al., 2018). For example, Abeles and Heggestad (1973) measured ethylene concentrations of 700 nL L^{-1} in the city centre and 39 nL L^{-1} in the city outskirts of Washington D.C. and suggested that these major concentration differences were due to traffic densities.

As it is well-known that avoiding ethylene exposure remains crucial for the fresh produce supply chain (Warton et al., 2000; Keller et al., 2013; Blanke, 2014; Janssen et al., 2014), ambient ethylene concentrations pose an additional challenge for fruit quality maintenance other than high temperatures under traditional marketing channels in tropical markets. Unlike controlled storage environments, wherein both ethylene monitoring and management (by scrubbing or ventilating) are possible, ambient ethylene although detectable is a challenge to be managed. The only available option for ambient ethylene management in open environments could be by blocking ethylene action using ethylene action inhibitors such as 1-MCP.

Previous investigations have elucidated the concentrations of ethylene prevalent under modern retailing systems. For example, Lu (2020) measured ethylene concentrations ranging 0.25-100 nL L^{-1} in retail display areas of supermarkets. Similarly, in investigations by Warton (2000) and Rees and Hipps (2011), ethylene concentrations at supermarket retail display areas ranged 11-23 and 2-35 nL L^{-1}, respectively. Since supermarkets consist of a closed-in environment, most of the measured ethylene concentration may be contributed from the displayed fresh produce while other sources may have minimal contributions to the measured ethylene concentrations.

Under traditional tropical marketing systems wherein fruit are sold in open environments, it is obvious that ethylene concentrations remain higher and that the measured ethylene concentrations are majorly contributed by anthropogenic sources. However, unlike knowledge of the prevalent ethylene concentrations under modern marketing system, concentrations of ethylene prevalent in the traditional retailing system is limited. To understand ethylene’s influence on fresh produce quality along the supply chain, an ideal way to start is by identifying ethylene concentrations prevalent at a point of the supply chain and later understanding the exposure impact in controlled experiments (Wills, 2021). Hence, in this study, in addition to gaining an understanding of kiwifruit response to high temperature, importance will be given to identifying ethylene's influence on kiwifruit quality under traditional tropical market conditions. These investigations will strengthen kiwifruit postharvest physiological understandings of ethylene exposure as well may further indicate an effective ambient ethylene management strategy under traditional marketing systems in tropical markets.

2.3.2 Overall conclusions

This chapter provides an overview of the New Zealand kiwifruit industry, addresses the fundamental knowledge of fruit ripening mechanisms and kiwifruit-specific postharvest metabolisms. The prevalent challenges for the New Zealand kiwifruit industry under traditional marketing systems in tropical markets are highlighted through existing literature. Available knowledge suggests high ambient temperatures in traditional markets pose a risk for kiwifruit quality maintenance. Additionally, higher ambient ethylene concentrations may also exist and further exaggerate the quality deterioration process.

A scientific understanding of kiwifruit responses to traditional market conditions is essential for establishing a suitable kiwifruit quality control strategy. While some knowledge on fruit responses to elevated temperatures exists, there remains a need for a more specific understanding towards traditional fruit marketing scenarios. These scenarios may include gaining an understanding of kiwifruit handling and storage practices, identifying the prevalent environmental conditions as well as the ripeness stage at which kiwifruit are handled under traditional marketing conditions. Hence, a stepwise approach to this study will be by first gaining knowledge on tropical traditional marketing conditions which is very crucial for conditions simulation in scientific experiments.

Exposing kiwifruit to simulated tropical traditional market conditions may enable identifying the safest exposure time frame to these conditions based on fruit physiology and quality responses. Further, postharvest strategies that may minimise the impact of traditional market conditions on kiwifruit quality could be experimented under simulated conditions. Overall, this research will aim in gaining a scientific understanding of kiwifruit responses to traditional marketing conditions which may enable the New Zealand kiwifruit industry in establishing a successful fruit quality maintenance strategy in tropical markets.

Chapter 3: A survey of retail conditions in the kiwifruit supply chains of India and Singapore

3.1 Introduction

New Zealand kiwifruit supply chain involves rigorous practices (Hewett, 2003) beginning from the production until overseas delivery, which not only ensures prolonged storage life but also facilitates product quality to synchronise with the export standards (Martin, 2003). Having said that, this doesn’t completely assure good quality fruit reaches the final overseas consumers as the fruit quality is also influenced by off-shore handling and distribution procedures (Ward and Courtney, 2013).

Kiwifruit in off-shore markets are handled either by modern or traditional retail formats. Better temperature control combined with a shorter distribution chain adopted within the modern retail formats may facilitate delivery of fresh produce in a state of good quality to end consumers. For example, a case study by Minten and Reardon (2008) conducted in multiple cities of Antananarivo region, the capital of Madagascar found tomatoes sold through modern retailers were of superior quality (judged based on size, ripeness and appearance) in comparison to that of traditional retail formats.

Traditional markets distinguish themselves from modern retails in various aspects such as product quality, handling and storage practices (Schipmann and Qaim, 2011; Najib and Sosianika, 2017). Traditional markets are operated by independent vendors or grocers or hawkers (Trebbin, 2014). Usually, fresh produce marketed in traditional markets may have reduced quality due to inefficient storage, transportation and marketing practices. It is very usual to spot street vendors selling fruit without any overhead shade or under an umbrella in many of the traditional retail markets. A secondary issue of traditional markets is the lengthy and fragmented supply channels (Singh et al., 2009; Halder and Pati, 2011; Negi and Anand, 2015) which not only increase the frequency of exposure to open conditions but could result in mechanical damage due to multiple handling procedures or longer duration of transport (Debela et al., 2011).

The knowledge on traditional market conditions or the influence of these conditions on fruit physiology or quality is limited. Mashau et al. (2012) assessed postharvest losses in 50 street vendor stores located in Limpopo province, South Africa and observed none of these vendors had refrigeration facilities and maximum fruit losses occurred due to over-ripening caused by high temperature (35-40 °C) exposure. Similarly, Bellavi Jayashiva (2012) investigated kiwifruit quality losses along supply chains in India and found that the fruit were often exposed to high temperatures (20-25 °C) during transportation, wholesale handling and at street vendor stores resulting in a drastic firmness decline before reaching the final consumers. Studies of Antunes and Sfakiotakis (2000) and Zhao (2017) have previously elucidated the influence of high temperatures (>30 °C) on kiwifruit physiology and quality after harvest or after a duration of coolstorage, respectively.

In addition to high temperatures, there is potential for elevated ethylene concentrations to exist in traditional markets which may further exaggerate quality deterioration in kiwifruit. Several investigations have previously identified the prevalent ethylene concentrations in modern fresh produce supply chains (Warton, 2000; Lu 2020). However, minimal information exists on the prevalent ethylene concentrations in traditional markets or ethylene's influence on kiwifruit (at ripe stage) at high temperatures. An initial approach for gaining understanding of these aspects would be by first determining the concentrations of ethylene in traditional markets and then understanding kiwifruit responses to those ethylene concentrations.

In this work, a case study of the kiwifruit supply chain is conducted in India and Singapore, the two tropical export markets for the New Zealand kiwifruit industry, to gain an understanding of environmental conditions prevalent under the tropical traditional marketing systems. The observations from this case study are expected to provide critical information on potential sale conditions for kiwifruit that can be later studied in simulated supply chain experiments in a laboratory environment.

3.2 Materials and Methods

3.2.1 Study locations

This case study was conducted from 15th June to 7th July 2019, a period of summer monsoon rainfall in India (Parthasarathy and Pant, 1985; Hrudya et al., 2020) and southwest monsoon season in Singapore. Storage conditions (temperature, relative humidity and ethylene concentration) were monitored at three street vendors stores in tier 1 cities of India (Delhi, Mumbai and Bengaluru) and at wet markets (Tekka wet market and Chinatown wet market) in Singapore.

3.2.2 Monitoring of storage conditions

Temperature and humidity were recorded using data loggers (I-button/1-wire DS1923, Maxim Integrated, USA) with a measurement accuracy of ± 0.5 °C and ± 5 % RH every ten minutes. Data loggers were calibrated before use. In the street vendor's store, loggers were attached on top of the kiwifruit punnets. A 24 h monitoring in three different street vendors stores in each of the locations (Delhi, Mumbai and Bengaluru) in India was completed. In Singapore, due to time constraints, 8 h monitoring of storage conditions was achieved.

Ethylene concentrations in the general atmosphere within street vendors stores were monitored using a MAC*View*® Portable Ethylene Postharvest Gas Analyser (Environmental Monitoring Systems (EMS) B.V., St. Annaland, Netherlands). This equipment is advantageous for supply chain studies in terms of portability, sensitivity (1 nL L^{-1}) as well as providing a wide range of detection (0-5000 nL L^{-1}) (Janssen et al., 2014; Verschoor, 2017). Details on calibration, mechanism of operation, and factors influencing measurements have previously been described (Janssen et al., 2014; Verschoor, 2017; Lu, 2020). The equipment was calibrated in New Zealand before being used and four "on the spot" ethylene concentration measurements were done at each street vendors stores in India only. In Mumbai and Bengaluru, ethylene measurements were done between 9:00-14:00 while in Delhi, measurements were done between 12:00-17:00.

Figure 3.1: Data loggers attached on kiwifruit punnets for monitoring storage conditions at street vendors stores (left). Setting up the ethylene monitoring equipment in one of the importers cool stores in India (right).

3.2.3 Fruit quality (firmness) assessment

Fruit are repacked from bulk to consumer packaging by the distributor and as a result, the information enabling traceability back to grower source is lost. Hence the firmness data could only be collected as a survey of what was available in the market and not associated back to the previous state of the fruit in the supply chain or at harvest.

The firmness of the fruit sold at street vendor stores in India was assessed using a GY-4 digital fruit penetrometer (GY-4, Yuchengtech, China) with an 8 mm probe fitted onto a manual fruit hardness test stand (GYD series, VTSYIQI, China). Fruit outer skin of 2 mm was removed at two equatorial regions perpendicular to each and the fruit was then held steadily by the left hand on an even solid surface. Using the right hand, the lever of the test stand was pressed downwards to enable the probe to penetrate the fruit until reaching the marked line of 8 mm depth. To obtain accurate measurements of equal force, a two-second press rule was followed. The values obtained from paired sides of each fruit were averaged and expressed in kg_f.

Figure 3.2: GY-4 digital fruit penetrometer used for kiwifruit firmness assessment.

3.2.4 Data presentation

Temperature and humidity data recorded at street vendor stores and at wet markets are presented in 24 h or 6 h line plots. As the ethylene analyser records 4 measurements per hour (15 minutes per measurement), ethylene concentrations are presented in 60 minutes line plots. Firmness at the point of sale are presented in the histogram to segregate different ranges of firmness. All of the obtained data were managed in Excel (64-bit Version, Microsoft, USA) and the graphs were plotted in OriginLab® (Version 2020, OriginLab Corporation, USA).

3.3 Results

3.3.1 General observations

Fruit exposure to open conditions occurred from the point of fruit arrival in wholesale markets until finally being sold to consumers at retail stores. At the wholesale market, exposure to open conditions was generally short-term (approximately 6 h) and happened during early hours of the day (between 4-10 AM) when fruit arrives from the importers cool stores and are displayed for retailers purchase (Figure 3.3A). The majority of the fruit brought into wholesale markets gets sold within 3-4 h while the remaining lots are held along with other fruits at a temporary refrigerated storage facility (with a set temperature of 4-5 °C) for next-day sale (Figure 3.3C-D). Since most of the wholesale handling happens for a short duration during early hours of mornings before temperature escalates to the highest range, its influence on quality is likely less than the final conditions of sale at the retail store. Likewise, since fruit arrives in wholesale markets in cooled conditions, fruit may remain cooler than the ambient conditions at the time of retailers purchase.

Figure 3.3: Fruit displayed for sale at wholesale market in Bengaluru (A), fruit transportation in a non-refrigerated vehicle from wholesale market to retail stores (B), temporary fruit storage facility at wholesale market in Mumbai (C-D), kiwifruit purchased by a street vendor (E) and kiwifruit displayed for sale in a cart vendor stall (F).

Traditional retailers mostly use non-refrigerated transport to transfer fruit from wholesale markets to retail stores (happens between 4-10 AM). Hence the possibilities of fruit reaching retailers store in cooled conditions are less and could be dependent on the proximity of retailers store to wholesale markets. The closer the proximity, the cooler the fruit remains as they reach the retailers store.

At the street vendors store, fruit are exposed to high temperatures for the longest duration of the supply chain. These vendors are highly heterogenous and hence difficult to generalise. On some occasions, fruit are sold under the overhead shade while others were in open conditions, but in both instances, refrigeration was almost always absent. Upon arrival from the wholesale market to retail store, fruit are displayed for sale either in bulk or in consumer packages.

Street vendors are generally aware that they cannot store fruit for long under these conditions and hence try to avoid losses by purchasing fruit sufficient enough for only 1 or 2 d of sales. Further, they try to keep the fruit as fresh as possible by frequently sprinkling water or covering fruits with moist gunny (burlap) bags, enabling some evaporative cooling. However, fruit losses are often frequent, especially during summers where most of the fruit are lost due to over-ripening within a short period. A response from one of the street vendors in Bengaluru was that it was quite challenging to determine the number of fruits sold per day which in most instances results in either fruit being sold quickly or remaining unsold for a couple of days subsequently resulting in fruit losses.

3.3.2 Temperature and humidity at street vendors store

In each of the selected cities (Delhi, Mumbai and Bengaluru), storage conditions in street vendors stores located at different locations were recorded. In

Delhi (Figure 3.4A), the mean day temperature ranged 36.1-36.3 °C, with the noon temperature reaching as high as 37.5-39.6 °C and night temperature dropping to a minimum of 34.5-36.5 °C. Corresponding humidity ranged between 40.5-42.9% being maximum (48.5 -59.3%) at early hours (00:00-8:00) of the day and minimum (26.5-37.5%) during midday.

In Mumbai (Figure 3.4B), the mean day temperature within street vendors stores ranged 30.7-32.4 °C, with the temperature being lowest during late night or early hours of the day (29.6-30.1 °C) and elevating to peak range (33.5-34.1 °C) during the late morning to early noon (11:00-15:00). Mean humidity ranged between 75.2-73.7%, elevating during night time (20:00-22:00) and remained maximum (81.6-88.6%) towards morning (until 8:00) and later dropped to lowest (57.7-64.9%) during early noon (12:00-14:00) when maximum temperature was recorded.

In Bengaluru (Figure 3.4C), the mean temperature ranged 27.8-28.5 °C, being maximum (28.14-32.1 °C) from noon towards evening (13:00-17:00) and lowest (25.1-28 °C) during early hours of the morning (7:00-8:00). The highest humidity range (74.5-86.3%) was recorded during early hours of the morning (00:00-8:00) and later declining during late morning (9:00-12:00) and recording the lowest range (39.8-41.6%) from afternoon to evening (12:00-17:00) and subsequently remained at elevated range during late-night until late morning.

In Singapore, environmental conditions were monitored at wet markets between 13:00-20:00 on 4th (Tekka wet market) and 5th (Chinatown wet market) of July 2019 (Figure 3.5). The temperature in the Tekka wet market ranged between 27.1-34.1 °C and averaged 32.2 °C and at Chinatown wet market, the temperature ranged between 32.6-34.6 °C and averaged 33.7 °C. Relative humidity remained almost constant averaging 81% in both these markets.

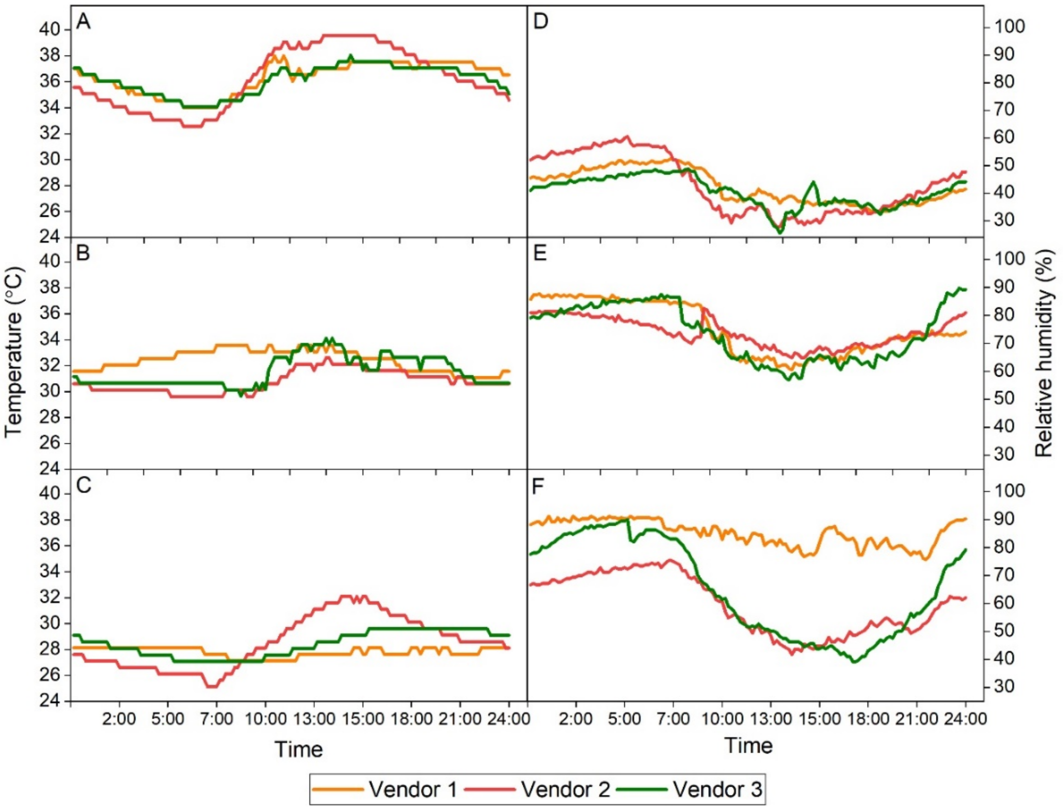


Figure 3.4: Temperature (A-C) and relative humidity (D-F) recorded in street vendors store in Delhi (A, D), Mumbai (B, E) and Bengaluru (C, F).

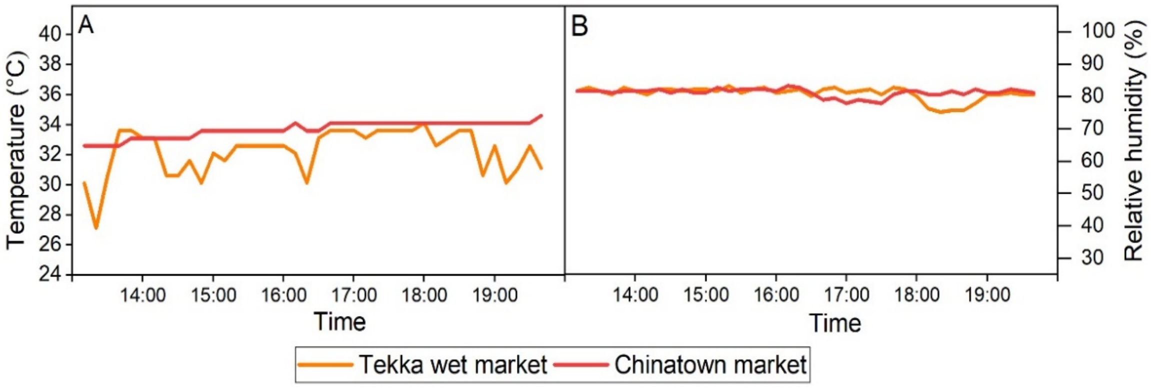


Figure 3.5: Temperature (A) and relative humidity (B) recorded around wet markets in Singapore.

3.3.3 Ethylene at street vendors stores and cool stores

Four “on the spot” ethylene concentration measurements were done at each of the street vendor stores. Concentrations ranged between 75-150, 70-112 and 60-100 nL L^{-1} in Delhi, Mumbai and Bengaluru, respectively (Figure 3.6). In Mumbai and Bengaluru, measurements were done between 9:00-14:00 while in Delhi, measurements were done between 12:00-17:00.

Ethylene concentrations were also monitored in coolstores located in Mumbai, Delhi, Bengaluru, and Singapore. In general, the cool rooms contained numerous pallets of kiwifruit and in most cases were stored separately from other fruit. In most cases, ethylene concentrations in the kiwifruit storage rooms ranged between 14-20 nL L^{-1} (Figure 3.7). However, in one of the cool rooms at Mumbai, kiwifruit were co-stored with pears resulting in substantially higher ethylene concentrations (120 nL L^{-1}) (Figure 3.7B). In Singapore, kiwifruit stored rooms had ethylene concentrations below 20 nL L^{-1} (data not presented).

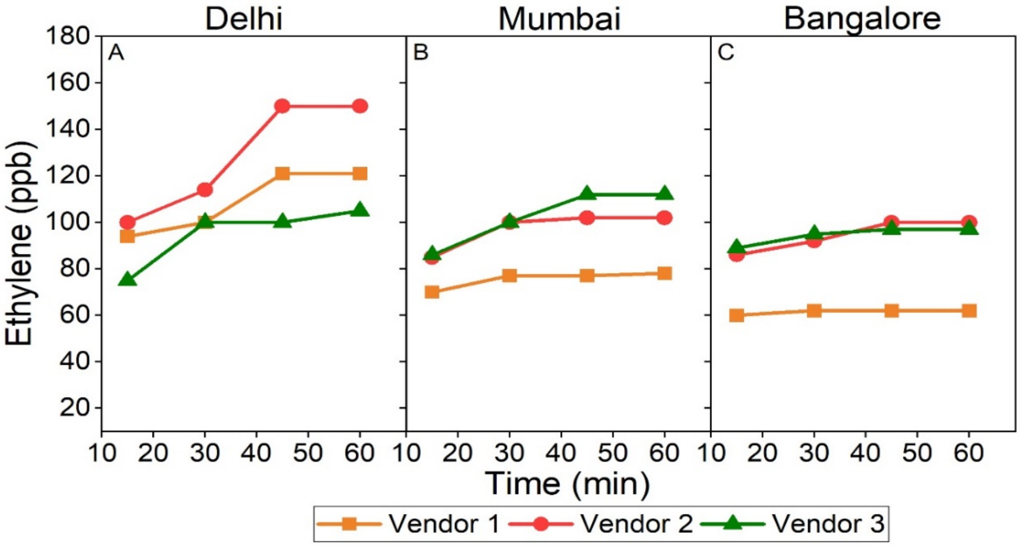


Figure 3.6: Ethylene concentrations at the vicinity of street vendors store in Delhi (A), Mumbai (B) and Bengaluru (C).

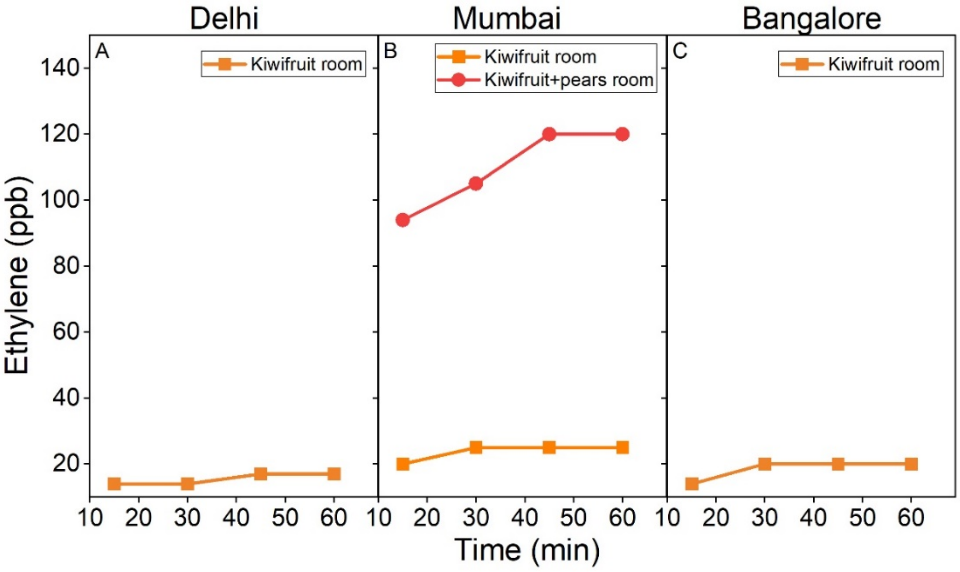


Figure 3.7: Ethylene concentrations in cool rooms containing kiwifruit in Delhi (A), Mumbai (B) and Bengaluru (C).

3.3.4 Firmness at street vendors store

The measured 'Hayward' fruit population consisted of 166 fruit (18-20 fruit per vendor in each city) of which 15% had firmness ranging between 1-1.5 kg_f, 52.4% ranged between 0.4 - 1 kg_f and 23.5% had firmness < 0.4 kg_f (Figure 3.8A). Similarly, for 'SunGold™', of the 144 fruit assessed (14-16 fruit per vendor in each city), 6.8% had firmness ranging between 1-1.4 kg_f, 66.6% had firmness ranging between 0.4 to 1 kg_f and 26.5% had firmness < 0.4 kg_f (Figure 3.8B). Most of the over-soft fruit (< 0.4 kg_f) in both 'Hayward' and 'SunGold™' populations were from Delhi.

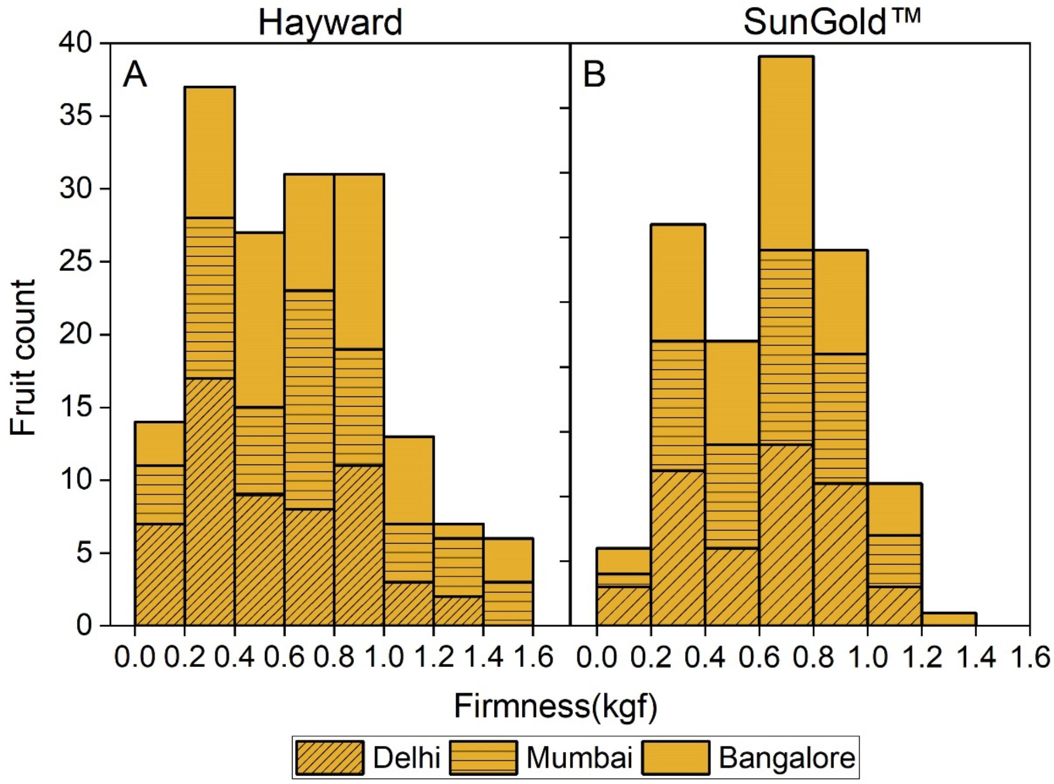


Figure 3.8: Histogram of firmness measured in Zespri™ 'Hayward' (A) and 'SunGold™' (B) kiwifruit marketed at street vendors stores in India.

3.4 Discussion

In a previous kiwifruit supply chain investigation of Bellavi Jayashiva (2012) in India, the maximum temperature abuse was observed to occur during long-distance transportation of kiwifruit (e.g. from Mumbai to Delhi or Bengaluru) resulting in firmness decline. They found that fruit core temperature at the point of sale ranged 19.8-21.3, 26.6-27.4 and 22.6-22.9 °C in Delhi, Mumbai and Bengaluru respectively in July (2011). The temperatures recorded at the street vendors store (measured within the store) in the current study was much higher than in the previous reports.

A potential reason for the lower fruit temperature recordings reported in the study of Bellavi Jayashiva (2012) may be due to fruit core temperature being recorded during heating from refrigerated temperature to ambient conditions. In a laboratory environment, high temperature conditions were created (without solar radiation), and centre temperatures of fruit in trays was monitored (continuously by thermocouples) upon transfer from refrigerated storage (0.5 °C) to high temperatures. These results (Figure 3.9) show that it took approximately 5 h for the fruit core temperature to equilibrate to the storage temperatures (36 and 40 °C). This data demonstrates the time lag for the fruit centre to equilibrate to the external temperature over a large temperature range as governed by heat transfer. It is possible for fruit temperature to be intermediary in the first few hours of exposure to a change of conditions. Hence, if fruit core temperature is measured during the initial hours of exposure, the values obtained may be less than the surrounding ambient conditions. Once the fruit is equilibrated to exposed temperatures, it is expected that the fruit temperature remains greater than the surrounding temperature due to the additional heat of respiration.

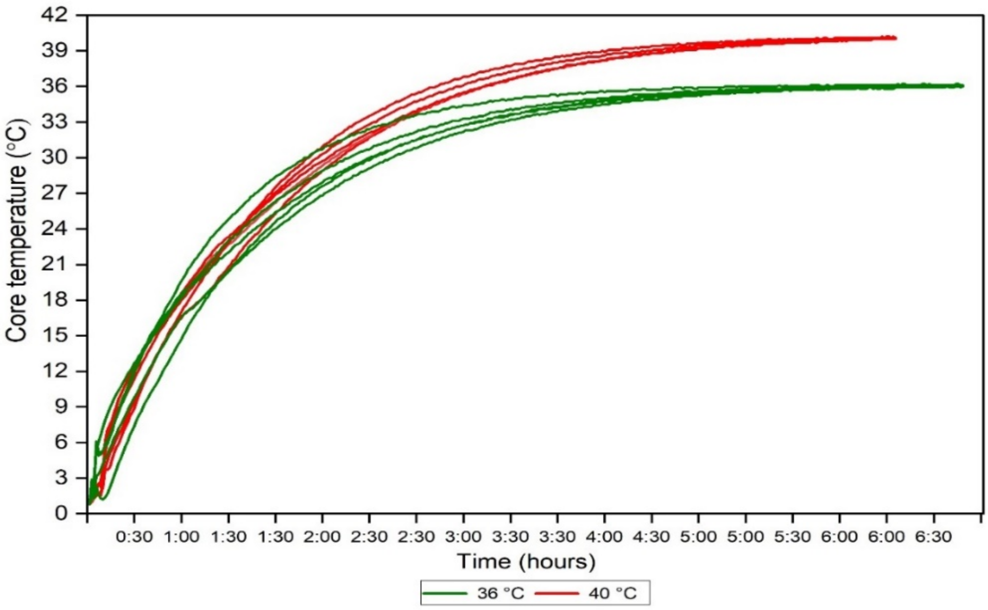


Figure 3.9: Rise in kiwifruit core temperature upon transfer from refrigerated storage (0.5 °C) to high temperatures (36 and 40 °C). Different lines of the same colour are different fruit.

An alternative reason could also be due to the varying temperature monitoring methodologies adopted between the two studies. In the current study, 24 h temperature monitoring in retail stores was conducted and the presented values are the mean day temperatures. However, in the previous study of Bellavi Jayashiva (2012), ‘on the spot’ fruit core temperature was measured only at a single time point (measurement time not elucidated). Observing the temperature values from the previous study, it could be that measurements were conducted during mornings before the temperature escalated to the highest range which may have yielded lower temperature values.

This case study briefly measures environmental conditions within the kiwifruit traditional marketing system in India and Singapore. Elevated temperatures (Figure 3.4) combined with higher ethylene concentrations (Figure 3.6) at the point of final sales were identified as potential challenges for maintaining kiwifruit quality. A drawback of this survey is that the measured environmental conditions were from limited street vendor stores in each of the focused cities which may not be representative of all scenarios.

Measured fruit quality data (Figure 3.8) indicates that most of the fruit at the point of sale were edible while approximately 25% could be considered as over-soft (< 0.4 kg_f). The resulting presence of over-soft fruit at the point of sale is a concern, potentially reflecting the consequences of these supply chain conditions. Previously, Antunes and Sfakiotakis, (2000) found that exposure to up to 35 °C accelerated softening, while 38 °C inhibited softening and caused abnormal ripening and heat injury, however, this work was done with initially firm (5.4 kg_f) fruit.

Most of the kiwifruit at street vendor stores were at an edible firmness (0.4-1.2 kg_f, Figure 3.8). This is potentially advantageous to the consumer, as fruit are ready to eat at purchase, whilst representing a challenge for the vendor, as fruit are close to becoming over ripe and hence unsalable. Given that refrigeration remains unlikely in these marketing channels, the only possible means to avoid losses at street vendor stores is to sell fruit rapidly.

In addition to high temperatures, elevated concentrations of ethylene as high as 150 nL L^{-1}, five times higher than that recommended for kiwifruit (Blanke, 2014) was measured. High ethylene concentrations within the fresh produce supply chains are often measured in-situ (Morris et al., 1978; Knee et al., 1985; Schouten, 1985; Warton et al., 2000; Blanke and Shekarriz, 2010; Lu, 2020). In this case, the high concentrations measured are thought to be from anthropogenic sources such as vehicle or factory exhausts.

The measured ethylene conditions could present an additional risk to kiwifruit quality deterioration reducing storage life in the hands of the vendor or final consumer (Keller et al., 2013). For kiwifruit, a number of studies have detailed postharvest responses to ethylene concentrations in low temperature conditions (Retamales and Campos, 1995; Pranamornkith et al., 2012; Jabbar and East, 2016; Tongonya et al., 2017). However, minimal knowledge exists on ethylene's influence on kiwifruit physiology and quality during high temperature exposure. Antunes and Sfakiotakis (2000) did previously find that propylene (an ethylene analogue) at 130 μL L^{-1} accelerated kiwifruit softening at 38-40 °C when initially firm (5.4 kg_f). Whether these findings transfer to softer kiwifruit at lower ethylene concentrations remains unknown. Should these ethylene exposures be contributing to accelerated softening, ethylene management with traditional markets may be challenging. One possible solution is to previously apply a technology (e.g. 1-MCP) that may restrict the response of the fruit and hence consequences on quality.

The observations in this work indicate a potential need for developing an understanding of kiwifruit responses to tropical temperatures (30-40 °C), particularly when at ready to eat ripening stage. Development of this knowledge may identify the need for handling strategies to minimise losses when fruit are exposed to these conditions.

3.5 Conclusion

This study was conducted to gain further information on the real kiwifruit sale conditions in regions dominated by traditional retailers. The obtained data suggest that kiwifruit may be continuously exposed to a temperature at or above 30 °C at an edible firmness (0.4-1.2 kg_f) under the traditional retailing systems. Further, the prevalence of higher ethylene concentrations in the vicinity of the retailers store could exaggerate the fruit quality deterioration process. Kiwifruit reaching the consumer at an overripe state in these markets might affect exporters reputation as well influence consumer’s perception.

Now that the fruit quality detrimental factors under traditional markets have been substantiated and the extent to which they occur is known (obtained in terms of data), the next step is to gain a scientific understanding of kiwifruit (at edible ripe stage) postharvest responses to traditional market conditions with high temperatures as well as higher ethylene concentrations. Further, postharvest strategies which minimise the impact of environmental conditions on kiwifruit quality and contribute to longer storage life under traditional market systems are essential for establishing a successful sales strategy.

Chapter 4: Postharvest responses of kiwifruit to tropical shelflife temperatures

4.1 Introduction

Market expansion has been one of the major goals for the New Zealand horticulture industry. In developed countries dominated by modern retail, market establishment or expansion may not be very strenuous since fruit quality is managed in a consistent cool chain through to the consumers and hence expected to reach consumers in a state of high quality (Porat et al., 2018). However, in other regions, traditional retail conditions (e.g. wet markets) continue to have a considerable share of fruit sales and make the process of delivering quality products more challenging (Punter et al., 2018).

The limited adoption or availability of refrigeration and the relatively high ambient temperature and humidity conditions may pose a considerable challenge in product quality maintenance under traditional marketing systems (Halder and Pati, 2011). In the previous chapter (Chapter 3), the prevalent detrimental factors for fresh produce quality under tropical traditional marketing systems in India and Singapore were identified. It was noted that fruits at the point of final retailing were continuously exposed to temperatures over 30 °C (Figure 3.4) and elevated ethylene concentrations (Figure 3.6).

Knowledge on fruit postharvest responses to prolonged high temperature exposure either solely or in combination with ethylene has been limited in the past. Few studies which have previously focused on this aspect include studies on kiwifruit (Antunes and Sfakiotakis, 2000; Bellavi Jayashiva, 2012; Zhao, 2017), pears (Hansen, 1942; Maxie et al.,1974), apples (Lurie and Klein, 1990; Johnston et al., 2001; Punter et al., 2018), avocados (Zauberman et al., 1977; Eaks, 1978), plums (Tsuji et al., 1984), guava (Bron et al., 2005) and tomatoes (Biggs et al., 1988).

Antunes and Sfakiotakis (2000) studied the influence of elevated storage temperatures (30-45 °C) on physiological and ripening mechanisms in 'Hayward' kiwifruit and observed 38 °C caused abnormal ripening and temperatures beyond 40 °C completely inhibited ripening and caused heat damage. Whilst this previous study provides insights into the influence of high temperatures on kiwifruit after harvest or before storage, knowledge on kiwifruit responses to elevated temperatures after long-term refrigerated storage as well as at a ripeness stage at which kiwifruit reach end markets is limited. An understanding of both these aspects is essential to match the real kiwifruit supply chain scenarios in which kiwifruit are refrigerated as well as softened to an edible firmness before finally being marketed.

Considering these facts, this investigation aims to understand postharvest physiological responses of kiwifruit to different simulated tropical conditions (hot and humid/hot and dry) after long-term refrigerated storage.

4.2 Materials and Methods

4.2.1 Fruit source and storage procedures

Kiwifruit of cultivars *Actinidia deliciosa* cv. 'Hayward' and *Actinidia chinensis* cv. 'Zesy002' (later referred to by the marketing name 'SunGold™') were sourced from three different growers located around the Bay of Plenty region, New Zealand. Fruit harvest dates were not controlled in the experiment and hence varied resulting in fruit maturity differences between growers at harvest. Fruit were class-1 grade, count size 33 and transported from commercial cool store to Massey University postharvest laboratory, Palmerston North under refrigerated conditions. 'Hayward' and

'SunGold™' fruit arrived packed within polyliners in 10.5 kg modular bulk (MB) and 6.5 kg modular loose (ML) boxes, respectively. Each grower line was considered as replicate and hence kept separate from each other. The fruit were randomised, packed into single-layered polypropylene trays of 25 fruit capacity with polyliners within the coolstore and stored (0.5°C and 90-95% RH) until high temperature exposure began. Information regarding harvest date, quality at harvest for each of the growers was collected from the Zespri® systems.

Three conditions: 20 °C and 75% RH (control), 33 °C and 87% RH (hot-humid) and 40 °C and 30% RH (hot-dry), were established in temperature and humidity-controlled rooms. The trials were conducted sequentially first for cultivar 'SunGold™' followed by 'Hayward'. Fruit of both these cultivars were subjected to long-term refrigerated storage (19-22 weeks for 'SunGold™' and 25-30 weeks for 'Hayward') for two reasons a) to simulate a period of refrigeration which occurs during on-shore storage, shipping and in off-shore storage before reaching the retail store in foreign markets b) obtain a stage of ripeness (edible ripe stage) at which kiwifruit are marketed at retail stores.

An initial respiration measurement (within coolstore) and quality assessment (after overnight fruit equilibration to 20 °C) before exposure were conducted. Before exposure, the fruit were divided into two packaging groups: with polyliners and without polyliners. For each grower, 10 trays (5 trays with polyliners and 5 trays without) were placed inside each of the conditions and one tray per day (25 fruit) under each of the packaging conditions was assessed for respiration rate and quality (firmness, total soluble solutes, acidity, disorders and rots) until the fruit were deemed unsalable. The samples of respiration rate were collected within the high temperature storage rooms and assessed under laboratory conditions whilst quality measurements were done after equilibrating fruit (for 3 h) to laboratory conditions. Temperature and relative humidity were monitored with data loggers (I-button/1 wire DS1923, Maximum integrated, USA) with an accuracy of ± 0.5 for temperature (°C) and ± 5 for RH (%).

4.2.2 Fruit physiology and quality measurements

4.2.2.1 Respiration rate

Respiration rate was measured as carbon dioxide production rate (r_{CO2}) considering the weight of fruit and expressed as nmol kg^{-1} s^{-1} using a static method. Individual fruit of pre-determined weight was enclosed inside an airtight glass jar (550 mL) for a particular period (5 minutes: hot-dry conditions; 15 minutes: control and hot-humid conditions). Gas samples were collected through a rubber septum from the headspace of the glass jar using a 1 mL syringe and injected into a gas analyser fitted with a CO_2 infrared transducer (Analytical Development Company, Hoddesdon, UK) that uses nitrogen as carrier gas at a flow rate of 35 mL min^{-1}. The amount of CO_2 present in the sample was recorded on an integrator (HP3396A, Hewlett Packard, California, USA). Before injecting the sample, the analyser was calibrated with a commercially available CO_2 β-standard (BOC Ltd., Auckland, New Zealand) of concentration 0.534 ± 0.011%. An initial measurement of CO_2 production in the cool store (0.5 °C and 90-95% RH) was conducted before exposure to experimental conditions.

4.2.2.2 Weight loss

An electronic balance (30000D, Presica, Switzerland) to an accuracy of ± 0.1 g was used to assess weight loss. Weight loss was monitored by recording tray weight (each tray consisting of 25 fruit and a plastic polypropylene tray). Measured weight was subtracted from the initial weight to determine a percentage of weight loss (Eq. 4.1) from the initial weight.

$$\text{Weight loss (\%)} = \frac{\mathrm{Wi} - \mathrm{Wf}}{\mathrm{Wi}} \ \mathrm{X} \ \ 100 \tag{4.1}$$

Where Wi represents initial fruit weight and Wf represents the weight of fruit at each measurement time.

4.2.2.3 Firmness

Firmness was assessed using a penetrometer (WEL Penetrometer, Willowbank Electronics Ltd., Napier, New Zealand) fitted with a standard 7.9 mm round Effegi probe which was linked to a computer. Fruit were equilibrated to 20 °C for at least three hours after which outer skin of 2 mm was sliced at two equatorial regions perpendicular to each other and later assessed for firmness. The settings used in the penetrometer were a depth of 8 mm at a speed of 20 mm s^{-1}. Firmness values of 25 fruit were averaged and expressed in kilogram-force (kg_f).

4.2.2.4 Total soluble solids (TSS)

TSS measured as °Brix was determined by using a digital refractometer (PR-32α, Atago Ltd, Tokyo, Japan). The proximal and distal end of the fruit was sliced to approximately 15 mm thickness and a few drops of juice from both ends was squeezed onto the refractometer. TSS was measured on 10 individual fruit.

4.2.2.5 Acidity

Acidity was assessed using a digital pH-meter (TitroLine easy, SI Analytics, Mainz, Germany). A 1 mL juice sample extracted from the remaining whole fruit flesh was filtered through a sieve and later diluted in 50 mL reverse osmosis water and titrated with NaOH (0.1 N) to an endpoint of pH 8.2. Acidity was measured on 5 individual fruit. The acidity percentage was calculated using Eq. 4.2 considering a milliequivalent factor of 0.064.

$$\%\ \text{acid} = \frac{[\text{mLs NaOH used}]\ \text{X}\ [0.1\ \text{N NaOH}]\ \text{X}\ [\text{milliequivalent factor}]\ \text{X}\ [100]}{\text{gms of sample}} \qquad (4.2)$$

4.2.2.6 Storage disorders and rots

All fruit were visually assessed for disorders and rots.

4.3 Data Analysis

Significant effects of treatments on quality parameters were analysed in Minitab (Minitab Inc., Version 16.1, State College, Pennsylvania, USA). Storage conditions, duration and packaging conditions were used as factors and hence data were analysed in a multiple factors ANOVA. Once significant differences were determined, Tukey’s honestly significant difference (HSD) test at 95% confidence was used to differentiate treatment means.

4.4 Results

4.4.1 Initial fruit quality attributes

At harvest quality attributes varied between growers in both kiwifruit cultivars. The variance in harvest dates resulted in different durations of coolstorage between growers. For ‘SunGold™’ grower 3, fruit was harvested three weeks later than the other growers and consequently, had a higher SSC at harvest. At the start of the experiment, fruit from grower 2 was softer than that of the other 2 growers. In ‘Hayward’ grower 5, due to its early harvest was less mature than other growers. At the start of the experiment, grower 5 was considerably softer than growers 4 and 6.

Table 4.1: Quality attributes of ‘SunGold™’ and ‘Hayward’ at-harvest and before exposure to experimental conditions. Dry matter was assessed only at harvest. Values appended by different letters in the same row are significantly different (LSD0.05). Presented are averaged values of 25 fruit (n=25).

		‘SunGold™’			‘Hayward’		
Grower Number		**GL1**	**GL2**	**GL3**	**GL4**	**GL5**	**GL6**
Harvest week (ISO)		16	16	19	22	17	22
Weeks of cool storage		22	22	19	25	30	25
Firmness (kg_f)	At harvest	5.82^{b}	6.25^{a}	5.63^{b}	7.43^{b}	8.23^{a}	6.97^{c}
	After storage	0.81^{a}	0.69^{b}	0.84^{a}	0.96^{a}	0.50^{b}	0.93^{a}
SSC (° Brix)	At harvest	8.84^{b}	8.55^{b}	12.25^{a}	10.84^{a}	6.45^{c}	10.05^{b}
	After storage	14.79^{a}	14.43^{a}	13.93^{b}	13.54^{b}	13.34^{b}	14.61^{a}
Dry matter (%)	At harvest	17.93^{a}	17.89^{a}	17.51^{a}	17.11^{a}	17.30^{a}	17.24^{a}
Fruit weight (g)	At harvest	125.9^{b}	144.4^{a}	143.4^{a}	125.9^{b}	144.4^{a}	143.4^{a}
	After storage	115.5^{b}	116.5^{a}	115.2^{b}	106.7^{c}	110.1^{a}	108^{b}

4.4.2 Storage conditions

As evident (Figure 4.1), good temperature control with ± 0.5 °C variations was achieved under 20 and 40 °C conditions. However, under 33 °C, a relatively larger variation in temperature existed. This larger variation at 33 °C may be due to the set higher humidity range. Fluctuations in storage humidity were noted under each of the storage conditions ranging 80-100%, 82-94%, and 29-45% under control, hot-humid and hot-dry conditions, respectively.

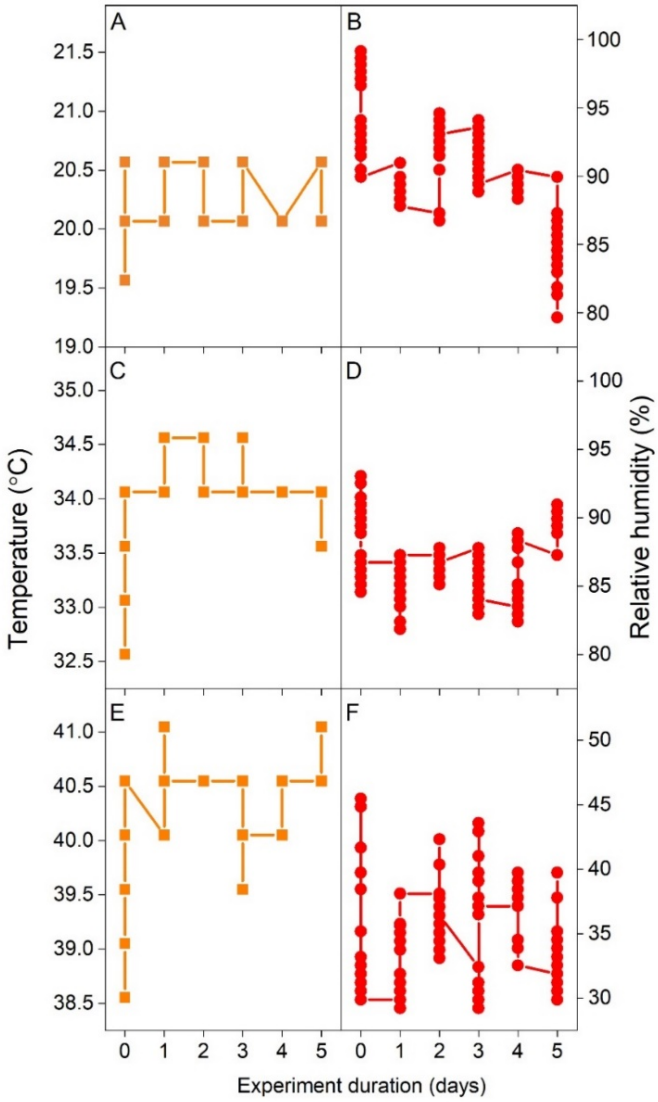


Figure 4.1: Storage conditions i.e. New Zealand (A-B), Singapore (C-D) and Dubai (E-F) monitored during kiwifruit experiments.

4.4.3 Respiration rate

For both 'SunGold™' and 'Hayward', respiration rate increased at high temperatures peaking in the first 24 h of storage at 33 and 40 °C (Figure 4.2). CO_2 production was maximum when measured at 12 h of exposure ranging 540 to 667 and 900 to 1258 nmol kg^{-1} s^{-1} at 33 and 40 °C, respectively in 'SunGold™'. At a similar time, CO_2 production in 'Hayward' ranged 508 to 572 and 948 to 1080 nmol kg^{-1} s^{-1} at 33 and 40 °C, respectively. A significant decline in CO_2 production followed with the 40 °C exposed fruit falling to below 200 nmol kg^{-1} s^{-1} on day 5 of exposure. At 20 °C, respiration rate reached a peak at 12 h and continued to remain at approximately the same value throughout the experimental duration.

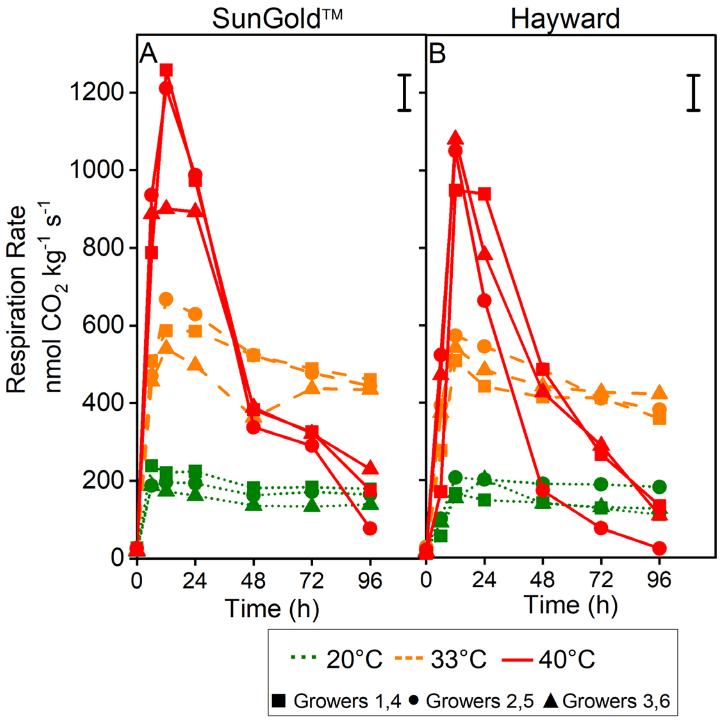


Figure 4.2: Respiration rate of 'SunGold™' (A) and 'Hayward' (B) kiwifruit at tropical conditions (n=15). Initial value at 0 h represents CO_2 production at 0.5 °C. Green dotted lines, orange dashed lines and red solid lines represent CO_2 production at 20, 33 and 40°C, respectively. The error bar represent $LSD_{0.05}$ for the influence of temperature*storage duration interaction on respiration rate.

4.4.4 Weight loss

As expected, weight loss (Figures 4.3-4.4) increased with the rise in storage temperature, with the use of polyliners restricting weight loss by a limited amount in both cultivars. After five days, weight loss in ‘SunGold™’ packed without polyliners ranged between 1.2 to 1.5% at 20 °C, 2.4-2.8% at 33 °C and 4.2-6.2% at 40 °C. Likewise, for ‘Hayward’ packed without polyliners, weight loss ranged between 1.5-1.9% at 20 °C, 2.2-2.9% at 33 °C and 4.6-5.4% at 40 °C.

The incidence of shriveling was observed in both cultivars at 40 °C with a small variation between packaging groups. Initial incidence of shriveling was observed on day three of storage at 40 °C in both ‘SunGold™’ and ‘Hayward’ wherein 40% of the ‘SunGold™’ fruit and 22% of ‘Hayward’ fruit packed without polyliners exhibited shriveling symptoms. By day five of storage at 40 °C, 100% shriveling was observed in both cultivars irrespective of the packaging conditions.

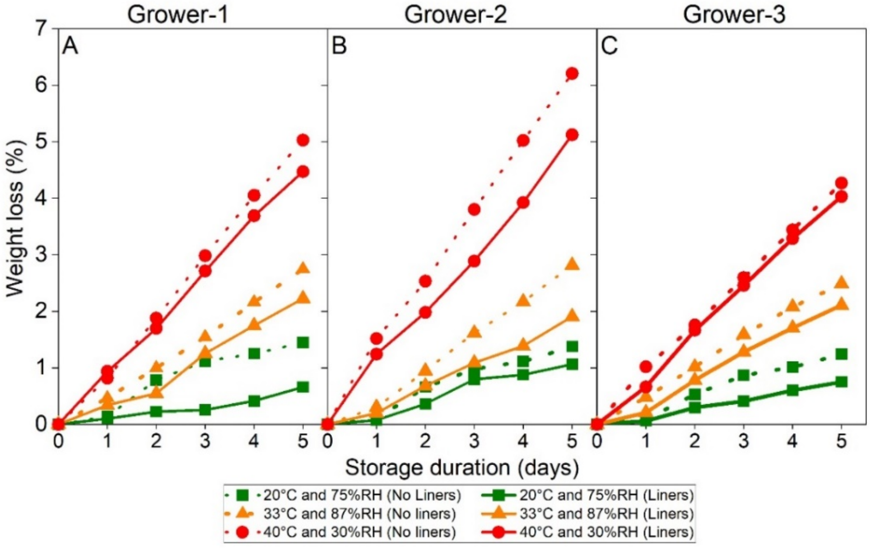


Figure 4.3: Weight loss (%) of ‘SunGold™’ kiwifruit at tropical conditions. Different colours (Green, orange and red) represents weight loss under different conditions. Solid and dotted lines represent package ‘with liners’ and ‘without liners’, respectively.

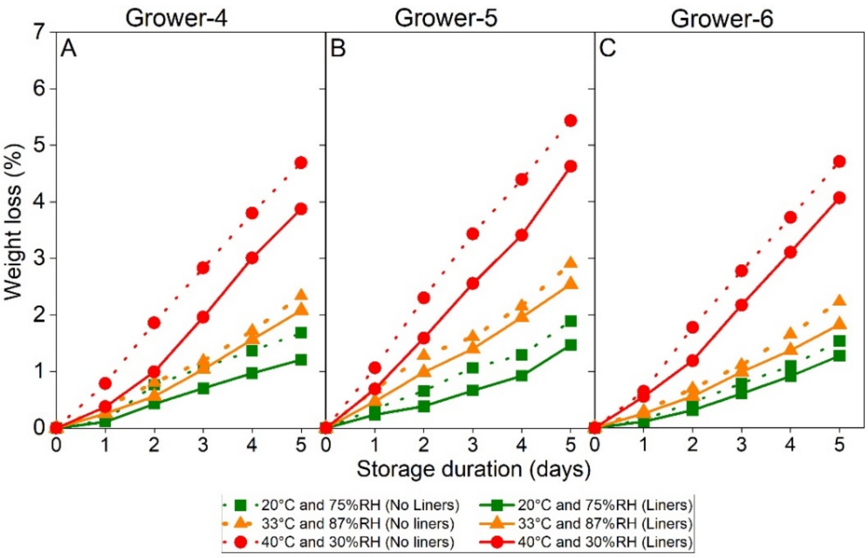


Figure 4.4: Weight loss (%) of 'Hayward' kiwifruit at tropical conditions. Different colours (Green, orange and red) represents weight loss under different conditions. Solid and dotted lines represent package 'with liners' and 'without liners' respectively.

4.4.5 Firmness

In both cultivars, a rapid decline in firmness was noted at 40 °C conditions (Figures 4.5-4.6). On day 3 of exposure to 40 °C, fruit of both cultivars were at an overripe state with firmness declining to below 0.4 kg_f. A very slow phase of softening in 'SunGold™' and a much faster softening in 'Hayward' was noted under 33 °C conditions. At 20 °C, minimal firmness changes happened in both cultivars. Under each of the storage conditions, no significant differences between packaging groups i.e. with polyliners and without polyliners were noted in both cultivars.

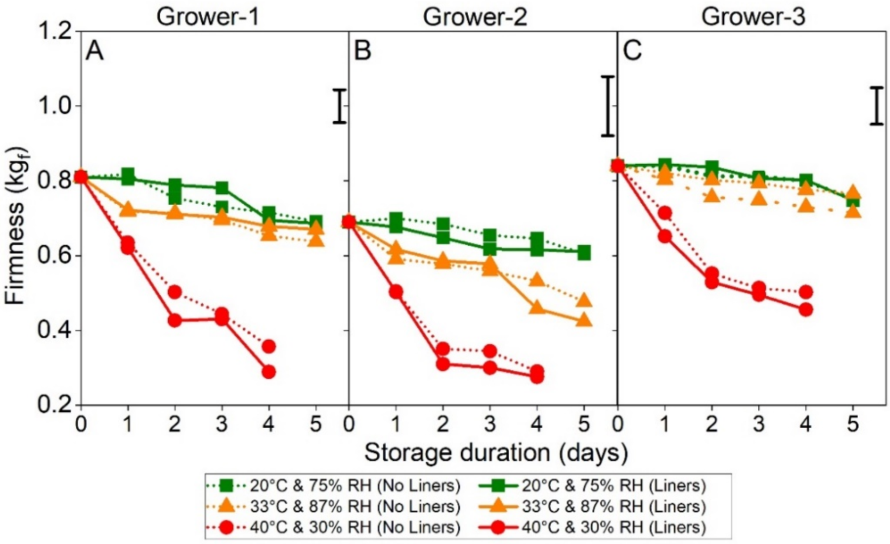


Figure 4.5: Average firmness of ‘SunGold™’ kiwifruit at tropical conditions (n=25). Different colours (green, orange and red) represent firmness changes at different conditions. Solid and dotted lines represent packaging ‘with liners’ and ‘without liners’ respectively. The error bar represent LSD$_{0.05}$ for the influence of temperature*storage duration interaction on firmness.

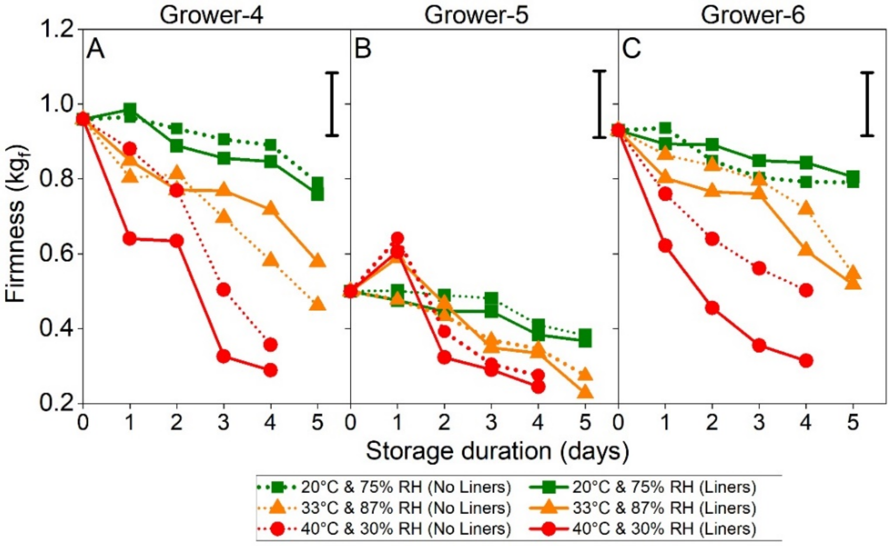


Figure 4.6: Average firmness of ‘Hayward’ kiwifruit at tropical conditions (n=25). Different colours (green, orange and red) represent firmness changes at different conditions. Solid and dotted lines represent packaging ‘with liners’ and ‘without liners’ respectively. The error bar represent LSD$_{0.05}$ for the influence of temperature*storage duration interaction on firmness.

4.4.6 Total soluble solids and acidity

No significant differences existed for TSS (Figures 4.7-4.8) or acidity (Figures 4.9-4.10) in either of the tropical conditions.

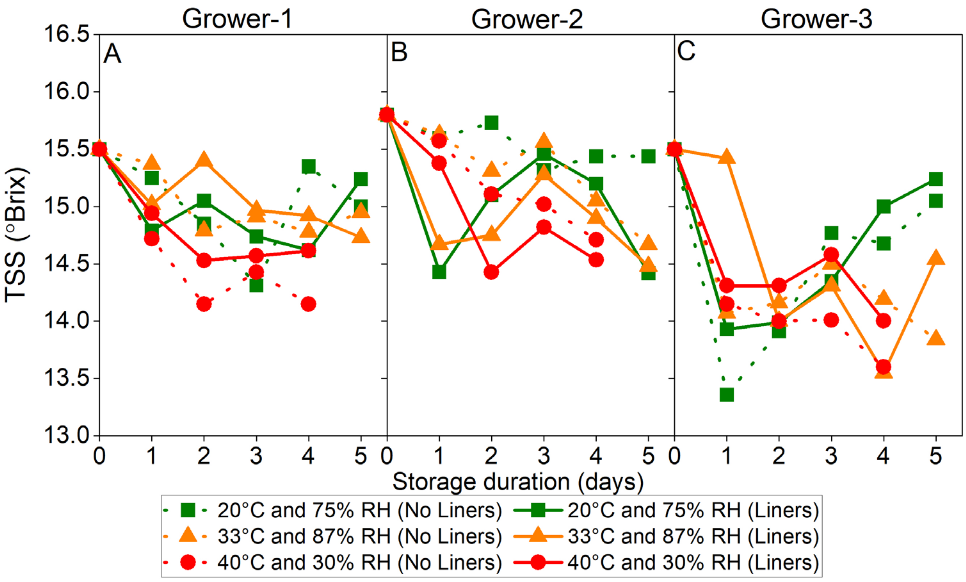


Figure 4.7: TSS (°Brix) in 'SunGold™' kiwifruit at tropical conditions. Each data point represents average value of 10 individual fruit.

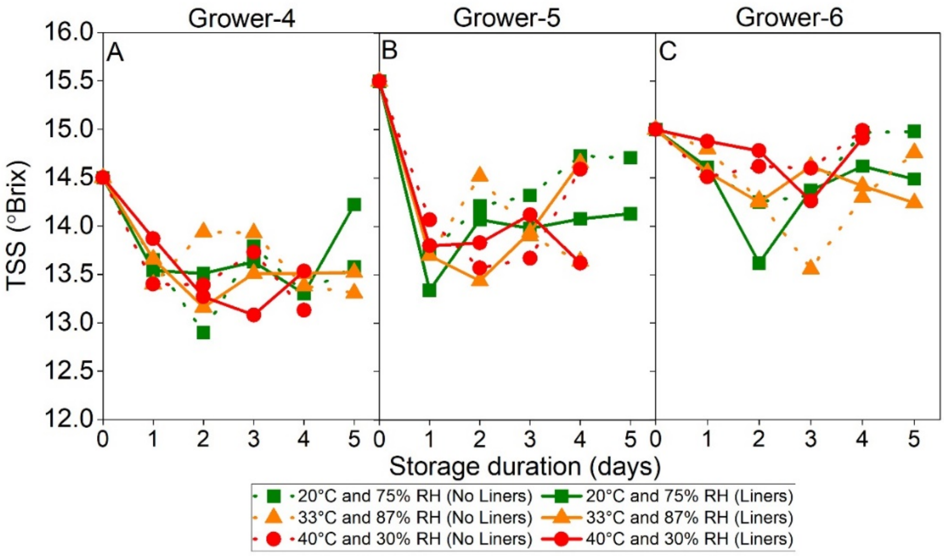


Figure 4.8: TSS (°Brix) in 'Hayward' kiwifruit at tropical conditions. Each data point represents average value of 10 individual fruit.

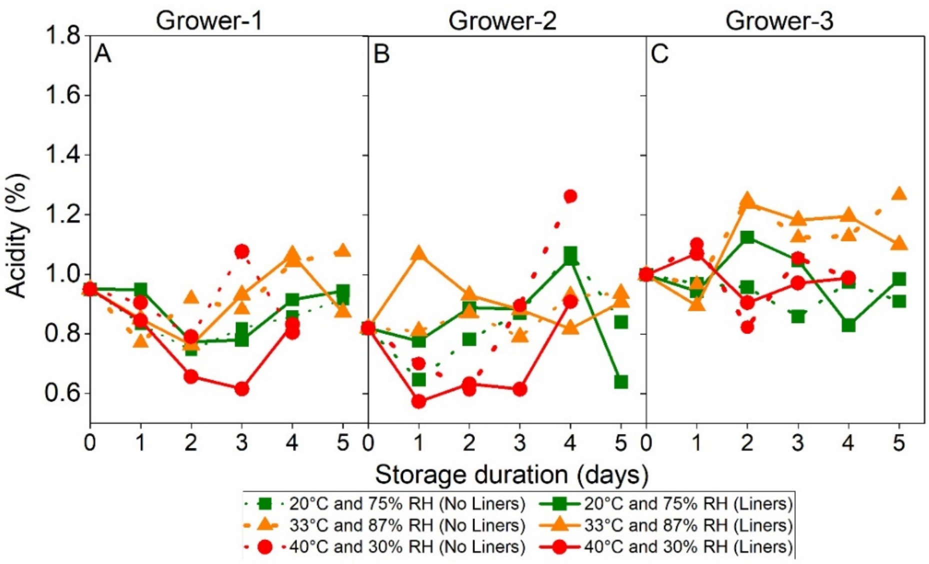


Figure 4.9: Acidity (%) in 'SunGold™' kiwifruit at tropical conditions. Each data point represents average value of 5 individual fruit.

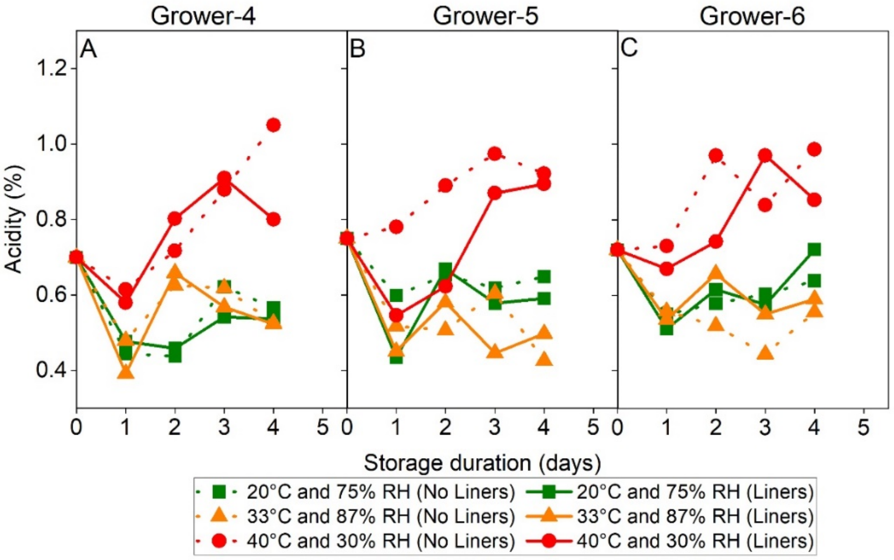


Figure 4.10: Acidity (%) in 'Hayward' kiwifruit at tropical conditions. Each data point represents average value of 5 individual fruit.

4.4.7 Storage disorders and rots

Heat injury symptoms were evident as flesh and skin discolouration and became evident from day 2 and 4 of exposure at 40 °C and 33 °C, respectively. Between 'SunGold™' and 'Hayward', the incidence (in 25 fruit population) ranged 8-20%, 32-48% and 96-100% on days 2, 3 and 4 at 40 °C. At 33 °C, only grower 2 of 'SunGold™' was susceptible to heat injury with symptoms evident on days 4 (16%) and 5 (32%). In 'Hayward', incidence ranged 32-40% on day 5 at 33 °C. Most fruits exhibiting heat injury on days 4 and 5 had developed rots.

4.5 Discussion

The influence of tropical conditions on the postharvest storage life of kiwifruit has been elucidated. While most of the observed physiological and quality responses are expected, this investigation mainly highlights the extent to which changes occur as a consequence of exposure to extreme conditions. Further, the obtained results are indicative of the fact that deterioration of fruits under tropical conditions is due to increased respiration rate, excess weight loss as well as rapid softening, all of which culminate in quality losses and deterioration. The observed visible symptoms of deterioration at 40 and 33 °C were flesh and skin discolouration, water soaked internal flesh, severe shrivelling and rots.

Respiration and transpiration are the two key physiological mechanisms influencing the storage life of fresh produce. However, of these two, respiration is of foremost importance since it is the only source of energy for fruits postharvest (Lance et al., 1965; Solomos, 1983). An inverse relationship exists between respiration rate and storage life in fruits (Dalrymple, 1969; Sekse, 1988; Tano et al., 2005) and prolonged storage can only be achieved by reducing the respiration rate to as low as possible using various storage techniques (Carson and East, 2018). Furthermore, respiration results in carbon loss which consequently contributes to weight loss (Mahajan et al., 2008). As evident in this study, high temperature accelerates both respiration and weight loss mechanisms resulting in undesirable changes which restrict storage life.

It is a well-established fact that the rise in respiration along with storage temperature is due to increases in the rate of respiratory reactions, which as described by Vant Hoff's law are two to three-fold higher for every 10 °C uprise (at temperatures within the normal physiological ranges) and the value of increase is determined by Q_{10} co-efficient (Smock, 1944). A strong dependency of respiration rate on storage temperatures has been elucidated in kiwifruit (Antunes and Sfakiotakis, 2000; East et al., 2010), cherries (Sekse, 1988) and blueberries (Nunez-Barrios et al., 2005; Sargent et al., 2017). As observed in this study, CO_2 production was proportional to exposed temperatures and was relatively swift under higher temperatures (Figure 4.2).

Higher respiration rate on the other hand indicates higher mitochondrial metabolism resulting in increased activity of malic and carboxylase enzymes (Hulme et al., 1963) and the subsequent decline in respiratory peak is due to reduced mitochondrial function and malic enzyme activity. As suggested by Hulme et al. (1963), the decline in respiration to a constant value after respiratory peak in apples could be due to a lack of acid substrates. The hypothesis of Hulme et al. (1963) points out that a definitive pattern of acidity decline should have been evident in the current experiment, especially at 40 °C under which respiration rate was relatively higher. Further, Plagge and Gerhardt (1930) proposed that the loss of acidity is greater under higher temperatures even when fruit's initial acid content is low.

In this study, no such relationship between acidity and respiration existed in either of the fruits and surprisingly in ‘Hayward’, acidity slightly increased along with storage duration at 40 °C. While the actual reason for the observed acidity increase in ‘Hayward’ is unclear, it could also be an indication of the existence of variability in acidity changes between cultivars as well as between fruit species as a response to heat stress. For example, in nectarines (Lay-Yee and Rose, 1994) and strawberries (Garcia et al., 1995), heat treatments caused a decline in acidity but in tomatoes (Lurie and Sabehat,1997) and grapefruit (Miller and McDonald, 1991) no such changes were evident. However, since the sample size adopted for acidity measurements was smaller in this study, the proposed theory of variability existence can only be confirmed after obtaining acidity results from a larger sample size.

The observed initial respiratory peak at higher temperatures may indicate fruit tissue trying to maintain normal homeostasis under the exposed conditions. Further, it is unknown whether ethylene production coincided with the observed initial respiratory peak during the initial hours of exposure. Observing the softening trend in kiwifruit at 40 °C, it could be that ethylene production occurred since the fruit were at the climacteric stage (< 1 kg_f firmness) and the possibility of refrigerated storage accelerating the onset of ethylene production exists (Hyodo et al., 1987; Ilina et al., 2010).

Conversely, ethylene production being completely inhibited at 40 °C due to heat stress (Antunes and Sfakiotakis, 2000) and softening being influenced directly by respiratory metabolism or thermal damage or a combination of both may have also occurred. The sharp decline of CO_2 from the peak at 40 °C suggests the existence of the latter to be more probable (i.e. softening influenced by respiration and heat damage) since the observed respiratory trend at 40 °C is an indication of stress exceeding beyond the normal compensatory level resulting in rapid respiratory decline due to irrecoverable physiological damage (Antunes and Sfakiotakis, 2000).

In both cultivars, a rapid decline in firmness was observed at 40 °C while at 33 °C, softening in 'SunGold™' matched the fruit at 20 °C, while for 'Hayward', softening was faster than at 20 °C. Less softening in 'SunGold™' than 'Hayward' at 33 °C could be an indication that 'SunGold™' may possess greater tolerance to heat stress than 'Hayward'. Increased tolerance in 'SunGold™' could be due to ethylene and softening metabolisms being differentially influenced by high temperature than in 'Hayward'.

Water loss affects the marketability of fresh produce due to reductions in salable weight as well as inducing undesirable visual changes such as shrivelling or wilting due to a decline in turgor pressure (Laurin et al., 2005). As the data indicates, weight loss increases with storage period under tropical conditions. The main factor influencing the weight loss of fresh produce is the variance of water vapour pressure deficit (WVPD) between fruit and external storage atmospheres (Smock, 1944). High storage temperatures enhance the differences in vapour pressure deficit between fruit and the storage atmosphere (Maguire et al., 1999; Schick and Toivonen, 2002). For example, the calculated WVPD under control, hot-humid and hot-dry conditions were 0.59, 0.65, 5.16 kpa, respectively. Thus, the high temperature and low humidity exhibited in hot-dry conditions increased WVPD and subsequently resulted in the highest weight loss. Furthermore, higher internal fruit temperature generates greater energy, subsequently promoting transpiration (Ben-Yehoshua and Rodov, 2002) and increased skin permeability (Nguyen et al., 2006).

As suggested by Robinson et al. (1975), a loss of 5-10% of the initial weight affects the marketability of fruits. In particular, weight loss ranging about 5% affects the marketability of kiwifruit (Minchin et al., 2013). However, under tropical conditions, weight loss may not be a good predictor of marketable life since larger physiological changes are induced by heat stress well before weight loss exceeds the unacceptable limit. For example in kiwifruit exposed to 40 °C, although the percentage weight loss reached unmarketable range (5%) on day 5, the incidence of flesh discoluration and water-soaked symptoms in internal flesh were evident from day 3. In addition to this, shrivelling symptoms also became evident from day 3 of storage at 40 °C when a 3% loss of weight occurred. This not only indicates that the incidence of shrivelling occurs fairly rapidly at higher storage temperatures but also suggests the possibility of alternative mechanisms influencing shrivelling under high temperatures.

The obtained results suggest that polyliners only reduced weightloss by a small proportion. The data obtained from within the polyliner microenvironment indicates a minimal difference in humidity existed around the fruit packed with or without polyliners under 33 and 40 °C storage conditions. For example in ‘Hayward’, the increase in RH within the polyliners was only by 2.7-4.3% at 33 °C and 3.2-5% at 40 °C in comparison to package without polyliners. A possibility for the lack of humidity accumulation within the polyliner microenvironment may be due to increased permeation of moisture through the polyliners which can occur at higher temperatures due to increased passage of polymer segment as well as higher energy of the diffusing molecule (Siracusa, 2012). However, since a similar effect of polyliners as that of 33 and 40 °C was observed at 20 °C, the existence of polymer permeation theory remains doubtful. It could be that a higher respiration rate had a significant influence on weight loss.

4.6 Conclusion

This study found that exposing kiwifruit to a short period (12 h) at 40 °C after long-term storage results in significant physiological changes. There remains a need to investigate if temperatures less than 40 °C (but > 33 °C) could induce a similar effect, and/or if short-term exposures of less than 48 h to 40 °C have a damaging effect in the long term. Firmness changes in ‘SunGold™’ at 33 °C were minimal in comparison to 20 °C, while for ‘Hayward’ 33 °C induced more rapid softening. This suggests that ‘SunGold™’ may be more tolerant to heat stress. However, to make this claim, a further investigation is necessary.

TSS and acidity development were not influenced by the high temperature conditions. The use of polyliners did not significantly reduce weight loss suggesting a need to identify alternative packaging techniques which minimise kiwifruit weight loss in tropical conditions. While this investigation elucidates the influence of tropical marketing conditions on kiwifruit physiology and quality, a further investigation aiming to understand ethylene's influence under tropical conditions is necessary since higher ethylene concentrations were found to exist under conditions of traditional retail (Figure 3.6) during the survey (Chapter 3).

Chapter 5: Inhibition of ethylene perception by 1-MCP treatment delays softening of kiwifruit in tropical marketing conditions

5.1 Introduction

Ethylene, the gaseous ripening hormone is essential for initiating a cascade of ripening events which are essential for climacteric fruits to reach their final edible quality (Giovannoni et al., 2017; Brizzolara et al., 2020). However, kiwifruit remains to be an exception as major ripening events are noted to happen in the absence of significant ethylene synthesis (Atkinson et al., 2011). Contrarily, kiwifruit is highly sensitive to ethylene exposure (after harvest) as very low concentrations of ethylene at storage or ambient temperatures can accelerate softening restricting long-term storage (Arapia et al., 1986; Retamales and Campos, 1997). Due to ethylene's detrimental role on kiwifruit quality, exposure to ethylene during postharvest, along the supply chain, is usually highly undesirable (Jeffery et al., 1991; Ritenour et al., 1999; Koukounaras and Sfakiotakis, 2007; Pranamornkith et al., 2012). Commercial application of ethylene to achieve accelerated and synchronised softening (Lallu et al., 1989; Crisosto et al., 1997) being an obvious exception.

To maintain better kiwifruit quality during storage and shelflife, monitoring as well as ventilating or scrubbing ethylene from the storage environment is essential (Defilippi et al., 2011). The New Zealand kiwifruit industry strictly monitors ethylene during storage in packhouses and shipping, considering concentrations of 30 nL L^{-1} as the upper limit for ethylene exposure (Jeffery et al., 1991; Blanke, 2014). The possibility of fruit getting exposed to higher ethylene concentrations during postharvest handling in New Zealand or during shipping is minimal due to regular monitoring which combined with good storage conditions enables ethylene concentrations to be kept below the upper limit. This being the fact, a challenge still exists in managing ethylene concentrations within the fruit packaging environment wherein the presence of a single diseased (major risk being *Botrytis cinerea*) or damaged (by mechanical injury) or disordered (e.g. chilling injury) fruit results in ethylene accumulation within the polyliner micro-environment which in turn triggers ethylene production and premature softening in healthy fruit resulting in fruit losses (Jeffery et al., 1991).

At the very end of the supply chain i.e. at wholesale storage or handling or at the point of sale (modern or traditional retail), it is more difficult to completely limit ethylene exposure. At the wholesale level, higher ethylene concentrations are expected to be mainly contributed from other climacteric fruits stored alongside kiwifruit (Warton et al., 2000; Lu, 2020). In an investigation conducted by Pathak et al. (2017), it was observed that kiwifruit stored with apples (a high ethylene producer) had higher rates of respiration and ethylene production and thereby had reduced storage life.

Similarly, during the kiwifruit supply chain survey (Chapter 3), it was found that in cool stores of major kiwifruit importers, ethylene concentrations were as high as 150 nL L^{-1} due to co-storage of pears along with kiwifruit (Figure 3.7B). In storage rooms with only kiwifruit, ethylene concentrations were approximately 25 nL L^{-1}. Further, environmental conditions around wet markets and street vendor stores in Delhi were 40 °C and 30% RH (Figure 3.4) with ethylene levels reaching as high as 150 nL L^{-1} (Figure 3.6).

Under conditions of retail, kiwifruit at “ready to sell” or “ready to eat” stage of ripeness is generally presented in display cabinets (Figure 3.8). These conditions expose the product to potential ethylene coming from adjacent produce, and other exogenous sources. Although ethylene exposure may be similar in both modern and traditional retail, better temperature control in modern retail facilitates comparatively better storage life. However, since most traditional retail markets have limited or no refrigeration facilities, exposure to elevated concentrations of ethylene under high temperature conditions could either (1) induce additional mechanisms resulting in accelerated ripening leading to more postharvest loss or (2) may not be significant in its effect given that the rate of ripening in ambient temperature conditions is already very rapid (Figures 4.5 and 4.6). Understanding ethylene's effect in these non-temperature-controlled retail conditions provides evidence as to the importance of the need to manage ethylene's detrimental action on kiwifruit quality as an essential strategy for reducing postharvest losses in tropical markets.

The ethylene antagonist 1-methylcyclopropene (1-MCP) has been widely used to understand ethylene's regulatory action during fruit ripening in addition to commercial application to extend the storage life of the produce (Blankenship and Dole, 2003; Sisler and Serek, 2003; Defilippi et al., 2011). Previously, Ilina et al. (2010) found 1-MCP treatment (1 µL L^{-1} for 24 h at 0 °C) after 80 and 120 days of refrigerated storage delayed climacteric ethylene production in 'Hayward' kiwifruit resulting in reduced softening under ambient conditions (20 ± 2 °C).

Since kiwifruit can be cool stored (0 °C and 90-95% RH) for up to 4-6 months in an ethylene free environment (Harvey et al., 1983; Ritenour et al., 1999; Burdon and Lallu, 2011), investigating 1-MCP efficacy beyond 120 days of refrigerated storage would be ideal for understanding 1-MCP efficacy after very long term storage. This would benefit in identifying if 1-MCP treatment would benefit in extending the eating window of kiwifruit since kiwifruit cool stored long term (≥ 12 weeks) generally soften to edible firmness (Burdon et al., 2017). Further, treatment on edible ripe kiwifruit will also clarify the action of 1-MCP on climacteric ethylene production which is generally expected to peak when kiwifruit firmness declines to below 1 kg_f (Stec et al., 1989;

Richardson et al., 2011; Atkinson and Schröder, 2016). In addition to this, little is known about the efficacy of 1-MCP on most climacteric fruit under tropical conditions.

In the initial survey (Chapter 3), kiwifruit at the edible ripe stage were found to be exposed to higher concentrations of ethylene (100 to 150 nL L^{-1}) at the end market conditions. In the subsequent study (Chapter 4), 'Hayward' and 'SunGold™' kiwifruit were exposed to tropical environments i.e. hot-humid and hot-dry after long-term storage (25 weeks at 0.5 °C and 90-95% RH), and it was observed that kiwifruit suffered significant heat stress and physiological damage within a short exposure duration (12 h) at 40 °C. While Chapter 4 provides information on the influence of tropical environments on kiwifruit physiology and quality, the impact of ethylene exposure under these tropical conditions is unknown. Consequently, this investigation aims to investigate the consequences of ethylene exposure on kiwifruit physiology and quality under simulated tropical market conditions and in addition determine if 1-MCP may be of commercial use as an effective kiwifruit quality control strategy in these tropical markets.

5.2 Material and Methods

5.2.1 Fruit source

Fruit from kiwifruit cultivars *Actinidia deliciosa* cv. 'Hayward' and *Actinidia chinensis* cv. 'Zesy002' (later referred to by the marketing name 'SunGold™'), grown in the Bay of Plenty region were sourced by Zespri® International Ltd, from commercial cool stores and received at Massey University postharvest laboratory, Palmerston North on two different dates, i.e. 'Hayward' grower 1 and 'SunGold™' arrived on 21st May 2020 (ISO week 21) and Hayward grower 2 arrived on 3rd November 2020 (ISO week 45). Most of the refrigerated storage for 'Hayward' grower 2 occurred at the packhouse. The fruit were class 1 grade, count size 30 (‘Hayward’ grower 1 and ‘SunGold™’) and 27 (‘Hayward’ grower 2). ‘Hayward’ kiwifruit arrived packed in loose packed 10.5 kg MB boxes and ‘SunGold™’ in loose packed 6.5 kg ML boxes. Fruit were cooled before and during transport and were immediately cool stored (0.5 °C and 90-95% RH) upon arrival at the laboratory. An initial quality measurement was done on the day of fruit received at the laboratory.

Since the fruit were subjected to long-term storage and to reduce heterogeneity at the start of the experiment, a round of manual sorting was done to remove unusable fruit. During manual sorting, soft fruit were removed based on slight palm pressure while visual symptoms were considered for the elimination of shrivelled and rotten fruit which existed in the stock. This sorting was done two days before the start of each experiment, after which fruit were randomised to treatments. Further, a non-destructive firmness measurement using the Softness Fruit Sensor (SFS), a non-destructive kiwifruit firmness sensor developed by The New Zealand Institute for Plant and Food Research Ltd was used to ensure only fruit above the desired firmness (SFS peak value ≥ 32) were used. Later, after SFS measurements, fruit were packed into labelled single layered polypropylene trays with polyliners (0.013 mm) and cool stored (0.5 °C and 90-95% RH).

5.2.2 1-MCP treatment

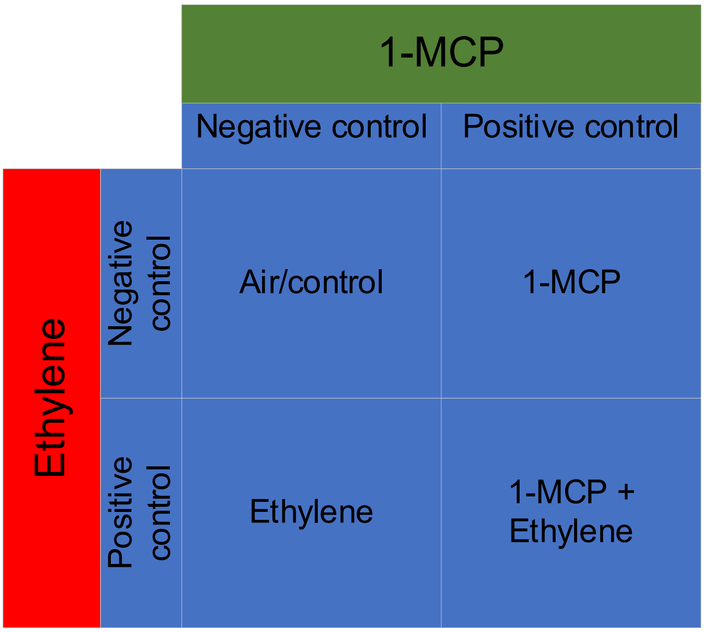
Fruit trays designated for 1-MCP treatment were transferred from the cool storage into an air-tight high-density polyethylene tub (820 x 530x 670 mm) which was maintained in a separate cool room (4 °C and 95% RH). Polyliners were removed from the treatment trays at this stage. Non-treated fruit trays remained under cool store conditions (0.5 °C and 90-95% RH) during the 1-MCP treatment period. A treatment of 1-MCP (0.14% 1-MCP SmartFresh™, AgroFresh Inc., USA) at 750 nL L^{-1} for 24 h at 4 °C was conducted. Lukewarm water was added to a 50 mL plastic vial that contained a predetermined quantity of 1-MCP powder and the vial was closed tight immediately and shaken vigorously to ensure 1-MCP powder mixes well with water to release the vapour. Later, the vial was placed inside the treatment tub which was subsequently sealed air-tight for 24 h. Additionally, to confirm the treatment, tomatoes (at breaker stage of maturity) were also treated with 1-MCP along with kiwifruit. The 1-MCP treated tomatoes exhibited delayed ripening confirming the activation of 1-MCP gas during the treatment process.

Temperature and humidity conditions inside the treatment tub were monitored using data loggers (I-button/1-wire DS1923, Maxim Integrated, USA). The carbon dioxide (CO_2) accumulation inside the tub was monitored twice during treatment to ensure either no extreme accumulation of CO_2 or leakage that would result in no accumulation. During the 24 h treatment period, CO_2 accumulation inside the tub ranged between 1-1.2%. After 24 h, the treatment tub was opened in a well ventilated area and later both 1-MCP treated and untreated fruit were repacked from IT trays into recycled polyethylene terephthalate (rPET) perforated punnets (178 x 140.5 x 55 mm) of 5 fruit capacity (approximately 600 to 650 g of fruit in each punnet) under refrigerated conditions and later the punnets were immediately transferred into the experimental conditions.

5.2.3 Storage procedure and experimental design

Two storage conditions i.e. 33 °C and 95% RH and 20 °C and 95% RH were established. The trial was first conducted at 33 °C followed by 20 °C. The 40 °C storage condition as adopted in the previous experiment (Chapter 4) was opted out due to the challenges in the experimental setup such as the requirement of higher flow rates within the barrels due to increased fruit CO_2 production rates.

A full matrix experiment consisting of a combination of treatments (1-MCP or control) and storage atmospheres (ethylene or air) was designed (Figure 5.1).



		1-MCP	
		Negative control	Positive control
Ethylene	Negative control	Air/control	1-MCP
	Positive control	Ethylene	1-MCP + Ethylene

Figure 5.1: Matrix design adopted for the experiment. The presence of 1-MCP treatment (1-MCP or 1-MCP+Ethylene) was considered as a positive control for 1-MCP treatment and absence of 1-MCP treatment (control or ethylene) was considered as a negative control for 1-MCP treatment. Similarly, the presence of ethylene in the storage atmosphere (Ethylene or 1-MCP+Ethylene) was considered as a positive control for ethylene exposure while the absence of ethylene (Air or 1-MCP) was considered as a negative control for ethylene exposure.

The experimental setup consisted of 36 barrels consisting of (3 barrels per treatment combined by 3 grower lines of fruit). Each barrel was 60 L capacity with a flow gas supply. A flowrate of 300 mL m^{-1} through each barrel was achieved using control valves. This flow rate ensured CO_2 concentrations within the barrels remained below 0.5% and limited further ethylene accumulation within the barrels. The outflow was continuously ventilated out of each barrel. Monitoring CO_2 and ethylene in the outflow was conducted. Relative humidity of 95% in each of the barrels was achieved by flowing the gas mix through sealed 1000 mL jars containing glycerol (21.1%) and water (78.9%) at both 33 and 20 °C. Temperature and humidity conditions inside each of the barrels were monitored using data loggers (i-button/1-wire DS1923, Maxim Integrated, USA) having an accuracy of ± 0.5 for temperature (°C) and ± 5 for RH (%) set at a measurement frequency of 30 minutes.

The maximum observed concentration of ethylene around the street vendors store during the kiwifruit supply chain survey (Chapter 3) was adopted as the treatment concentration (Figure 3.6). As such, a concentration of 150 nL L^{-1} was selected. Exposure of fruit to continuous exogenous ethylene at the concentration of 150 nL L^{-1} was achieved by diluting 92 ± 4 µL L^{-1} ethylene β-standard (BOC Ltd., Auckland, New Zealand) with dry air using a flow-controlled mixer. The final gas concentration from each of the barrels was checked through the outflow on the alternative days to fruit quality measurements using MAC*View*® Portable Ethylene Postharvest Gas Analyser (Environmental Monitoring Systems (EMS) B.V., St. Annaland, Netherlands).

For ‘Hayward’, for each grower, three barrels per treatment combination was established. Each barrel consisted of 30 fruit (6 punnets) at 33 °C or 50 fruit (10 punnets) at 20 °C (more fruit at 20 °C due to additional measurement days). At each measurement occurrence, 10 fruit (2 punnets) were removed from each barrel and assessed for physiology and quality parameters. ‘SunGold™’ comprised of only a single grower of three replicate barrels.

Assessments on fruit physiology and quality were conducted after 1-MCP treatment at 1, 3 and 5 days at 33 °C. At 20 °C, assessments occurred after 1,3,6,10 and 15 days. Quality was also measured a day before 1-MCP treatment (d -1).

Respiration rate measurement (CO_2 production) was done at the storage temperatures immediately after the removal of the fruit from the barrels. For quality measurements, the fruit were equilibrated to 20 °C for 3 h (only for 33 °C stored fruit) before assessment. Weight loss measurement was done immediately when the fruit were brought to 20 °C before equilibration.

5.2.4 Fruit respiration rate

Respiration rate was measured as previously described in Chapter 4 (section 4.2.2.1). A set of 12 fruit (4 fruit per barrel or 2 fruit per punnet) under each treatment/grower/cultivar were measured individually for respiration rate. The time interval between the initial and final gas sample collection was 15 minutes at 33 °C and 30 minutes at 20 °C. Respiration rate was calculated from the change in CO_2 production by taking into consideration the weight of fruit, free volume of the glass jar and storage temperature and expressed as nmol kg^{-1} s^{-1}. An initial assessment of respiration rate at the coolstore was done on both treated and untreated fruit before and after 1-MCP treatment before transferring the fruit to storage conditions.

5.2.5 Fruit weight loss

Weight loss measurements were done on individual fruit. The same set of 12 fruit used for respiration assessments were subsequently weighed to estimate weight loss. At the start of the experiment after 1-MCP treatment, all the fruit designated for weight loss measurements were recorded for weight (initial weight) inside the cool store (0.5 °C and 90-59% RH), labelled and then packed into punnets. Later, on the day of measurement after exposure, the final weight was recorded at room temperature. An electronic balance (TW423L, Shimazdu corporation, Japan) with an accuracy of ± 0.001 g was used to measure fruit weight. The percentage loss in weight of individual fruit was estimated by Eq. 4.1.

5.2.6 Flesh colour

Flesh colour was measured using a reflectance spectrophotometer (CM-2600D, Konica Minolta Sensing Inc., Osaka, Japan) with an 8 mm aperture diameter. Spectramagic NX software was used to calculate °hue. The illuminate source D65 was selected for the instrument and the spectrophotometer was set to measure with spectral component included (SCI). A single reflectance measurement was recorded on one side of individual fruit after double slicing the fruit.

5.2.7 Destructive firmness

Flesh firmness was measured as described in Chapter 4 (section 4.2.2.3).

5.2.8 Fruit rots

The fruit were cut into halves and visually assessed for rots.

5.3 Statistical analysis

For 'Hayward', data was analysed separately for each grower (considered as replicates) in Minitab (Minitab Inc., Version 16.1, State college, Pennsylvania USA). Since 'SunGold™' consisted of a single grower, barrels (n=3) were considered as replicates. Significant effect of treatments (1-MCP or control) or storage atmosphere (ethylene or air) or interaction between treatments and storage atmosphere in influencing kiwifruit physiology and quality parameters at each measurement point was analysed except for rot incidence. Once significant differences were determined, Tukey’s honestly significant difference (HSD) test at 95% confidence was used to differentiate sample means at each of the time points.

5.4 Results

5.4.1 Initial fruit quality attributes

Harvest date, as well as quality attributes (at harvest and after storage), varied between growers/cultivars. At the start of the experiment, ‘Hayward’ grower 2 had the highest firmness in comparison to ‘Hayward’ grower 1 while no significant differences existed in TSS content between these two growers (Table 5.1). ‘SunGold™’ had the lowest firmness and highest TSS content at harvest and at the start of the experiment. Fruit from both cultivars were at edible ripe stage (0.8 to 1 kg_f) at the start of the trial.

Table 5.1: Initial average quality of fruit upon arrival to laboratory and at the start of the experiment. Dry matter was assessed only after harvest. Values appended by different letters in the same row are significantly different (LSD 0.05). Presented are averaged values of 30 fruit (n=30).

Grower Number		**‘Hayward’ Grower 1**	**‘Hayward’ Grower 2**	**‘SunGold™’**
Harvest week (ISO)		18	22	17
Weeks of cool storage		28	24	29
Firmness (kg_f)	At harvest	6.26^{b}	7.11^{a}	4.62^{c}
	After storage	0.93^{b}	1.02^{a}	0.82^{c}
SSC (°Brix)	At harvest	10.12^{b}	10^{b}	14.45^{a}
	After storage	15.03^{b}	14.61^{b}	15.42^{a}
Dry matter (%)	At harvest	17.71^{b}	17.51^{b}	19.54^{a}
Colour (°hue)	At harvest	-	-	102.71
	After storage	97.88^{a}	98.08^{a}	90.18^{b}

5.4.2 Respiration Rate

As observed previously, a rapid increase in respiration rate happened on the initial day of exposure in both temperatures. At 33 °C, CO_2 production rate ranged between 528 to 601 nmol kg^{-1} s^{-1} on day 1 (Figure 5.2). An approximate 1.3-fold drop in CO_2 production rates was observed in 1-MCP treated fruit on day 3 in both growers of 'Hayward'. This respiration reduction was further extended to day 5. In the untreated fruit, the CO_2 production rate remained higher on days 3 and 5 with the rates being closer to the peak value. For 'SunGold™', the respiration rate almost remained similar for all treatment combinations. In 'Hayward', significant differences ($p < 0.05$) between 1-MCP treated and untreated fruit was observed on days 3 and 5.

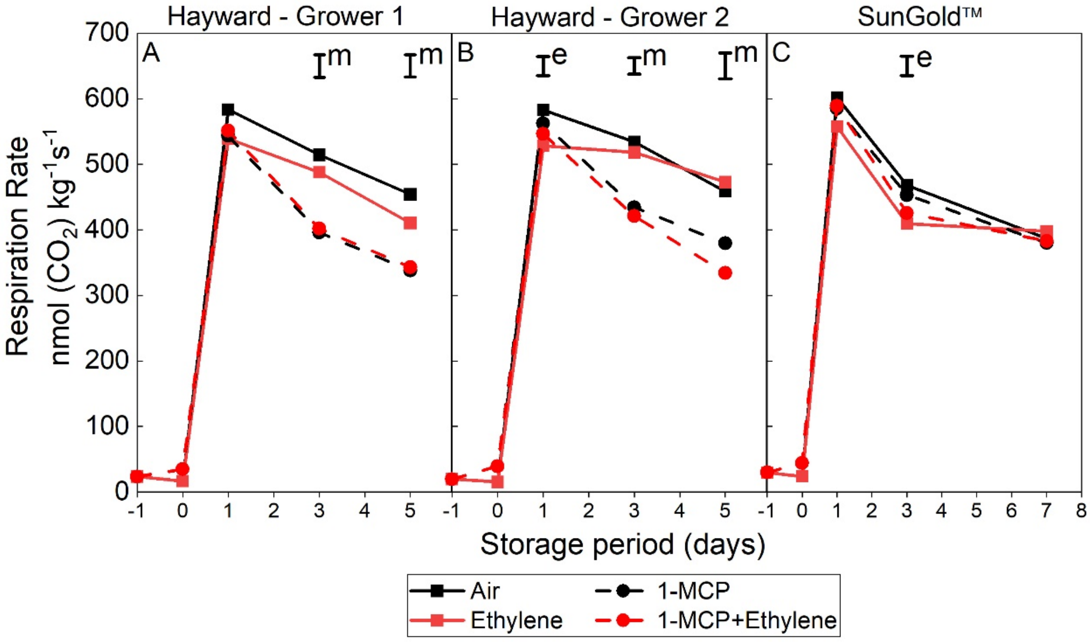


Figure 5.2: Respiration rate (CO_2 production) of 'Hayward' (A & B) and 'SunGold™' (C) kiwifruit as influenced by different treatment combinations at 33 °C and 95% RH after long-term refrigerated storage. Each data point represents average value of 12 fruit. Values at day -1 and 0 are CO_2 production at 0.5 and 4 °C respectively. The error bar represent LSD $_{0.05}$ at time points wherein 1-MCP (m) or ethylene (e) effect exists in influencing CO_2 production.

At 20 °C (Figure 5.3), the CO_2 production rate was highest on the initial day of exposure and ranged between 215 to 259 nmol kg^{-1} s^{-1} and 265 to 320 nmol kg^{-1} s^{-1} in grower 1 and 2 of 'Hayward' respectively and 236 to 283 nmol kg^{-1} s^{-1} in 'SunGold™'. From day 3 to day 16, CO_2 production ranged between 150 to 250 nmol kg^{-1} s^{-1} in all the treatment combinations in both cultivars. In 'Hayward' grower 1, 1-MCP treated fruit had reduced CO_2 production in comparison to the untreated fruits ($p < 0.05$). In 'SunGold™', 1-MCP treated fruit had reduced CO_2 production on day 1 while on day 16, the presence of ethylene in the storage atmosphere resulted in increased CO_2 production in both treated and untreated fruits.

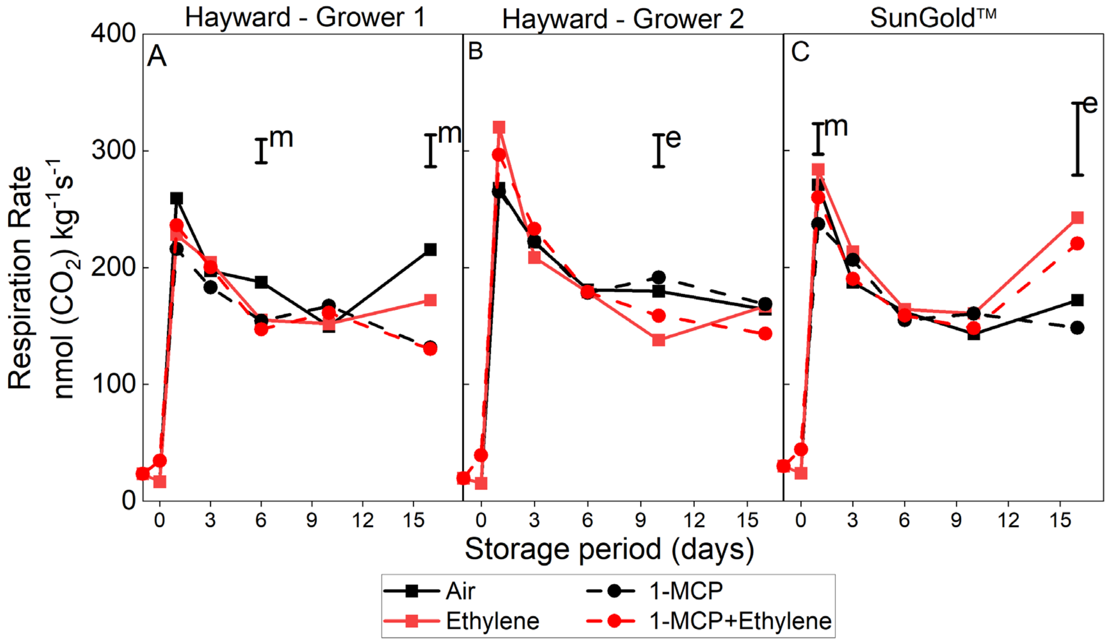


Figure 5.3: Respiration rate (CO_2 production) of 'Hayward' (A & B) and 'SunGold™' (C) kiwifruit as influenced by different treatment combinations at 20 °C and 95% RH after long-term refrigerated storage. Each data point represents average value of 12 fruit. Values at day -1 and 0 are CO_2 production at 0.5 and 4 °C respectively. The error bar represent LSD $_{0.05}$ at time points wherein 1-MCP (m) or ethylene (e) or treatment combinations (m*e) effect exists in influencing CO_2 production.

5.4.3 Destructive firmness

At 33 °C storage conditions, 1-MCP treated ‘Hayward’ fruit retained firmness throughout the experimental duration irrespective of the presence of 150 nL L^{-1} of exogenous ethylene (Figure 5.4). ‘Hayward’ fruit not treated with 1-MCP showed a drastic firmness drop at 33 °C reaching closer to overripe stage (0.4 kg$_f$) after 5 days. ‘SunGold™’ fruit were exposed to 33 °C at a lower firmness than ‘Hayward’ but failed to soften dramatically in any of the treatment combinations over 7 days.

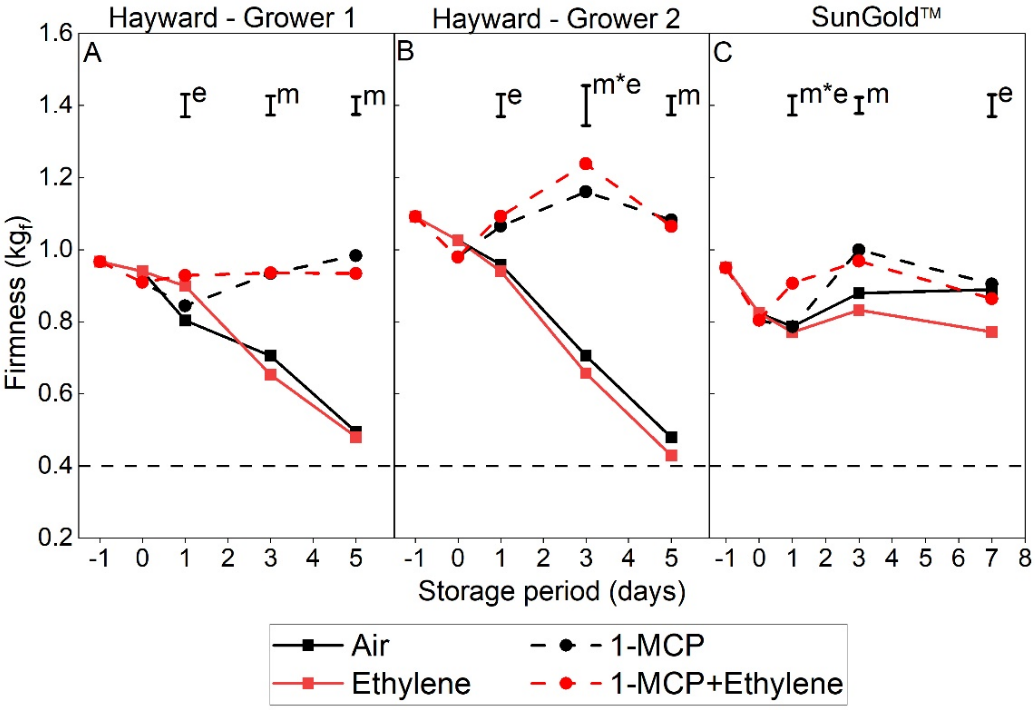


Figure 5.4: Firmness of ‘Hayward’ (A & B) and ‘SunGold™’ (C) kiwifruit as influenced by different treatment combinations at 33 °C and 95% RH after long-term refrigerated storage. Each data point represents average value of 30 fruit. The dashed horizontal line represents the lowest firmness value of the eating window. The error bar represent LSD $_{0.05}$ at time points wherein 1-MCP (m) or ethylene (e) or treatment combinations (m*e) effect exists in influencing firmness changes.

At 20 °C, in both cultivars, untreated fruit exposed to ethylene showed the highest firmness decline mostly being evident in ‘Hayward’ grower 2 and ‘SunGold™’ from day 6 to 16 of storage. In ‘Hayward’ grower 1, the firmness of 1-MCP treated fruit remained unaffected even in the presence of ethylene while in untreated fruit stored in either air or ethylene, firmness declined reaching closer to 0.6 kg$_f$ by day 16 of storage. In ‘Hayward’ grower 2 and ‘SunGold™’, firmness of both untreated and treated fruit dropped but was highest in untreated fruit exposed to ethylene.

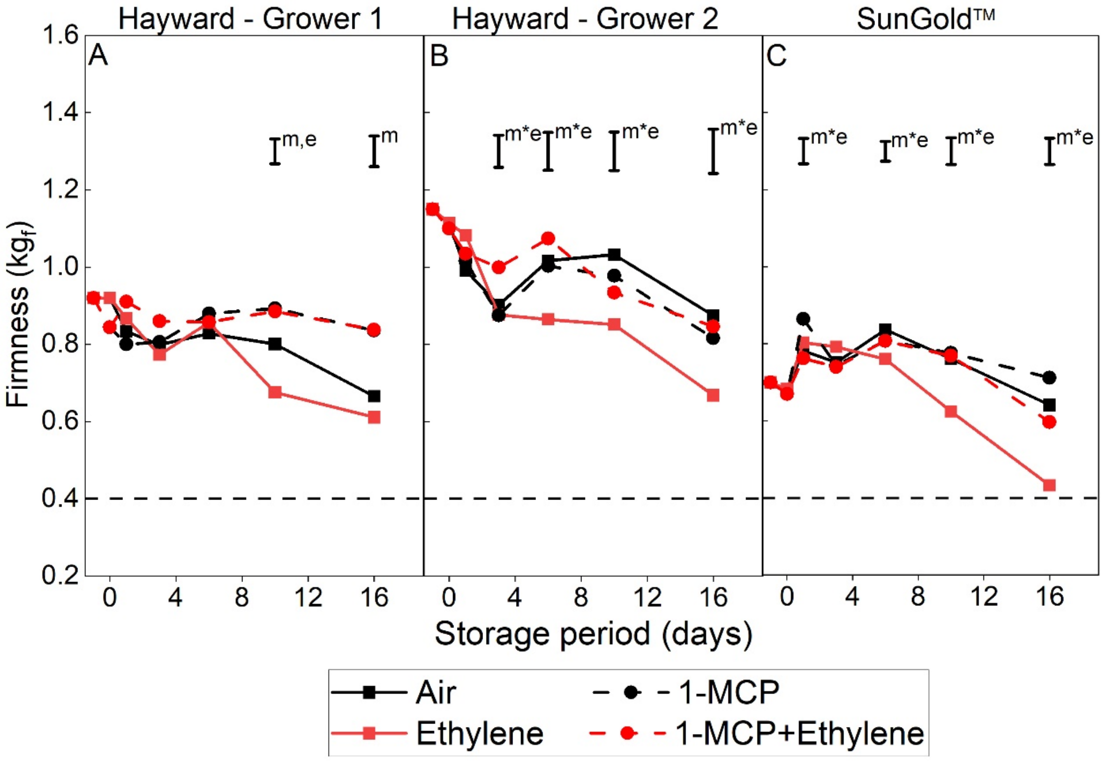


Figure 5.5: Firmness of ‘Hayward’ (A & B) and ‘SunGold™’ (C) kiwifruit as influenced by different treatment combinations at 20 °C and 95% RH after long-term refrigerated storage. Each data point represents average value of 30 fruit. The dashed horizontal line represents the lowest firmness value of the eating window. The error bar represent LSD $_{0.05}$ at time points wherein 1-MCP (m) or ethylene (e) or treatment combinations (m*e) effect exists in influencing firmness changes.

5.4.4 Flesh colour

Under both storage conditions for both cultivars, internal flesh °hue declined. At 33 °C (Figure 5.6), 1-MCP treated 'Hayward' fruit stored in air recorded the lowest flesh °hue in comparison to other treatment combinations at the end of storage. In 'SunGold™', untreated fruit exposed to ethylene had the lowest flesh °hue at the end of storage at 33 °C.

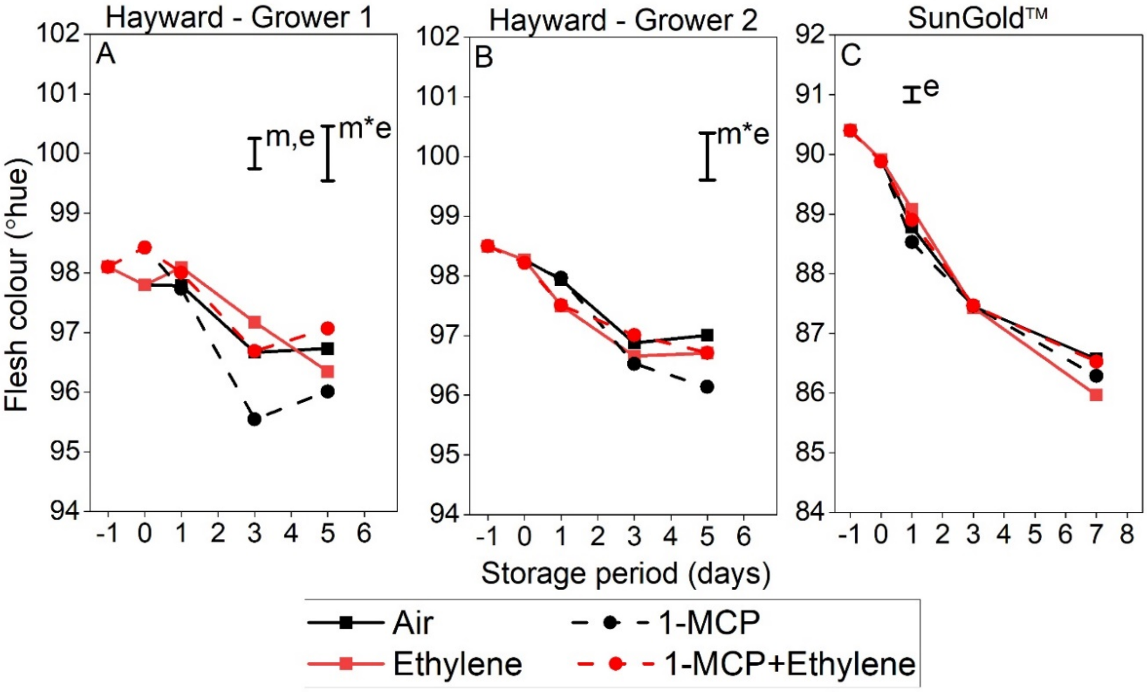


Figure 5.6: Flesh colour (°hue) in 'Hayward' (A & B) and 'SunGold™' (C) kiwifruit as influenced by different treatment combinations at 33 °C and 95% RH after long-term refrigerated storage. Each data point represents average value of 30 fruit. The error bar represent LSD $_{0.05}$ at time points wherein 1-MCP (m) or ethylene (e) or treatment combinations (m*e) effect exists in influencing flesh °hue.

At 20 °C (Figure 5.7), no significant difference in either of the treatment combinations existed for 'Hayward' grower 1. In 'Hayward' grower 2, on day 10 where significant difference existed between ethylene conditions, both treated and untreated fruit stored under ethylene free conditions recorded the lowest flesh °hue. In 'SunGold™', treatment combinations (m*e) was found to influence decline in flesh °hue on day 10 and 16 wherein untreated fruit exposed to ethylene recorded the lowest flesh °hue.

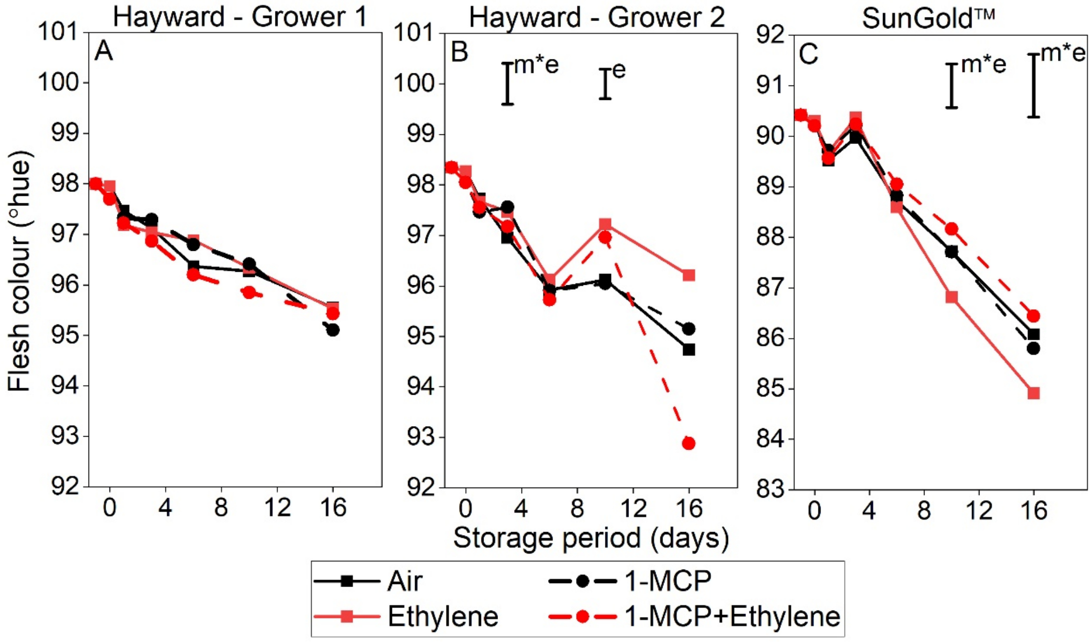


Figure 5.7: Flesh colour (°hue) in 'Hayward' (A & B) and 'SunGold™' (C) kiwifruit as influenced by different treatment combinations at 20 °C and 95% RH after long-term refrigerated storage. Each data point represents average value of 30 fruit. The error bar represent LSD $_{0.05}$ at time points wherein 1-MCP (m) or ethylene (e) or treatment combinations (m*e) effect exists in influencing flesh °hue.

5.4.5 Weight loss

As expected, weight loss increased over time reaching a range of 1.2 to 1.8% after 5 days at 33 °C (Figure 5.8) and 0.6 to 1% at 20 °C (Figure 5.9). Ethylene exposure (150 nL L^{-1}) and 1-MCP treatment had no influence on weight loss in either of the cultivars under both storage conditions.

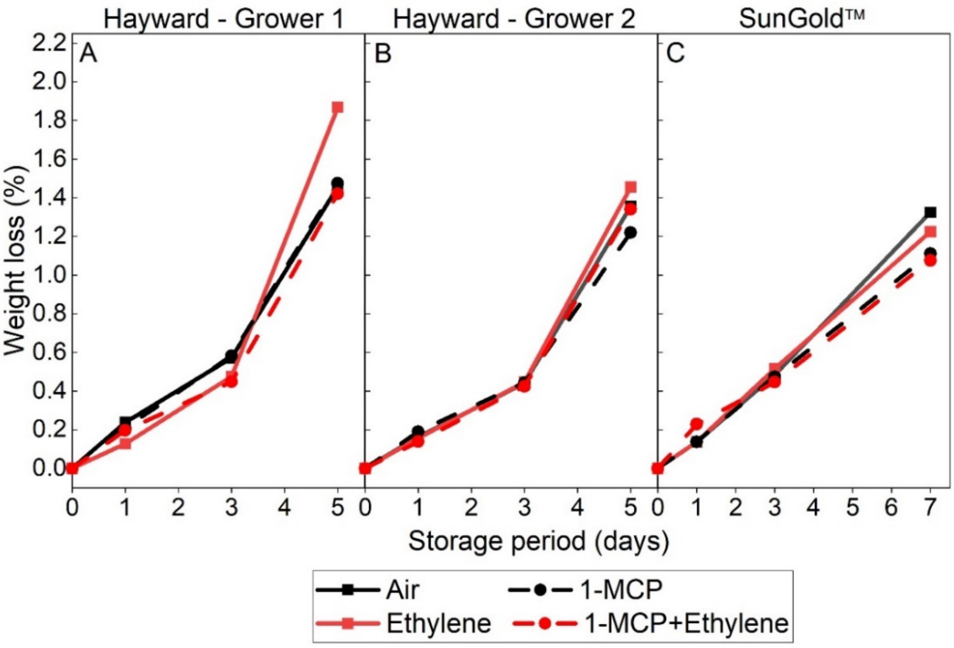


Figure 5.8: Weight loss (%) in 'Hayward' (A & B) and 'SunGold™' (C) kiwifruit as influenced by different treatment combinations at 33 °C and 95% RH after long-term refrigerated storage. Each data point represents average value of 12 fruit.

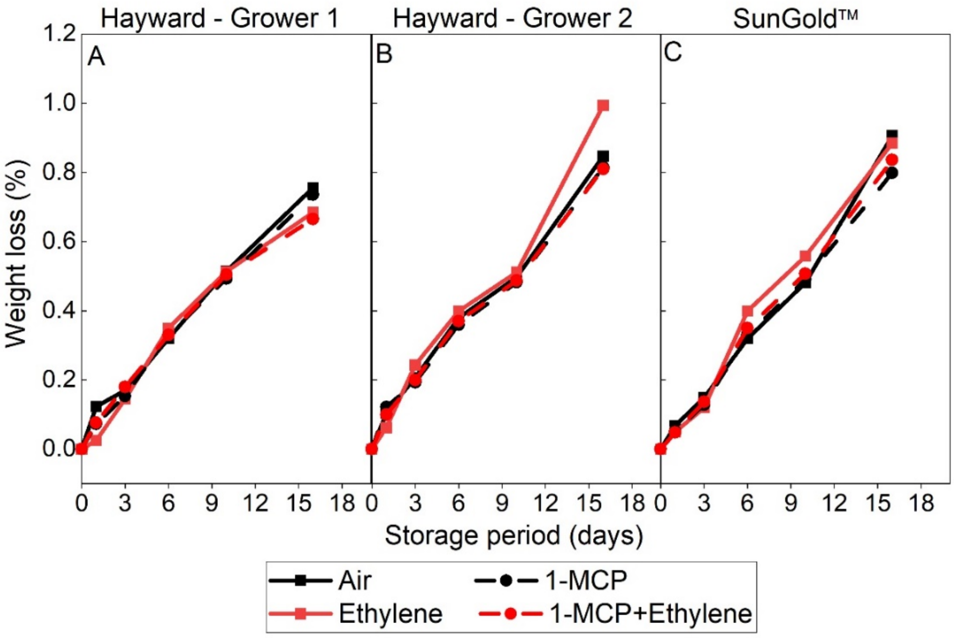


Figure 5.9: Weight loss (%) in 'Hayward' (A & B) and 'SunGold™' (C) kiwifruit as influenced by different treatment combinations at 20 °C and 95% RH after long-term refrigerated storage. Each data point represents average value of 12 fruit.

5.4.6 Storage rots

At both 33 and 20 °C storage conditions, highest incidence of rot was noted in ‘SunGold™’. In ‘Hayward’, incidence of rot was minimal at both 33 and 20 °C. In ‘SunGold™’, at 33 °C, highest rot incidence (15%) was noted on day 7 in untreated fruit exposed to ethylene. Similarly, at 20 °C, 1-MCP treated ‘SunGold™’ fruit exposed to ethylene recorded the highest incidence of rot (15%) on day 16 of storage.

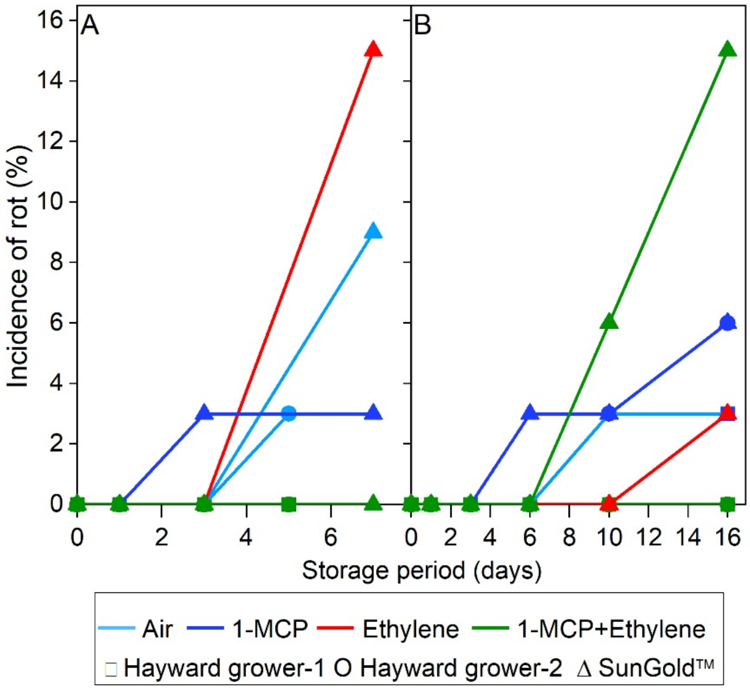


Figure 5.10: Incidence of rot (%) at 33 °C (A) and 20 °C (B) storage conditions. Assessment on rots were done from a total fruit population of 30 fruit under each measurement point under each treatment. Different treatment combinations are indicated by different colours and different growers or cultivars are indicated by different symbols.

5.5 Discussion

This investigation suggests that by suppressing ethylene perception by 1-MCP treatment, the eating firmness of kiwifruit at shelflife temperatures of 33 °C (Figure 5.4) can be extended. Moreover, our finding also elucidates that 1-MCP is effective in delaying the induction of autocatalytic ethylene synthesis in kiwifruit under conditions of continuous ethylene exposure even when applied after very long-term refrigerated storage. The response to exogenous ethylene was observed to be cultivar dependent with ‘Hayward’ being more susceptible to the ethylene exposure at both 20 and 33 °C. ‘SunGold™’ exhibited softening as a response to ethylene at 20 °C but interestingly remained less responsive to ethylene at 33 °C.

The softening trend observed in ‘Hayward’ at 33 °C elucidates that endogenous ethylene plays a major role in regulating softening for this cultivar at elevated temperatures. It was observed that when untreated ‘Hayward’ fruit were transferred to 33 °C, an immediate induction in autocatalytic ethylene production happened both at ethylene and ethylene free air resulting in rapid firmness decline. For example, ethylene concentration measured in untreated ‘Hayward’ fruit barrels (stored in ethylene free air) on day 2 of exposure at 33 °C was as high as 1000 nL L^{-1} confirming the initiation of autocatalytic ethylene production. In contrast, the maximum ethylene concentration recorded in 1-MCP treated ‘Hayward’ fruit barrels during 5 days of storage was 25 nL L^{-1}. A maximal ethylene concentration of 36 nL L^{-1} was recorded in ‘SunGold™’ stored barrels (measured in untreated fruit stored in ethylene free air) through 5 days of storage at 33 °C.

With ‘SunGold™’ not significantly responding to ethylene unlike ‘Hayward’ at 33 °C thus suggests that there may be a decline in sensitivity of ethylene receptors thereby delaying softening. The decline in sensitivity to ethylene analogue propylene at higher storage temperatures (above 35 °C) has previously been reported in ‘Hayward’ kiwifruit by Antunes and Sfakiotakis (2000). Similarly, reduced sensitivity to ethylene or propylene at higher storage temperatures have been reported in ‘Bartlett’ pears (Hansen, 1942; Maxie et al., 1974), 'Hass' avocados (Eaks, 1978) and tomatoes (Biggs et al., 1988), although the actual mechanism is not well elucidated.

Heat stress has been reported to affect membrane fluidity and functionality in plants (Bukhov et al., 1999; Balota et al., 2004; Dias et al., 2010). Cell membrane and in the specific endoplasmic reticulum is the location site for the ethylene receptors within the plant cell (Chen et al., 2002; Ma et al., 2006). The changes induced by heat stress on the cell membrane could plausibly alter either the composition or function of the ethylene receptors resulting in an insensitive response to ethylene as observed in 'SunGold™' at 33 °C. However, due to a lack of in-depth information, this just remains speculation. Although the efficacy of 1-MCP on delaying softening was not clear on 'SunGold™' at 33 °C, the treated fruit retaining firmness in the presence of ethylene at 20 °C confirmed the treatment efficacy on this cultivar.

The immediate initiation of ethylene autocatalysis in 'Hayward' kiwifruit (especially in fruit at ethylene free air) could be influenced by multiple factors. Firstly, the fruit were very close to the ripeness stage (≤ 1 kg_f firmness) at which ethylene autocatalysis is observed to happen (Stec et al., 1989; Ritenour et al., 1999; Schroder and Atkinson, 2006; Richardson et al., 2011; Atkinson and Schröder, 2016). Further, the duration of coolstorage could have contributed to rapid ethylene production since the lag phase for maximal ethylene production in 'Hayward' is shortened when exposed to higher storage temperatures after refrigerated storage (Hyodo et al., 1987; Ilina et al., 2010). This is due to the increased activity of aminocyclopropane-1-carboxylic acid synthase (ACS) and aminocyclopropane-1-carboxylic acid oxidase (ACO) enzymes after cool storage (Hyodo et al., 1987; Ilina et al., 2010). In addition, immediate ethylene induction in 'Hayward' could also be promoted to an extent as a stress response as generally evident in plants (Yang and Hoffman, 1984;

Vanderstraeten and Van Der Straeten, 2017). All these factors collectively might have led to an increased ethylene production in untreated ‘Hayward’ kiwifruit resulting in a drastic firmness decline at 33 °C.

The phase of transition from eating ripe to overripe stage in kiwifruit is observed to be accelerated when autocatalytic ethylene production is initiated (Bonghi et al., 1996; Ilina et al., 2010; Kim, 1999; Ritenour et al., 1999; Asiche et al., 2015) which synchronises to our study wherein a rapid transitions from eating ripe (1 kg_f) to over ripe (< 0.4 kg_f) stage happened in untreated ‘Hayward’ kiwifruit within 5 days. Ethylene accelerates softening in kiwifruit due to upregulation of genes involved in cell wall breakdown (Wang et al., 2000; Atkinson et al., 2011; Richardson et al., 2011; McAtee et al., 2015).

Interestingly the presence of ethylene in the storage environment did not further exaggerate the softening in ‘Hayward’ at 33 °C (Figure 5.4). A possibility for this could be the saturation of ethylene concentration within fruit tissue due to autocatalytic ethylene production and exogenous ethylene not causing any further changes in firmness as previously elucidated in apples by Johnston et al. (2009). However, this proposed theory remains speculation and needs further investigation.

1-MCP treated ‘Hayward’ fruit retained firmness throughout storage duration both at 33 and 20 °C indicating the inhibition of autocatalytic ethylene initiation throughout both storage conditions. The observed insensitive response of treated fruit to ethylene exposure proves that 1-MCP effectively blocked all the active ethylene receptors which were synthesised during cool storage and thereby prevented softening as previously postulated by Ilina et al. (2010) and Kim (1999).

It is known that 1-MCP represses ethylene regulated ripening processes not only by its receptor binding action but also by suppressing the expression of ethylene biosynthesis genes (Tatsuki and Endo, 2006). It is well understood that 'System 2' ethylene controls the expression of genes coding ethylene related receptors as well as the genes involved in ethylene autocatalysis (Whittaker et al., 1997; Xu et al., 2000; Alexander and Grierson, 2002; Ilina et al., 2010; Harb et al., 2012; Van de Poel et al., 2012). As observed by Yin et al. (2008), of the five receptors genes identified in kiwifruit, expression of *AdERS1a*, *AdETR2* and *AdETR3* increased with a concomitant rise in ethylene production and expression of these genes were repressed by 1-MCP treatment. Similar action of 1-MCP in suppressing ethylene receptor genes has been reported in other climacteric fruits such as in mangoes (Li et al., 2020), persimmons (Kou et al., 2020), durians (Thongkum et al., 2018) and apples (Varanasi et al., 2013; Tatsuki and Endo, 2007).

As stated above, 1-MCP is also known to inhibit the activity of aminocyclopropane-1-carboxylic acid synthase (ACS) and aminocyclopropane-1-carboxylic acid oxidase (ACO) enzymes which are involved in ethylene biosynthesis (Zhu et al., 2015; Facanha et al., 2019) by suppressing the accumulation of genes coding these enzymes. Ilina et al. (2010) observed in 'Hayward' kiwifruit that the activities of two ethylene synthesis related genes were repressed by 1-MCP treatment after 40 and 80 days of cold storage. A similar role of 1-MCP in suppressing genes related to ethylene autocatalysis has been reported in other climacteric fruits such as apples (Tatsuki et al., 2007; Yang et al., 2013) and pears (Yamane et al., 2007; Xu et al., 2018).

In kiwifruit, key biochemical changes concerning cell wall breakdown happening at the later stage of softening are increased bulging of the cell wall, depolymerisation of solubilised pectin and finally disintegration of middle lamella all of which are aided by autocatalytic ethylene production (MacRae and Redgwell, 1992). Of the several cell wall degrading enzymes present in kiwifruit, the activity of polygalacturonase (PG) enzyme was observed to increase at the later stage of ripening in concomitant to rise in autocatalytic ethylene (Bonghi et al., 1996; Wang et al., 2000). PG is involved in depolymerization of solubilised pectin at the later softening stage of kiwifruit (MacRae and Redgwell, 1992).

Of the three PG genes identified in kiwifruit, i.e. *CkPGA*, *CkPGB*, and *CkPGC*, the expression of *CkPGA*, *CkPGB* was observed to be associated with autocatalytic ethylene production. As observed by Atkinson et al. (2011), the expression of PG genes increased rapidly and peaked 12 h after ethylene treatment indicating the activity of this enzyme is modulated by ethylene. Therefore, by delaying the autocatalytic ethylene production using 1-MCP treatment, the suppression of genes relating to PG could be achieved resulting in the delay of the later phase of softening in kiwifruit.

In climacteric fruits, the efficacy of 1-MCP is found to decline with advancement in the stage of ripeness (Blankenship and Dole, 2003; Tatsuki et al., 2007; Jung and Watkins, 2014). It is hypothesised that with the advancement in ripening, the internal ethylene concentration (IEC) rises and contends with 1-MCP for binding receptors resulting in diminished 1-MCP treatment effect (Tatsuki et al., 2007; Nock and Watkins, 2013). Ilina et al. (2010) observed 1-MCP delayed softening in soft ‘Hayward’ kiwifruit (1-1.5 kg_f) even when applied after 120 days of coolstorage but concluded that the efficacy could diminish with the progression of softening.

Findings from this experiment partially agree with Illina et al. (2010) and further suggests that the efficacy of 1-MCP could be achieved on both ‘Hayward’ and

'SunGold™' kiwifruit even after a very long-term storage duration of 200 days without any diminished treatment effect as no differences existed in softening in 1-MCP treated fruit stored either in the presence or absence of ethylene. The results from this investigation also suggest that 1-MCP application any time before autocatalytic ethylene induction might result in the extension of the eating window.

It is postulated that in climacteric fruits, the rise in respiratory peak as a response to high temperature is a stress response mechanism (Lee and Young, 1984; Inaba and Chachin, 1989; Antunes and Sfakiotakis, 2000). This increased respiratory response may be independent of climacteric ethylene production since these two processes were observed to happen independently of each other under high temperatures (Hansen, 1942; Maxie et al., 1974; Eaks, 1978; Antunes and Sfakiotakis, 2000). The observation in this investigation agrees to the previous hypothesis that these two mechanisms happen independently since both 1-MCP treated and untreated fruit showed a similar rise in respiratory peak on the initial day of exposure although no ethylene production was observed to happen in 1-MCP treated fruit.

It was noted that the presence of propylene increased CO_2 production in 'Hayward' kiwifruit at 30 to 34 °C when compared to fruit stored under propylene-free conditions (Antunes and Sfakiotakis, 2000). However, no such respiratory variations were noted in this experiment although differences in softening were evident between ethylene and ethylene-free conditions. This might indicate that in kiwifruit, softening mechanism is highly sensitive to ethylene than the respiratory mechanism. Also, there could be a possibility that the ethylene concentration used in this experiment was not as high to induce significant stress on the kiwifruit respiratory mechanism. Although no differences in the respiratory peak were observed between treatments in both cultivars on the initial day of exposure, 1-MCP treated 'Hayward' kiwifruit exhibited reduced respiration rate on the later stage of storage while no treatment effect was noted in ‘SunGold™’.

It is reported that higher respiration rate causes increased accumulation of ethanol at the cellular level resulting in the development of off-flavours (Boeckx et al., 2019). A recent investigation by Ali et al. (2021) has showcased that 1-MCP treatment limited ethanol accumulation in ‘Bruno’ kiwifruit by suppressing the activity of pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH) enzymes which are involved in fermentative metabolism as well as resulted in reduced respiration rate compared to the untreated fruit.

The main reason for monitoring colour in this experiment was to identify whether exposure to 33 °C results in the incidence of flesh discolouration in ‘Hayward’ kiwifruit as observed previously (Chapter 4). The decline in °hue of 1-MCP treated fruit was rapid in comparison to untreated fruit in ‘Hayward’.1-MCP treatment is known to delay the degradation of chlorophyll by inhibiting the activity of genes involved in the chlorophyll degradative process (Boquete et al., 2004; Lv et al., 2020; Zhao et al., 2020). However, it is also reported that 1-MCP could induce flesh browning as observed by Jung and Watkins (2011) in ‘Empire’ apples and these authors postulated that the inhibition of ripening metabolism could have resulted in stress resulting in increased activity of polyphenol oxidase activity (PPO) subsequently causing flesh browning incidence.

In the current study, no visible symptoms of flesh discolouration were noted and the actual mechanism leading to the rapid decline in °hue because of 1-MCP treatment is unknown. The similar pattern of rapid decline in °hue in ‘SunGold™’ at both 33 and 20 °C could be an indication that it may be due to natural ripening process since ethylene treated fruit in 20 °C showed more rapid decline in °hue in concomitant to firmness loss.

In kiwifruit, significant amount of water loss results in shrivel incidence (Burdon et al., 2014b). There was no incidence of shrivelling observed in the current study under both storage conditions. It is presumed that the higher humidity range (95%) maintained could have resulted in minimal weight loss and this could have also led to not much differences in weight loss between the 1-MCP treated and untreated fruit. Therefore, a better conclusion on the efficacy of 1-MCP treatment on preserving weight loss in kiwifruit could not be confirmed from the current experiment.

5.6 Conclusion

This chapter showcases the influence of ethylene on postharvest physiology and quality of kiwifruit under tropical conditions. The existence of a differential pattern of ripening responses between ‘Hayward’ and ‘SunGold™’ under high temperature is also elucidated. The results indicate 1-MCP at a concentration of 750 nL L^{-1} is effective on kiwifruit even after very long-term refrigerated storage as well as at tropical shelflife conditions. Investigations involving exposure of kiwifruit to different concentrations of ethylene at a wider range of tropical temperatures are essential for gaining a broader understanding of kiwifruit physiological mechanisms as a response to heat stress. The proposed reason for ethylene exposure not exaggerating softening of eating ripe ‘Hayward’ kiwifruit at high temperatures needs to be further confirmed. In addition, different 1-MCP application strategies which are industrially adoptable such as cool storing 1-MCP treated soft kiwifruit and later exposure to high temperatures could be investigated along with organoleptic studies to identify the impact of 1-MCP on kiwifruit taste under tropical conditions.

Chapter 6: High-temperature-time regime causing detrimental outcomes in kiwifruit

6.1 Introduction

Temperatures exceeding the optimum growth range are perceived as heat stress by plants (Kotak et al., 2007; Wahid et al., 2007; Hassan et al., 2021). Plants due to their sessile nature have developed an ability to survive at temperatures closely above optimal range due to basal thermotolerance and in addition, may survive at lethal temperatures due to acquired thermotolerance (Larkindale et al., 2005; Ruelland and Zachowski, 2010; Song et al., 2012). However, a sudden rise in temperatures to a very extreme range or prolonged exposure to supra-optimal temperatures could lead to irrecoverable deleterious consequences causing cell damage and cell death (Wahid et al., 2007; Driedonks et al., 2015; Jagadish et al., 2021). Cell death under heat stress is due to several processes such as loss of membrane integrity, oxidation of proteins and lipids and damage to the DNA and RNA (Schöffl et al., 1999; Wahid et al., 2007; Driedonks et al., 2015).

The extent of tissue damage caused by heat stress is dependent on the exposure duration. Short-term exposure could be recoverable, whilst long-term exposure is unrecoverable (Schöffl et al., 1999; Wahid et al., 2007; Golam et al., 2012). Postharvest fruit responses to short-term heat stress (either as hot water, air or vapour treatments) have extensively been investigated due to the beneficial effect of heat treatments on pest and disease reduction as well as to improve fruit responses to various stresses during storage (Lay-Yee and Whiting, 1996; Lurie, 1998; Beirao-da-Costa et al., 2006). While sufficient information exists on the impact of acute heat stress on postharvest fruit ripening mechanisms, studies focusing on the consequences of chronic heat stress on fruit physiological mechanisms as well as its influence on quality are limited.

Prolonged heat stress suffered by fruit becomes apparent in the form of skin or flesh discolouration (Klein and Lurie., 1992; Song et al., 2001) either upon exposure or during subsequent storage (Fan et al., 2005). Exposure of fruit to high temperatures for a longer duration is often prevalent in countries wherein traditional retailing systems such as wet markets dominate fruit sales (Punter et al., 2018). Further, due to temperature breaks in the supply chain, fruit may also get exposed to intermittent high temperatures before retail sales, which is an issue in both traditional and modern fruit supply chains (Tsai and Lin, 2019; Loisel et al., 2021).

Temperature breaks often occur at the points of fruit loading or unloading, during transportation and wholesale handling (Freiboth et al., 2013; Goedhals-Gerber et al., 2017). Fruit exposure to high temperatures even for a short duration before returning to optimal storage temperatures could plausibly result in detrimental outcomes. Hence identifying the safest time frame of exposure to high temperatures beyond which fruit are deemed unsaleable even if subsequently cool stored could be crucial for the fruit industries to reduce fruit losses in supply chains wherein temperatures breaks are frequent.

Earlier, in Chapter 4, the influence of tropical conditions i.e. 33 °C and 87% RH (hot/humid) and 40 °C and 30% RH (hot/dry) on kiwifruit physiology and quality was investigated. At 40 °C, the CO_2 production peaked after the initial 12 h of exposure and later plummeted to close to nil by after 120 h (Figure 4.2). This reduction in CO_2 production could potentially be an indicator of cell death. Meanwhile, at 33 °C, CO_2 production remained closer to the peak throughout 120 h of storage. While there is evidence that 40 °C may have a lethal impact on kiwifruit, and 33 °C may not, what is not known is the responses of kiwifruit (at edible ripeness) to intermediate conditions. Hence, this investigation aims to identify the combination of high temperatures and time of exposure that may significantly trigger detrimental physiological and quality outcomes for kiwifruit. Besides, the consequences of different durations of high temperature exposure in influencing kiwifruit quality changes upon subsequent storage will also be investigated.

6.2 Materials and Methods

6.2.1 Experimental design

Four high-temperature storage conditions i.e. 33, 36, 38 and 40 °C with ± 0.5 °C were established. Relative humidity was chosen not to be controlled in this experiment to achieve a consistent temperature throughout the experimental period. The experiment was conducted first for ‘Hayward’ followed by ‘SunGold™’. A total of 10 individual fruit trays of 30 fruit/grower packed without polyliners were transferred into each of the storage conditions.

Fruit physiology (CO_2 production), quality parameters (weight, colour, firmness) and heat injury incidence were initially recorded at time point 0 (initial CO_2 production measured at 0.5 °C and initial quality after overnight equilibration to room temperature) and monitored twice on the first day of exposure (at 6 and 12 h) and once on subsequent days (24 to 96 h) of the experiment. During exposure, CO_2 production was measured within the storage rooms and later the fruit were equilibrated to room temperature for 3 h before quality assessments.

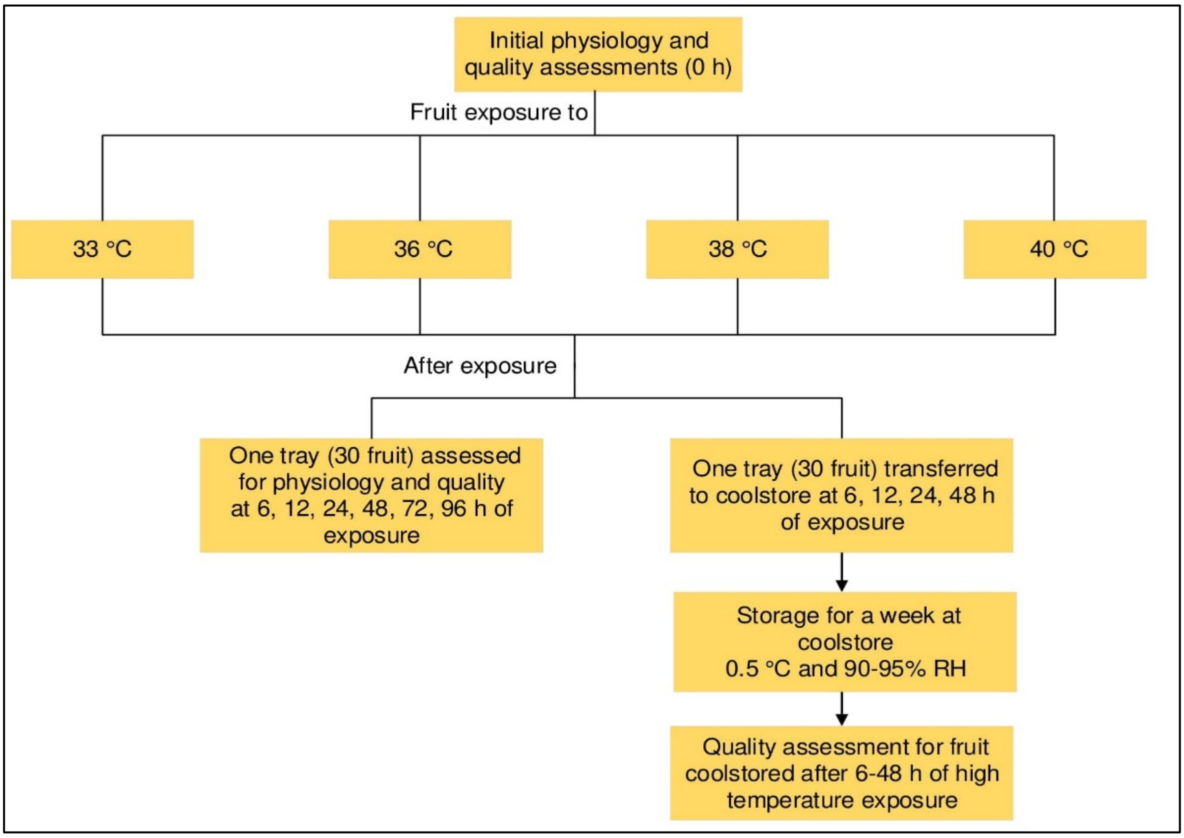


Figure 6.1: Schematic representation of the experimental plan. One set of fruit (one tray of 30 fruit/grower/cultivar) were assessed for physiology and quality after 0, 6, 12, 24, 48, 72 and 96 h of exposure to 33-40 °C. Another set of fruit (one tray of 30 fruit/grower/cultivar) were transferred to coolstore after 0, 6, 12, 24, 48 h of exposure to 33-40 °C and assessed for quality after a week of storage.

In addition, another set of fruit (one tray of 30 fruit/grower/cultivar) exposed high temperatures (33-40 °C) for 6, 12, 24 and 48 h were transferred back to coolstore (0.5 °C and 95 ± 5% RH) and assessed for quality a week later (Figure 6.1). Comparisons in fruit quality parameters between fruit assessed immediately after high temperature exposure or fruit coolstored for a consequent week after equivalent high temperature exposure was conducted to identify if these short-term exposures to high temperatures influenced quality changes during consequent coolstorage. Ethylene concentrations within the cool room in which high temperature exposed fruit were stored was monitored to check for any potential influence on fruit quality change caused by exogenous ethylene. Room concentrations were measured in continuous flow mode in photoacoustic ethylene analysing equipment (ETD- 300, Sensor Sense B.V., Nijmegen) which has a sensitivity of 0.3 nL L^{-1} to ethylene (Gwanpua et al., 2018a).

6.2.2 Plant material

Kiwifruit of cultivars 'Hayward' *(Actinidia deliciosa*) and 'Zesy002' ('SunGold™', *Actinidia chinensis*) each from three different growers were sourced from commercial coolstores located in the Bay of Plenty region, New Zealand. The fruit arrived in a refrigerated vehicle at Massey University postharvest laboratory, Palmerston North on 3rd of September 2019 (ISO week 36). The fruit were class 1 grade and count size 33. 'Hayward' arrived packed in loose packed 10.5 kg MB boxes while 'SunGold™' were in loose packed 6.5 kg ML boxes. Immediately upon arrival, fruit were placed into coolstore (at 0.5 °C and 95 ± 5% RH). Information regarding harvest date and quality attributes at harvest was retrieved from Zespri® information systems.

A week before the start of the experiment, fruit from each grower were randomised under ambient conditions (20 °C and 75 % RH) and repacked from MB/ML boxes into labelled single-layered IT trays of 30 fruit with polylines and transferred back to the cool store (0.5 °C and 95 ± 5% RH). The fruit trays were labelled according to the temperature to which they are exposed during the experiment as well as the time point at which a tray is drawn for assessments. A day before start of the experiment, respiration rate measurement was conducted within the coolstore and later, the fruit were equilibrated to room temperature before assessing for initial quality.

On the start day of the experiment, after removal of the polyliners, the initial weight of each fruit tray was recorded within coolstore and later the fruit trays were transferred into temperature-controlled rooms maintained consistently at either 33, 36, 38 and 40 °C. Data loggers (I-button/1 wire DS1923, Maximum integrated, USA) with a measurement accuracy of ± 0.5 °C and ± 5% for RH, set at a measurement frequency of 10 minutes were placed in fruit trays to monitor storage conditions.

6.2.3 Fruit physiology and quality assessments

6.2.3.1 Respiration rate

Respiration rate was measured as described in Chapter 4 (Section 4.2.2.1) with a few modifications. A total of six replicates (each consisting of 4 fruit) per grower under each of the storage conditions were enclosed separately within an 1800 mL airtight glass jar and assessed for CO_2 production. The samples were selected on the initial day, weighed, labelled and the same set of samples were assessed for respiration rate throughout the experimental duration.

6.2.3.2 Fruit weight loss

Weight loss of fruit trays was assessed as described in Chapter 4 (Section 4.2.2.2).

6.2.3.3 Flesh colour (°hue)

Flesh colour (°hue) was measured as described in Chapter 5 (Section 5.2.6) with a few modifications. First slices of the skin of 2 mm at two equatorial regions perpendicular to each other was removed. Two measurements from each side of the sliced surface were taken and averaged to obtain a single measurement. At each assessment point, 15 fruit per grower were assessed.

6.2.3.4 Fruit firmness

Flesh firmness was assessed as described in Chapter 4 (Section 4.2.2.3).

6.2.3.5 Heat injury incidence

Fruit were cut at the equatorial region and assessed visually for any incidence of heat injury and expressed as a percentage of the total fruit population (30 fruit per measurement).

6.2.4 Data Analysis

Significant effects of treatments on fruit physiology and quality were determined using the General Linear Model (GLM) procedure in Minitab (Minitab Inc., Version 16.1, State College, Pennsylvania, USA) except for weight loss and incidence of heat injury. Data obtained from each of the grower was analysed separately, considering storage temperature and exposure time as controlled variables. Once significant differences were determined, Tukey's honestly significant difference (HSD) test at 95% confidence was used to differentiate treatment means. A two-sample t-test in Minitab (Minitab Inc., Version 16.1, State College, Pennsylvania, USA) was used to identify significant differences in fruit quality parameters between fruit that were assessed immediately after high temperature exposure and fruit coolstored for a consequent week, after equivalent high temperature exposure.

6.3 Results

6.3.1 Initial fruit quality attributes

In 'Hayward', fruit from grower 3 recorded the highest at-harvest firmness while fruit from grower 1 was the firmest at the start of the experiment. For 'SunGold™', fruit from grower 5 were the firmest at-harvest and fruit from grower 6 were the firmest at the start of the experiment (Table 6.1). No significant differences ($p > 0.05$) in SSC between growers existed for either of the cultivars at start of the experiment. Fruit from growers 1 and 6 of ‘Hayward’ and ‘SunGold™’, respectively were less ripe in comparison to other growers at the time of exposure to high temperatures.

Table 6.1: Average initial fruit quality attributes after harvest and after storage. Values appended by a different letter in the same row are significantly different ($p < 0.05$). Presented are averaged values of 30 fruit (n=30).

		Hayward			**SunGold™**		
Grower Number		G1	G2	G3	G4	G5	G6
Harvest week (ISO)		16	16	16	20	20	20
Weeks of cool storage		21	21	21	19	19	19
Firmness	At harvest	7.6^{b}	7.7^{ab}	7.9^{a}	7.2^{a}	7.4^{a}	6.6^{b}
	After storage	1.5^{a}	1^{c}	1.2^{b}	0.8^{b}	0.7^{c}	1^{a}
SSC (°Brix)	At harvest	8.8	8.3	8.6	11.1^{a}	9.3^{c}	10^{b}
	After storage	14.4	15	14.3	16.1	15.8	15.5
Dry matter (%)	At harvest	18.5^{a}	17.9^{b}	18.3^{ab}	19.4^{a}	18.5^{b}	18.7^{b}
Fruit weight (g)	At harvest	129.8^{a}	125.3^{a}	117.9^{b}	137.7^{a}	141.1^{a}	125.9^{b}
Flesh colour (°hue)	At harvest	-	-	-	101.2^{b}	102.3^{a}	101.5^{b}
	After storage	98.9	98	100.3	91.4	91.3	91.6

6.3.2 Storage conditions

A week before the start of the experiment, high temperature conditions were established to check for consistency. Set temperatures were achieved in each of the storage rooms throughout the experiment with ± 0.5 °C variations (Figure 6.2), except for the 33 °C conditions (Figure 6.2A). For the 33 °C conditions, the temperature dropped to 30 °C for approximately 4 h on day 4 of the experiment. Relative humidity was not controlled in this experiment and as a result, variation in relative humidity existed under each of the conditions and ranged 15 to 38%, 26 to 52%, 35 to 53% and 22 to 38% at 33, 36, 38 and 40 °C, respectively.

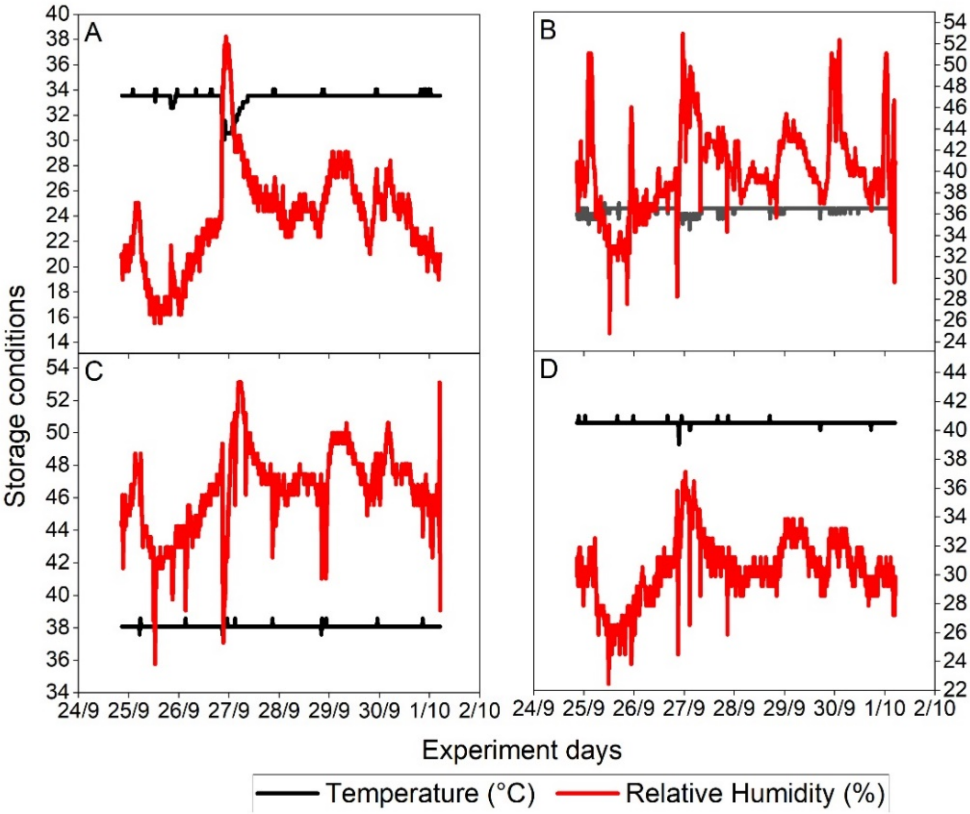


Figure 6.2: Storage conditions (temperature and relative humidity) monitored for the treatments described as 33 °C (A), 36 °C (B), 38 °C (C), and 40 °C (D) during the experiment.

6.3.3 Respiration rate

In both 'Hayward' and 'SunGold™', the CO_2 production was maximum after an initial 12 h of exposure (Figure 6.3). Later a consistent decline at 33-38 °C and a rapid decline at 40 °C was observed. As expected, the CO_2 peak observed in the initial 12 h was highest at 40 °C followed by 38, 36 and 33 °C. After 120 h of exposure, CO_2 production in fruit stored at 33-38 °C remained consistent and closer to the peak respiration rate but at 40 °C, respiration rate plummeted closer to 0 nmol kg^{-1} s^{-1} as observed in the earlier investigation (Figure 4.2). In both cultivars, temperature and time significantly influenced CO_2 production rate ($p < 0.05$) whereas no significant differences existed between growers ($p > 0.05$).

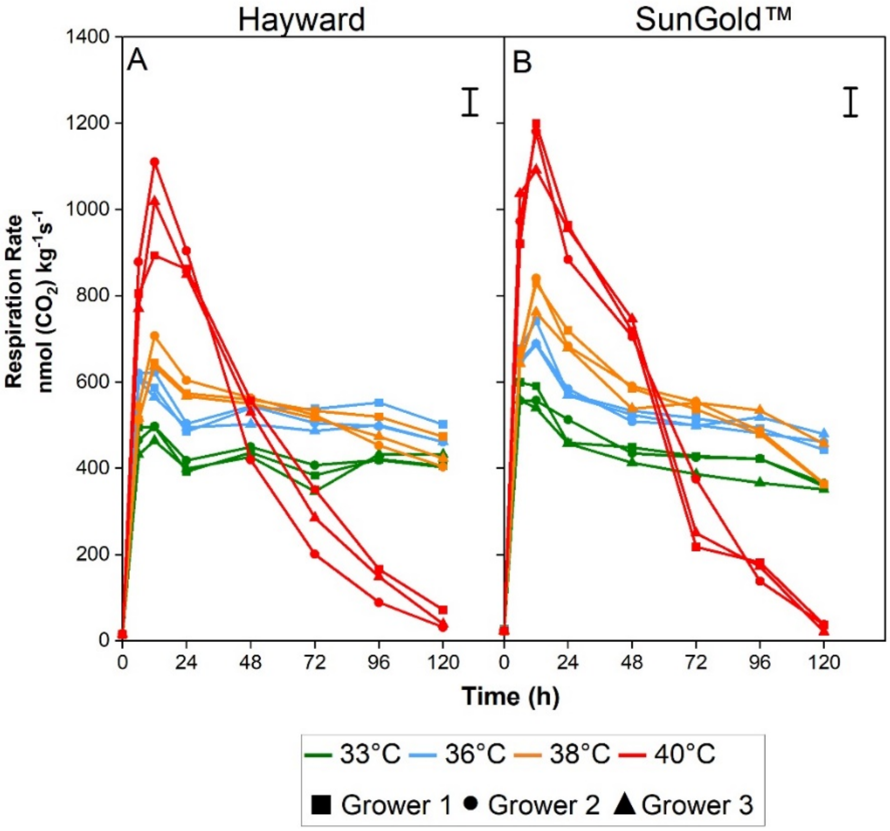


Figure 6.3: Respiration rate of 'Hayward' (A) and 'SunGold™' (B) kiwifruit at high temperatures. Each data point represents the average CO_2 production of six replicates (n=6). The initial value at time point 0 represents CO_2 production at 0.5 °C. The error bar represent $LSD_{0.05}$ for the influence of temperature-time interaction on CO_2 production.

6.3.4 Weight loss (%)

Percentage loss in weight was concomitant to exposed temperature, increasing linearly along with storage time (Figure 6.4). After the initial 12 h of exposure, approximately 0.5% loss in weight was recorded under all four storage conditions in both cultivars, which subsequently increased with storage period reaching approximately 4% at 40 °C, 3.5% at 38 °C, 3% at 36 °C and 2.5% at 33 °C at the end of 96 h storage period. Water vapour pressure deficit (WVPD) under each storage condition was calculated by considering the averaged value of temperature and relative humidity prevalent during the experiment period. A WVPD of 3.53, 3.74, 3.92 and 5.13 was obtained for 33, 36, 38 and 40 °C conditions, respectively indicating that with increase in WVPD, weight loss increased.

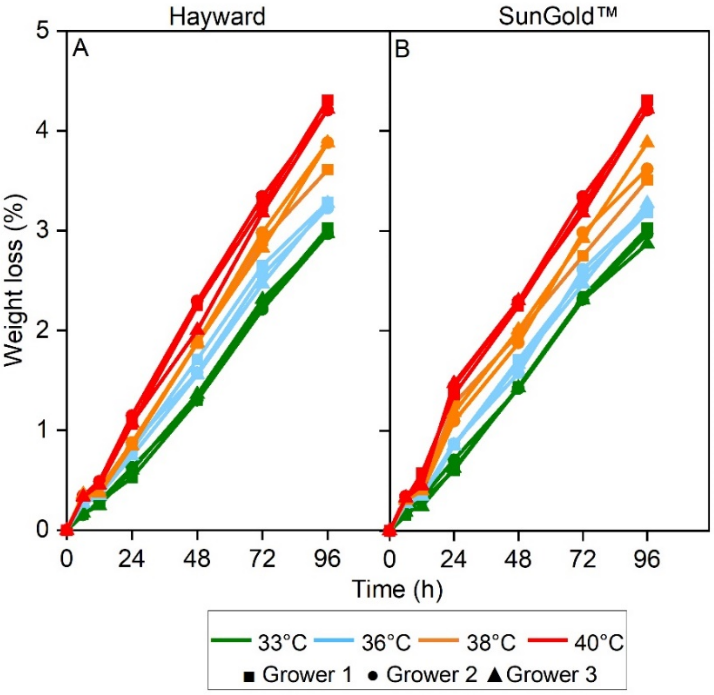


Figure 6.4: Weight loss (%) in Hayward (A) and SunGold™ (B) at different ranges of high temperatures.

6.3.5 Fruit firmness

In ‘Hayward’ (Figure 6.5), after 12 and 24 h of exposure, fruit stored at 40 °C recorded the lowest firmness followed by fruit at 38 °C. Later, during subsequent storage, fruit stored at 33 and 36 °C continued to reduced firmness with fruit stored at 33 °C recording the lowest firmness (0.42 to 0.5 kg$_f$) after 96 h of exposure followed by fruit at 36 °C (0.52 to 0.62 kg_f). Fruit stored at 38 and 40 °C however exhibited a slower firmness decline from 24-96 h and ended remaining firmer than the fruit at 33 and 36 °C at 96 h. After 96 h of storage, firmness in fruit stored at 38 and 40 °C ranged 0.61 to 0.74 and 0.61 to 0.96 kg_f, respectively.

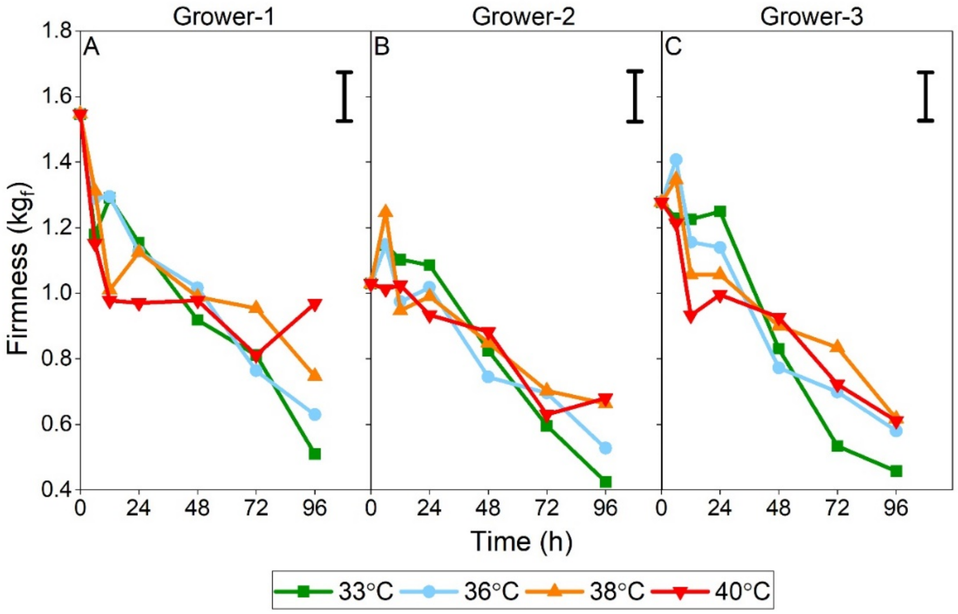


Figure 6.5: Firmness of 'Hayward' kiwifruit during exposure to high temperatures. Each data point represents an average value of 30 fruit (n=30). The error bars represent $LSD_{0.05}$ for the influence of temperature-time interaction on firmness changes.

In 'SunGold™' (Figure 6.6), firmness decline was highest in fruit stored at 40 °C followed by 38 °C, while fruit stored at 33 and 36 °C remained at a similar to initial firmness throughout the experimental period. Grower 6 which was the firmest (1.04 kg_f) at experiment initiation did not have differential softening irrespective of storage conditions ($p > 0.05$).

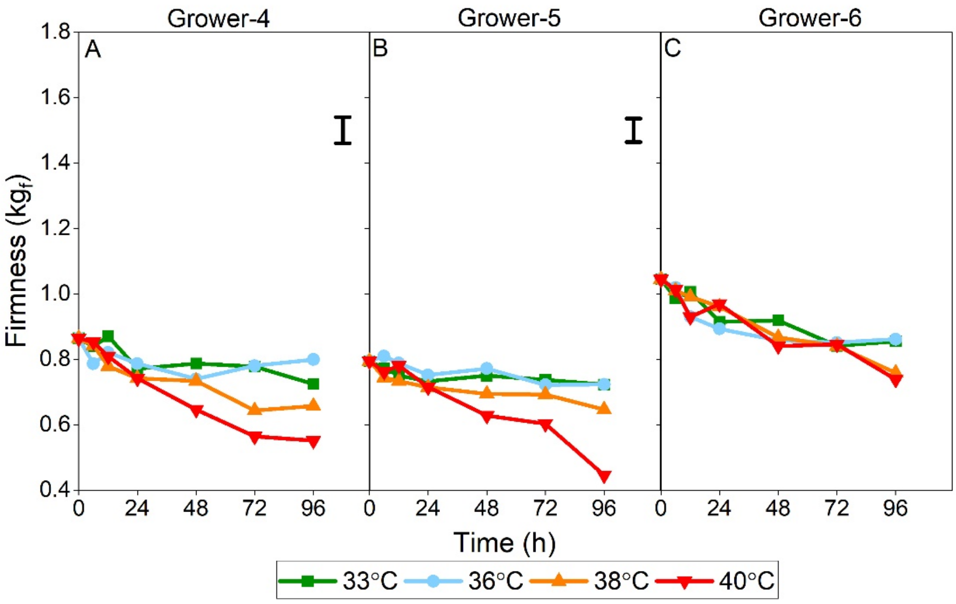


Figure 6.6: Firmness of 'SunGold™' kiwifruit during exposure to high temperatures. Each data point represents an average value of 30 fruit (n=30). The error bar represent LSD$_{0.05}$ for the influence of temperature-time interaction on firmness changes.

6.3.6 Flesh colour (°hue)

In both cultivars, exposure to high temperature conditions caused a decline in °hue with storage time (Figures 6.7-6.8). At 40 °C, a higher magnitude drop in °hue was observed in all three growers for 'Hayward' in comparison to other conditions (Figure 6.7). Storage temperatures-time interaction significantly influenced flesh colour changes for both cultivars.

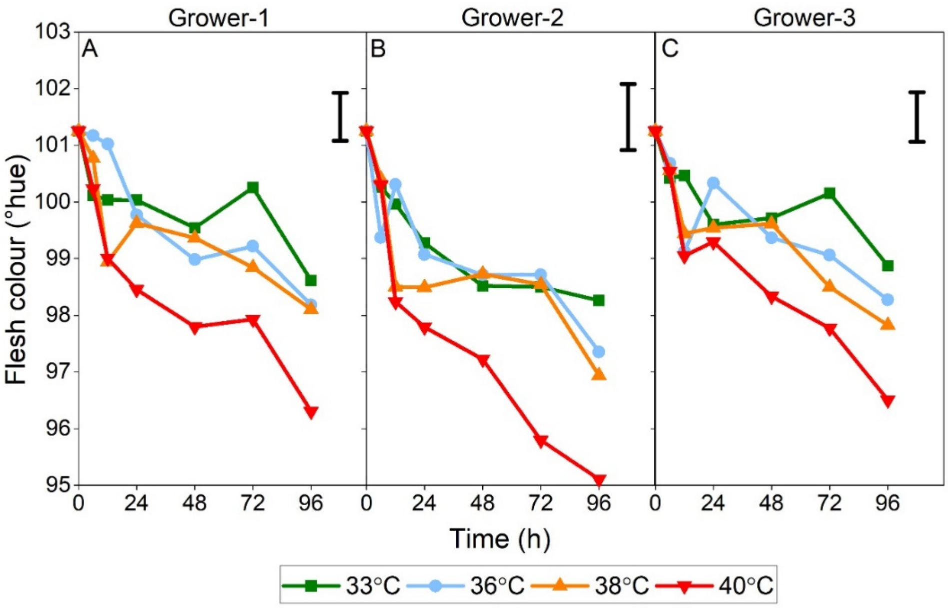


Figure 6.7: Flesh colour (°hue) in 'Hayward' kiwifruit during exposure to high temperatures. Each data point represents an average value of 15 fruit (n=15). The error bar represent LSD$_{0.05}$ for the influence of temperature-time interaction on flesh °hue changes.

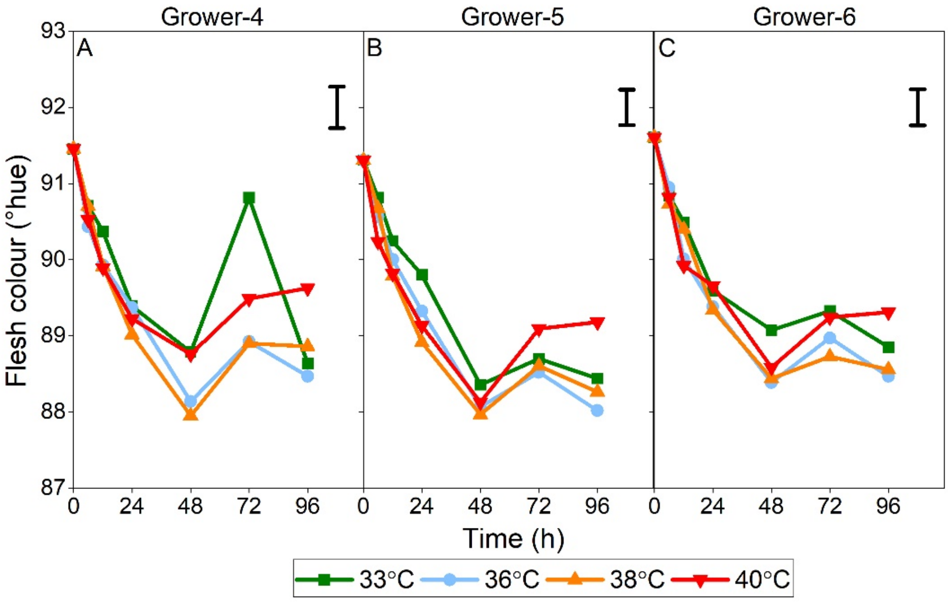


Figure 6.8: Flesh colour (°hue) in 'SunGold™' kiwifruit during exposure to high temperatures. Each data point represents an average value of 15 fruit (n=15). The error bar represent LSD$_{0.05}$ for the influence of temperature-time interaction on flesh °hue changes.

6.3.7 Heat injury incidence

The most common visible symptoms of heat injury noted in this experiment were water soaking (in both cultivars) and flesh discolouration (in 'Hayward'). In 'Hayward', symptoms of flesh discolouration (in the form of yellowing) along with water soaking was observed to spread from the centre to the peripheral region of the fruit (Figure 6.11A) and first became evident in fruit from grower 2 after 48 h at 40 °C and later in all fruit at 33-40 °C. Most of the fruit that exhibited flesh yellowing incidence at 72 and 96 h at 40 °C had developed a cavity airspace close to the core (Figure 6.12A).

For 'SunGold™', fruit from grower 4 was observed to be more susceptible to flesh water soaking symptoms (Figure 6.11B) at 40 °C under which the incidence reached close to 80% after 96 h of storage. For growers 5 and 6 fruit, the incidence was closer to 40% after 96 h at 40 °C. Like 'Hayward', most of the fruit exhibiting water-soaked symptom at 72 and 96 h at 40 °C had also developed cavities (Figure 6.12B).

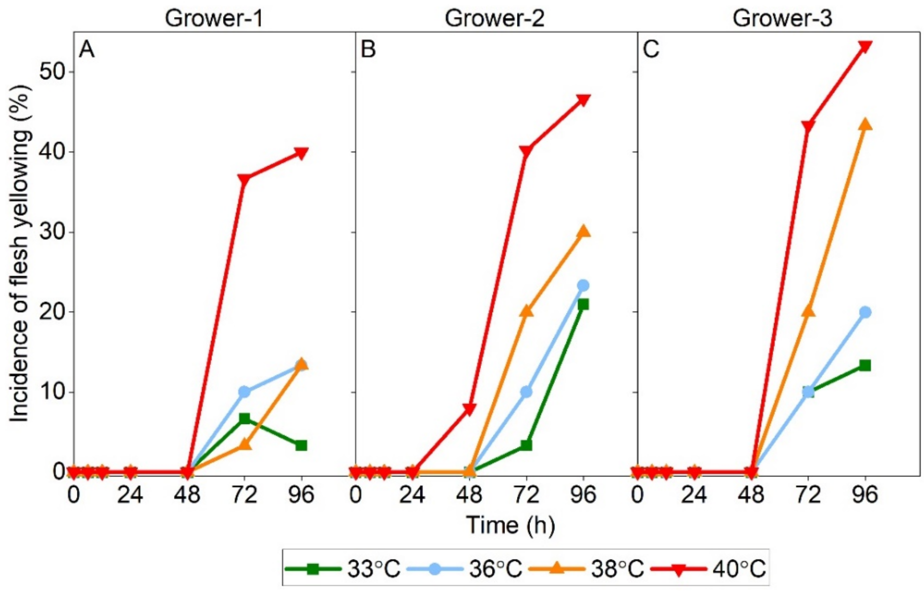


Figure 6.9: Incidence of flesh yellowing observed in 'Hayward' under different high temperature conditions. Each data point represents the incidence of heat injury in a population of 30 fruit (n=30).

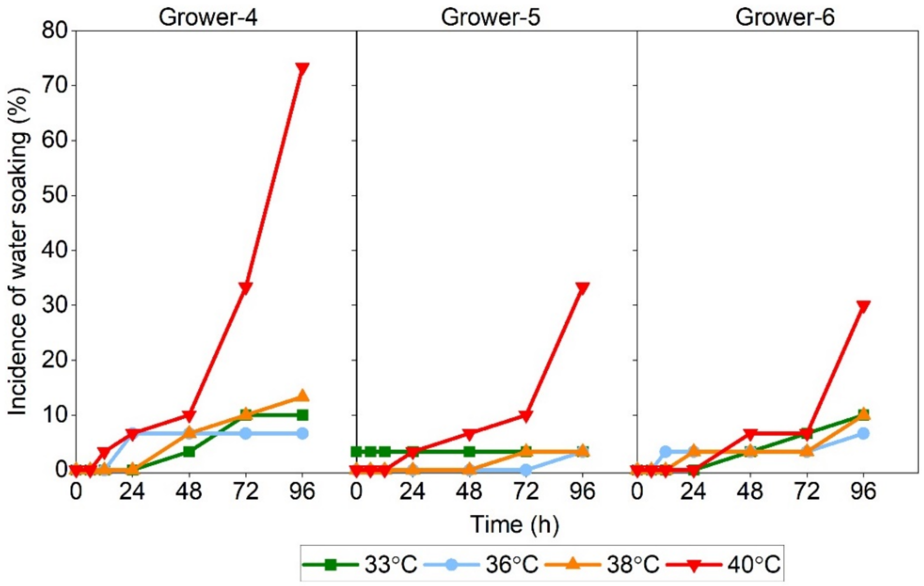


Figure 6.10: Incidence of flesh water soaked symptoms observed in 'SunGold™' under different high temperature conditions. Each data point represents the incidence of heat injury in a population of 30 fruit (n=30).

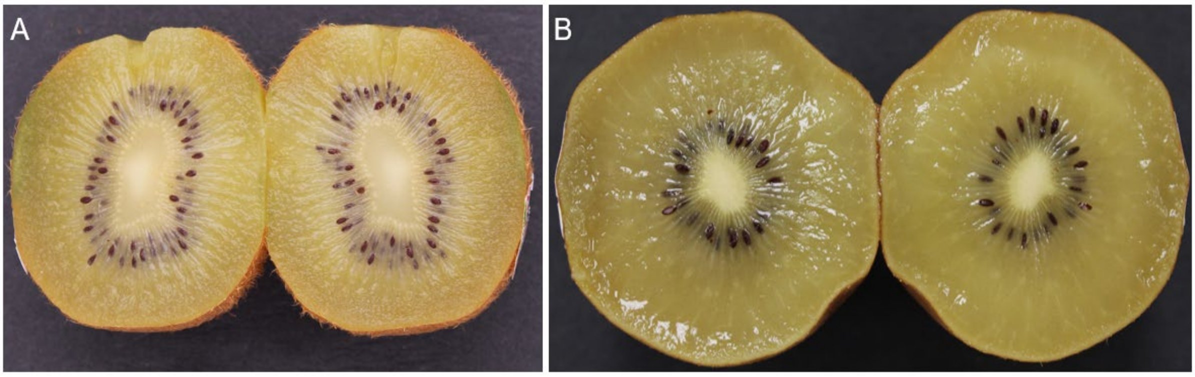


Figure 6.11: Internal symptoms of heat injury in 'Hayward' (A) and 'SunGold™' (B) kiwifruit after 96 h of exposure to 40 °C.

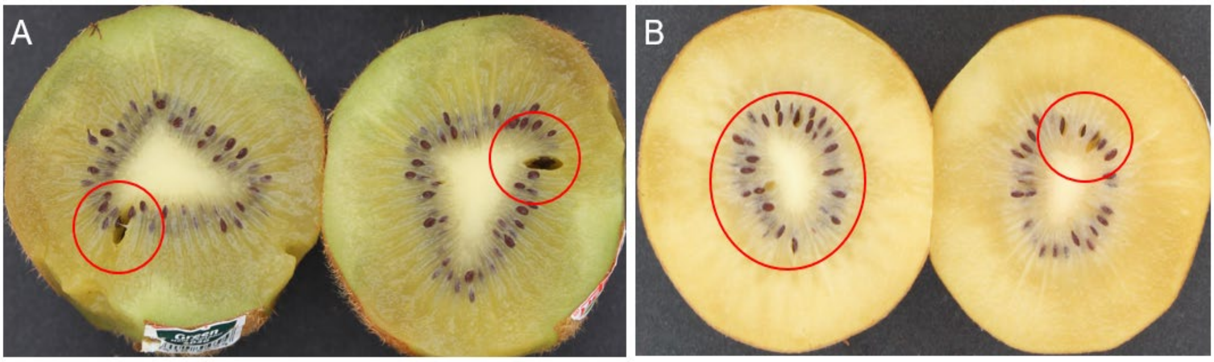


Figure 6.12: Symptoms of cavity formation (encircled) observed in 'Hayward' (A) and 'SunGold™' (B) kiwifruit after 96 h of exposure to 40 °C.

6.3.8 Impact of high temperature exposure on low temperature quality changes

A two-sample t-test was used to identify the changes in fruit quality (firmness and flesh colour) between fruit assessed immediately (Fe/Ce) after exposure and fruit cool stored for a consequent week (Fcs/Ccs), after equivalent 6, 12, 24 and 48 h of high temperature exposure. Under both scenarios, an initial fruit quality measurement (0 h) was done to keep track of the quality changes occurring in between Fe/Ce and Fcs/Ccs fruit measurements. Significant changes in initial fruit quality (firmness) occurred only for 'Hayward' grower 1 in which fruit at the point of high temperature exposure recorded an average firmness of 1.54 kg_f but later declined in firmness to 1.1 kg_f by the time quality measurements were conducted for fruit cool stored after high temperature exposure.

In terms of quality changes during low temperature storage after high temperature exposure, no significant changes in fruit firmness happened at low temperature in both 'Hayward' and 'SunGold™' cultivars after different durations of high temperature exposure (Figures 6.14-6.15) ($p > 0.05$). However, an only exception was for 'Hayward' grower 1 in which fruit cool stored (Fcs) after 48 h of exposure to 40 °C had softened significantly to 0.65 kg_f in comparison to that of fruit assessed immediately after high temperature exposure (Fe) which had firmness of 0.97 kg_f (Figure 6.14A-C).

Significant changes in flesh colour at low temperatures after high temperature exposure was evident only for 'Hayward' fruit (Figure 6.16). In fruit from 'Hayward' grower 1, significant differences in flesh colour between Ce and Ccs fruit was evident at 48 h at 33 and 40 °C and 12 h at 36 and 40 °C. In fruit from 'Hayward' grower 2, significant differences between Ce and Ccs fruit was evident at 48 h at 33 and 38 °C and 12 h at 36 °C. Similarly, in fruit from 'Hayward' grower 3, significant differences between Ce and Ccs fruit was evident at 24 and 48 h at 33 and 38 °C.

In both cultivars, fruit that were exposed to beyond 24 h to high temperatures (33-40 °C) and consequently cool stored had developed a 100% incidence of internal breakdown symptoms (Figure 6.13) evident as water soaking and flesh discolouration spreading from the internal to the peripheral region of the fruit. Neither of the observed internal breakdown symptoms were evident in fruit that were cool stored after 6, 12 and 24 h of high temperatures exposure (33-40 °C).

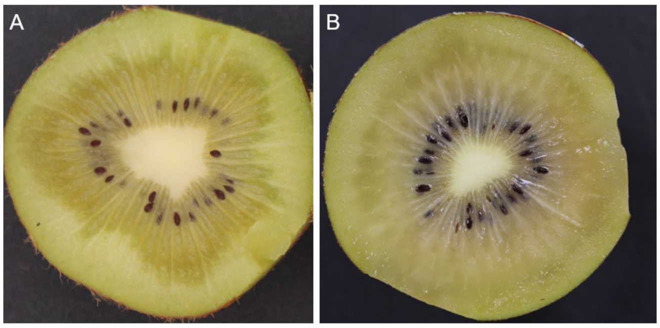


Figure 6.13: Internal breakdown symptoms observed in 'Hayward' (A) and 'SunGold™' (B) kiwifruit that were cool stored consequently for a week after 48 h of exposure to 33-40 °C.

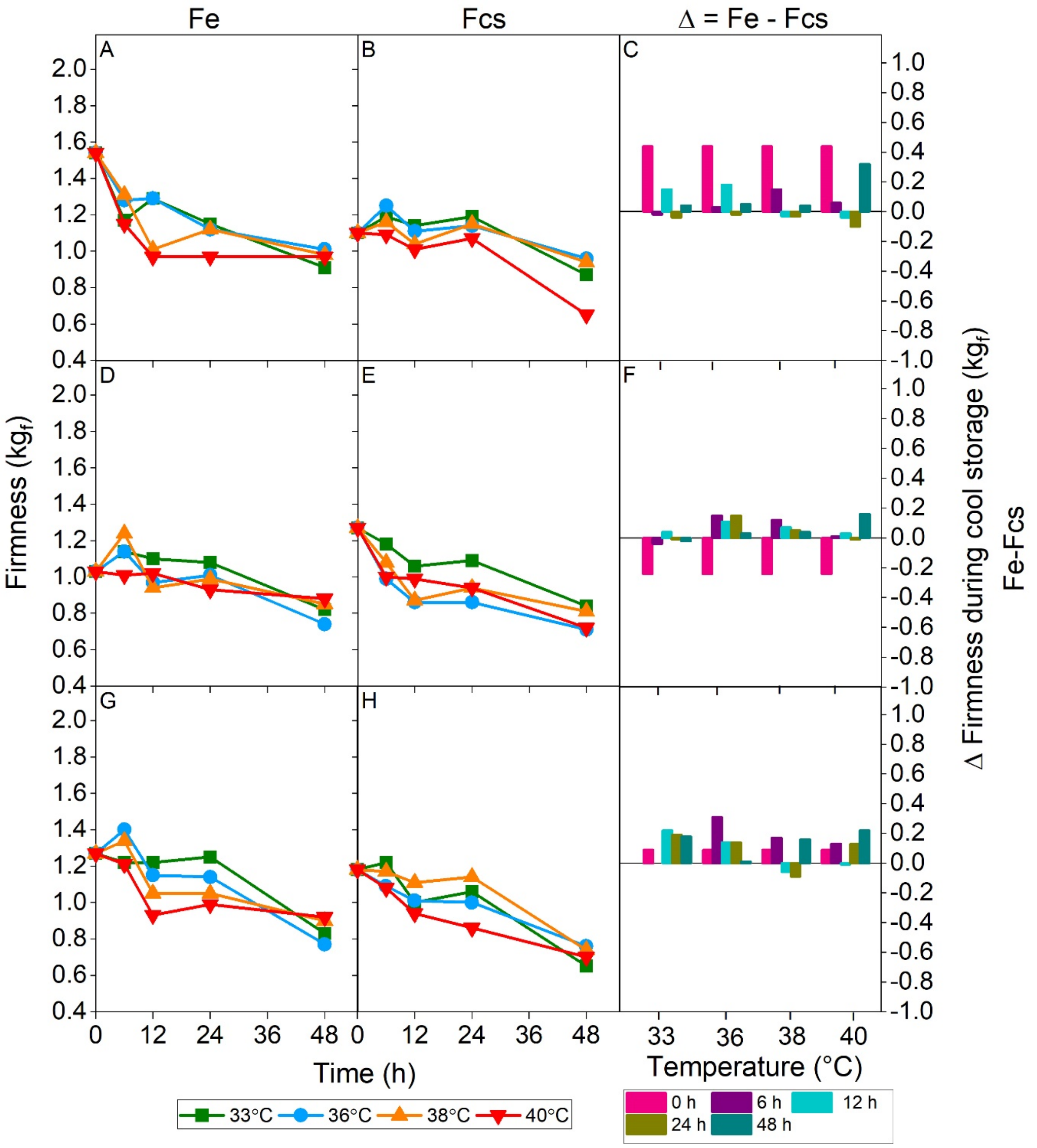


Figure 6.14: 'Hayward' firmness (kgf) changes in fruit assessed immediately (Fe) and fruit cool stored consequently for a week (Fcs), after 6, 12, 24 and 48 h of high temperature exposure. Graphs A-C, D-F and G-I are for growers 1, 2 and 3, respectively. Graphs C, F and I represent the differences in firmness between Fe and Fcs fruit (Δ = Fe-Fcs). Each data point represents the averaged value of 30 fruit (n=30).

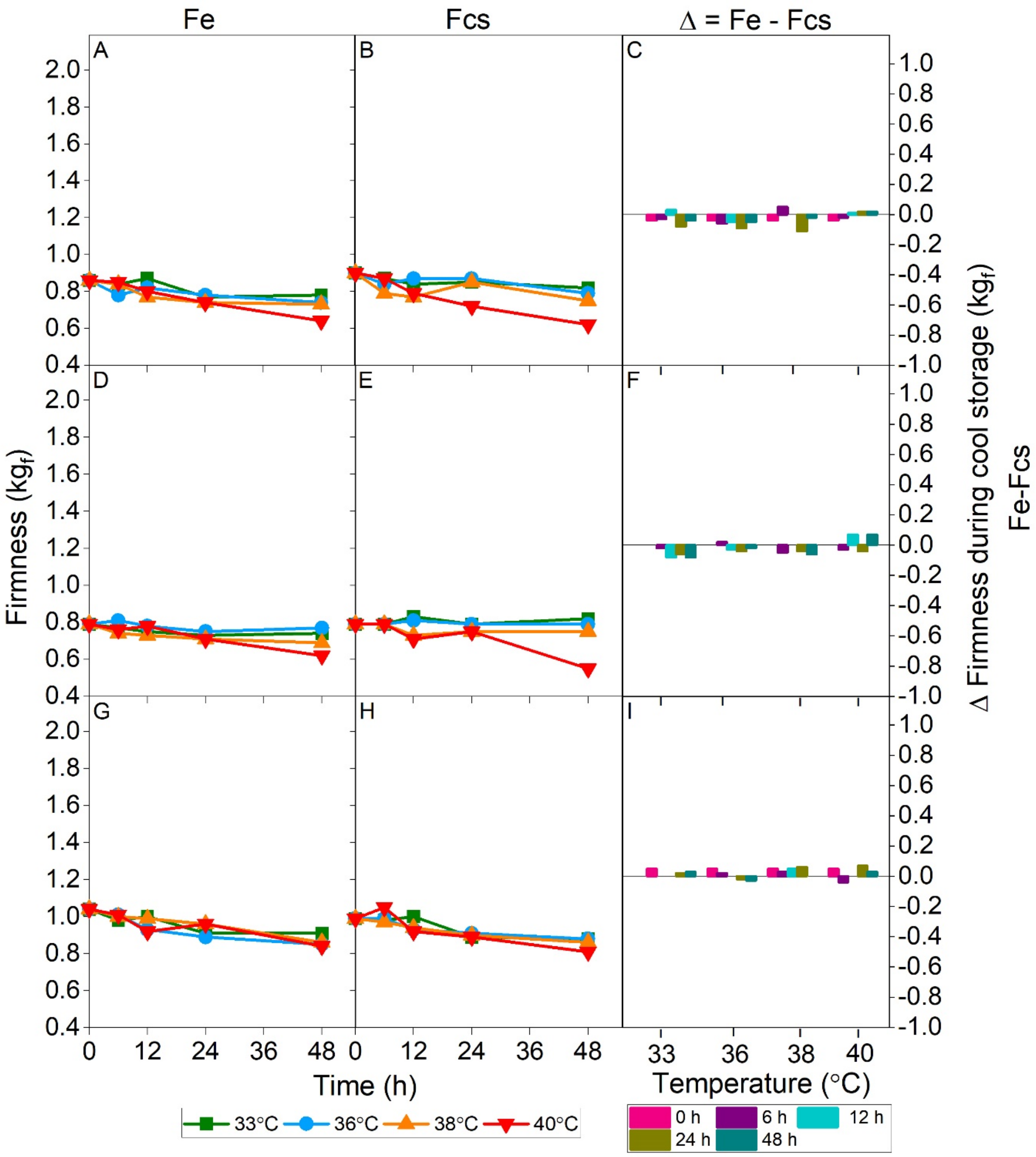


Figure 6.15: 'SunGold™' firmness (kgf) changes in fruit assessed immediately (Fe) and fruit cool stored consequently for a week (Fcs), after 6, 12, 24 and 48 h of high temperature exposure. Graphs A-C, D-F and G-I are for growers 4, 5 and 6, respectively. Graphs C, F and I represent differences in firmness between Fe and Fcs fruit (Δ = Fe-Fcs). Each data point represents the averaged value of 30 fruit (n=30).

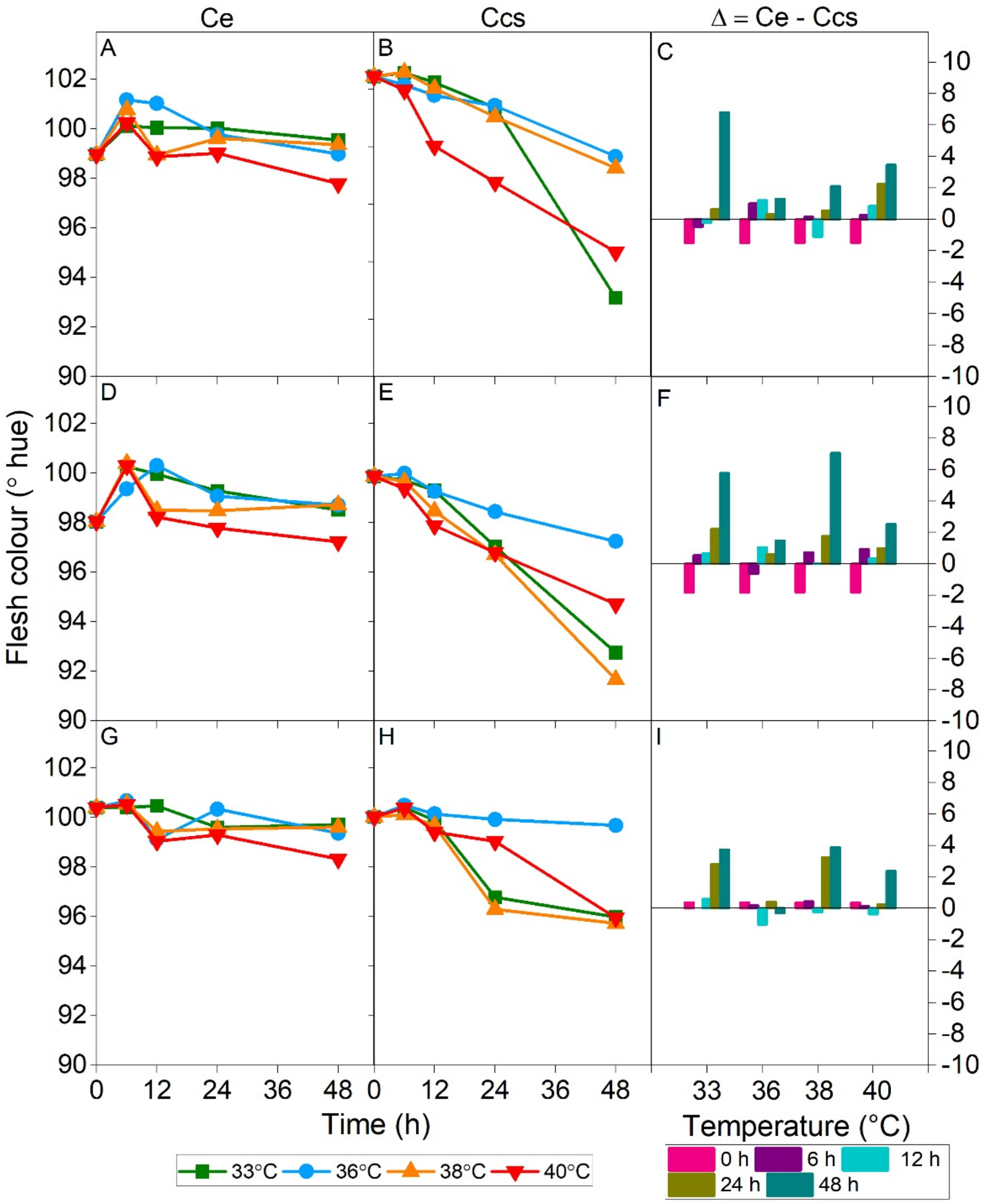


Figure 6.16: 'Hayward' flesh colour (°hue) changes in fruit assessed immediately (Ce) and fruit cool stored consequently for a week (Ccs), after 6, 12, 24 and 48 h of high temperature exposure. Graphs A-C, D-F and G-I are for growers 1, 2 and 3, respectively. Graphs C, F and I represent differences in flesh colour (°hue) between Ce and Ccs (Δ = Ce-Ccs). Each data point represents the averaged value of 15 fruit (n=15).

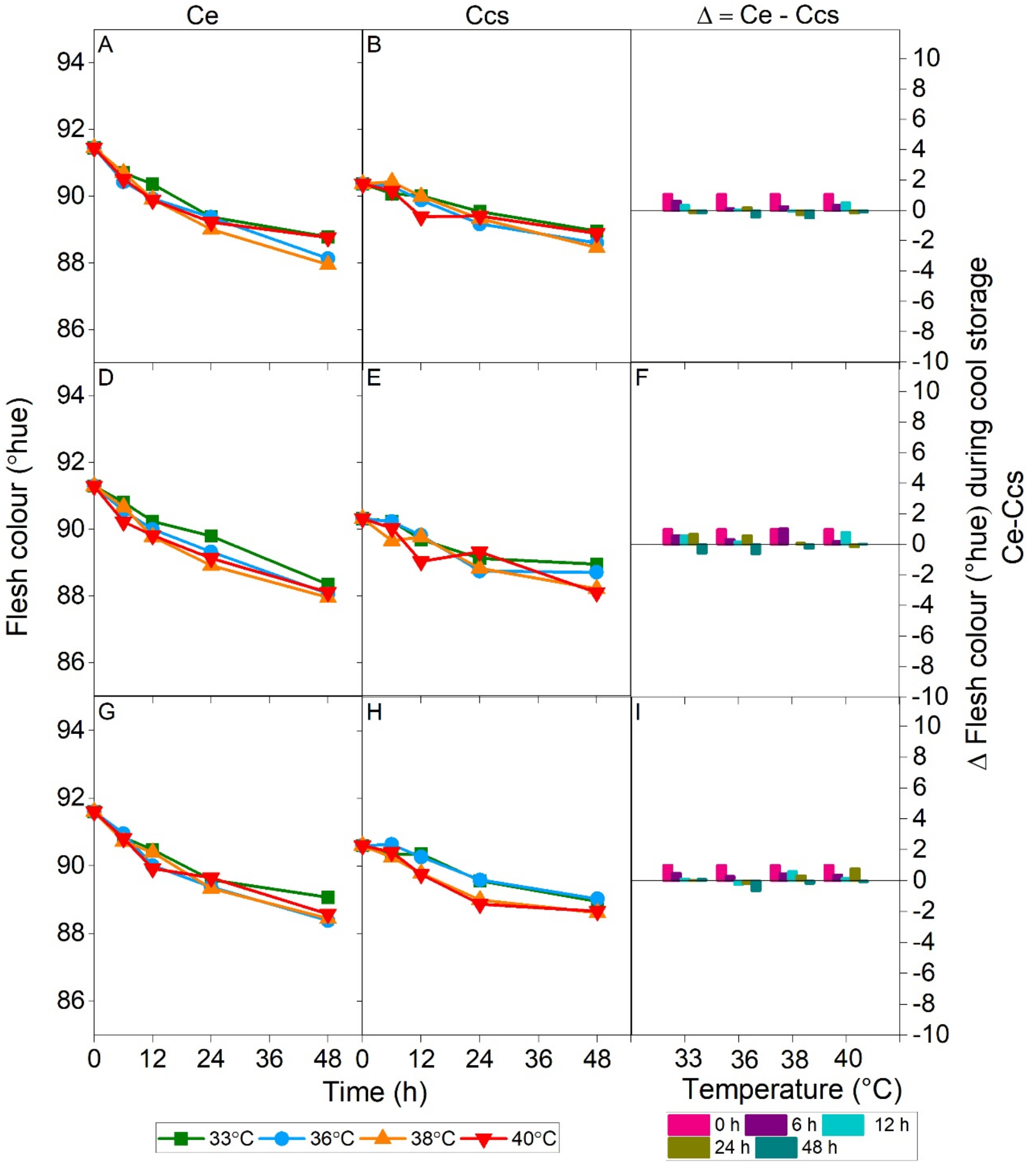


Figure 6.17: 'SunGold™' flesh colour (°hue) changes in fruit assessed immediately (Ce) and fruit cool stored consequently for a week (Ccs), after 6, 12, 24 and 48 h of high temperature exposure. Graphs A-C, D-F and G-I are for growers 4, 5 and 6, respectively. Graphs C, F and I represent differences in flesh colour (°hue) between Ce and Ccs (Δ = Ce-Ccs). Each data point represents the averaged value of 15 fruit (n=15).

6.4 Discussion

This investigation was conducted to identify a temperature-time treatment interaction that would significantly induce irrecoverable damage on kiwifruit after long-term storage. Considering the CO_2 production results from both earlier (Figure 4.2) and the current study (Figure 6.3), a short period of exposure < 24 h to 40 °C could potentially cause death of kiwifruit. Exposure of kiwifruit to temperatures 33-38 °C may not have a lethal impact but prolonged exposure (72-96 h) to this temperatures range could induce stress and cause injury. While visible symptoms of heat injury in fruit assessed immediately after exposure to 33-38 °C were evident only after 72 h (Figures 6.9-6.10), the observed internal breakdown symptoms (Figure 6.13) in fruit consequently cool stored beyond 24 h of exposure indicate that irrecoverable non-visible degradative processes are induced beyond 24 h of exposure.

Respiration rate is used to indicate fruit metabolic rate and is strongly influenced by storage temperature. The influence of medium (1-20 °C) and elevated range temperatures (30-45 °C) on kiwifruit respiration rate (CO_2 production) has previously been elucidated by East et al. (2010) and Antunes and Sfakiotakis (2000), respectively. Antunes and Sfakiotakis (2000) observed CO_2 production in freshly harvested ‘Hayward’ kiwifruit to increase linearly with temperature from 30 to 45 °C. These authors noted that the CO_2 production in fruit stored at 30-42 °C remained close to the peak values throughout 72 h while the CO_2 production in fruit stored at 45 °C plummeted to closer to 0 nmol kg^{-1} s^{-1} after 72 h. Further, Antunes and Sfakiotakis (2000) found that fruit exposed to 45 °C exhibited flesh yellowing symptoms after 24 h with the incidence increasing with declining CO_2 production and reached 100% after 72 h of exposure. It was concluded that kiwifruit suffered extreme stress at 45 °C which resulted in highest CO_2 production and the subsequent sharp decline was due to tissue breakdown caused by heat stress.

A similar CO_2 production trend as that of Antunes and Sfakiotakis (2000) at 45 °C was evident in the current (Figure 6.3) and previous investigation (Figure 4.2) at 40 °C indicating that heat induced tissue damage occurred at 40 °C. This observation of a lower temperature to induce damage than that observed by Antunes and Sfakiotakis (2000) may be a result of a decline in the upper-temperature tolerance limit due to advancement in ripening. The physiological state or stage of ripeness is a known factor of influence of fruit responses to high-temperature exposure (Paull and Chen, 2000). In 'Jonagold' and 'Cortland' apples, post climacteric fruit were more susceptible to heat injury than the pre-climacteric fruit (Fan et al., 2011). According to Vierling (1991), susceptibility or tolerance of plants to heat stress is proportional to the amount of heat shock proteins (HSPs) synthesised. Salzano et al. (2019) observed a decline in the expression of several biotic or abiotic stress-related proteins in cool stored 'Hayward' kiwifruit in comparison to freshly harvested fruits. Hence, the decline in tolerance of kiwifruit to high temperatures with advancement in ripening could be due to limited expression of stress related proteins.

The mechanisms by which heat stress induces tissue damage in either plants or fleshy fruit is diverse and include cellular and physiological manifestations (Paull and Chen, 2000). Internal breakdown symptoms evident as water-soaked tissue observed in both 'Hayward' and 'SunGold™' fruit either after high temperature exposure (Figure 6.11) or upon subsequent cool storage (Figure 6.13) strongly suggest that the loss of cell membrane integrity is a prominent symptom of heat injury in kiwifruit. Electrolyte leakage is an indicator of membrane permeability and is a phenomenon that accompanies senescence (Marangoni et al., 1996; Saltveit, 2005;

Antunes and Sfakiotakis, 2008; Dea et al., 2010). A rise in electrolyte leakage upon exposure to high temperatures has previously been reported in apples (Lurie et al., 1995) and mangoes (Mitcham and McDonald, 1993; Nyanjage et al.,1999).

Proteins and lipids, which are the major constituents of the cell membrane, undergo a series of compositional changes to enable the cell membrane to maintain its normal physiological function under stressful conditions (Quinn, 1988). For example, in apples, storage at 38 °C for four days resulted in increased cell membrane micro viscosity due to an increase in sterol to phospholipid ratio which is suggested to be an adaptive strategy to heat stress (Lurie et al., 1995).

Prolonged stress or stress above tolerance limits dissembles cell membrane components, mainly lipids, resulting in the loss of membrane function (Quinn, 1988). The peroxidation of unsaturated membrane lipids is an important phenomenon initiating senescence in plant tissue. Exposure to high temperatures is one of several factors which accelerates this phenomenon (Dat et al., 1998). Active oxygen species (AOS) which are mainly synthesised during photosynthesis and respiration are known to induce this phenomenon in plants. Moreover, peroxidation of lipids further promotes the production of AOS (McKersie et al., 1988; Thompson, 1988). Increased accumulation of AOS in fleshy fruits as a response to high temperature exposure has been confirmed (Yu et al., 2019; Zhou et al., 2019). In 'Hongyang' kiwifruit, senescence was accompanied by an increased accumulation of AOS, lipid peroxidation and protein denaturation (Xia et al., 2016).

AOS may not be the only cause for cell membrane deterioration under heat stress. Additional possibilities include anaerobic metabolites such as ethanol, acetaldehyde and ethyl acetate which accumulate in fruit under elevated storage temperatures (Mitcham and McDonald, 1993; Fan et al., 2011; Spadoni et al., 2015).

Increased production of anaerobic metabolites could lead to off-flavours and internal breakdown disorders in fruit (Tadege et al., 1999; Ho et al., 2013; Boeckx et al., 2019; Ali et al., 2021; Joseph et al., 2021).

At elevated temperatures, an uprise in CO_2 production in fruit results in more demand for O_2 and since this increase in demand for O_2 cannot be met within fruit's internal atmosphere, fermentation occurs even under normal external O_2 availability (Mitcham and McDonald, 1993). Gaseous transport in and out of fruit is influenced by factors such as the presence of intercellular spaces which decline as fruit ripen and restrict movement of O_2 and CO_2 causing fermentation (Kader et al., 1989; Burdon et al., 2005). In this work, the high respiration rate and the advanced ripeness stage of fruit (edible ripe) both favour the possibility of the occurrence of anaerobic respiratory metabolism. Further, the pattern of internal breakdown incidence observed in fruit cool stored beyond 24 h high temperature exposure i.e. spreading from the core to the peripheral region (Figure 6.13) suggests the possibility of anaerobiosis as gas transfer impacts central locations of the fruit bodies the most.

The increased incidence of flesh yellowing described by the rapid decline in °hue was observed in 'Hayward' at 40 °C. These symptoms of flesh yellowing evident in 'Hayward' fruit has previously been reported in investigations of Antunes and Sfakiotakis (2000), Chea et al., (1992) and Lay-Yee and Whiting (1996) and is presumed to be a consequence of tissue damage. Degradation of chlorophyll present in the flesh of 'Hayward' kiwifruit (Pilkington et al., 2012) could be the root cause. While chlorophyll naturally degrades in plants as part of growth, maturation and senescence (Hendry et al., 1987), unfavourable growth conditions such as extreme or prolonged heat stress can result in chlorophyll destruction (Adelusi and Lawanson, 1978; Ellis, 1981; Doley, 1983). Chlorosis (the reduction in chlorophyll concentration) is considered to be an initial symptom of senescence in plants (Ono et al., 2019) and is induced under heat stress due to the breakdown of the thylakoid membrane, a site where chlorophyll resides within the chloroplast (Feierabend and Schrader-Reichhardt, 1976; Feierabend, 1977; Djanaguiraman et al., 2011). AOS accumulation is linked with chlorophyll degradation due to membrane breakdown (Maina et al., 2008).

An additional symptom of heat stress observed in both cultivars was formation of a cavity which became evident in the locular region of fruit stored for 96 h at 40 °C (Figure 6.12). The increased CO_2 accumulation within fruit internal atmosphere may have resulted in cavity formation. Lay-Yee and Whiting (1996) had previously reported similar symptoms (4.7% incidence) of cavity formation in ‘Hayward’ kiwifruit after exposure to high temperature (40 °C) controlled atmosphere (0.2% O_2 and 20% CO_2) storage conditions for 10 h. In apples, internal cavity formation is linked to high internal CO_2 concentrations (Smock, 1977; Elgar et al., 1998; James and Jobling, 2009). In ‘Cripps Pink’ apples, observations under the scanning electron microscope (SEM) revealed that high CO_2 related cavities occurred due to the disintegration of vascular bundles originating from the core to cortex tissue (James and Jobling, 2009).

Firmness is an important quality trait of kiwifruit and is strongly influenced by the storage temperature (Hertog et al., 2004). For ‘Hayward’, firmness decline at 33 and 36 °C was more rapid than at 38 and 40 °C (Figure 6.5). However, this softening trend occurred only after 24 h of exposure before which 38 and 40 °C stored fruit displayed a rapid firmness drop at 6 and 12 h of exposure. The initial rapid decline in firmness at 38 and 40 °C might have been influenced by the time taken for the fruit to reach the ambient exposed temperature. It was observed in the previous investigation (Chapter 3) that kiwifruit transferred from cool store took approximately 6 h to reach the ambient exposed temperatures (Figure 3.9). However, the reason for the observed rapid firmness decline in 'Hayward' at 12 h at 38 and 40 °C remains unknown and also further suggests the possibilities of other unspecified physiological mechanisms in influencing the softening trend at initial hours of exposure to 38 and 40 °C.

A decline in firmness loss in 'Hayward' kiwifruit upon exposure to high temperatures (> 34 °C) either after harvest or after a period of cool storage has been reported by Antunes and Sfakiotakis (2000) and Zhao (2017), respectively. Reduced ripening rate at higher storage temperatures as observed for 'Hayward' in this experiment, has been attributed to a decline in the activities of enzymes involved in ethylene biosynthesis (Klein and Lurie, 1992) and cell wall degradation (Klein and Lurie, 1990; Ben Shalom et al., 1993; Johnston et al., 2001; Lurie and Tonutti, 2014). For example, Antunes and Sfakiotakis (2000) found the activities of ethylene biosynthesis enzymes (ACC synthase and ACC oxidase) to decline at temperatures over 38 °C resulting in reduced softening in 'Hayward' kiwifruit.

In 'SunGold™', firmness of fruit at 33 and 36 °C remained almost unaffected throughout storage while a slight and rapid drop in firmness was noted at 38 and 40 °C, respectively. Interestingly, no significant differences ($p > 0.05$) in firmness was observed in grower 6 of 'SunGold™' at 33-40 °C (Figure 6.6C). Fruit from this grower line were firmer at the start of the experiment suggesting that firmer fruit may be more tolerant to high temperature exposure.

In 'SunGold™', firmness decline in any of the high temperatures was not as drastic as 'Hayward'. For example, at 40 °C, a maximum of 0.4 kg_f drop over 96 h was observed in 'SunGold™' (Figure 6.6B) whereas, for 'Hayward', a maximum of 0.7 kg_f firmness decline was observed over 96 h at 40 °C (Figure 6.5C). This result suggests

‘SunGold™’ retains firmness better than ‘Hayward’ at elevated temperatures. However, the reason for this observed cultivar difference is unknown. In apples, a differential softening response between cultivars at elevated temperatures (20-35 °C) was observed to be influenced by internal ethylene concentrations (Johnston et al., 2001). A few of the possibilities for the observed differential softening response between ‘Hayward’ and ‘SunGold™’ cultivars at high temperatures could be due to differences between cultivars in the initiation or the rates of climacteric ethylene production at these temperatures or softening in ‘SunGold™’ to be more impeded by heat stress than Hayward.

6.5 Conclusion

A temperature-time treatment combination of 40 °C for 12 h was confirmed to have a lethal impact on kiwifruit physiology. Incidence of internal breakdown disorders in fruit cool stored after exposure to 33-40 °C for 48 h suggests that an exposure period beyond 24 h to temperatures above 30 °C has the potential to cause quality deterioration in eating ripe ‘Hayward’ and ‘SunGold™’ kiwifruit. As differences in softening response were observed between cultivars and between grower lines (in ‘SunGold™’), identifying factors that control or influence softening under elevated temperatures would be beneficial to elucidate the physiological mechanisms that cause the observed differential softening responses. While the possible mechanisms that could have caused the observed effect of heat injury in kiwifruit has been discussed, there remains a need for more detailed investigations to elucidate the mechanisms. Hence, the upcoming study will investigate the influence of high temperatures in inducing anaerobic respiratory metabolism in kiwifruit and will further aim to identify whether a relationship exists between anaerobic metabolites (if any) and high temperature induced tissue injury.

Chapter 7: High-temperature storage activates anaerobic respiratory metabolism in 'Hayward' kiwifruit

7.1 Introduction

Gaseous exchange between plants or plant organs and the external environment occurs through diffusion, a process in which gas moves from higher to lower concentrations as defined by Fick's law of diffusion (Burg and Burg, 1965; Cameron and Yang, 1982; Banks, 1985; Ho et al., 2006; Ho et al., 2018; Joseph et al., 2021). In the internal atmosphere of dense plant organs such as fruit, hypoxic conditions can exist due to the restricted diffusion of oxygen within fruit tissue, even if oxygen is available in normal concentrations (Yearsley et al., 1997; Bower et al., 2000; Biais et al., 2010; Bessemans, 2018; Bessemans, et al., 2020; Nugraha et al., 2021). However, hypoxia in plants may still occur even when internal O_2 diffusion remains unrestricted due to an increase in the plant's metabolic rate (van Dongen et al., 2003; Weits et al., 2019; Loreti, 2020; Dukowic-Schulze et al., 2021; Jethva et al., 2022).

In the internal atmosphere of fruit where O_2 transport is limited, increasing external storage temperature can further exacerbate O_2 diffusion (Ke and Kader, 1992). High temperatures (within physiological range) as known, upregulate fruit metabolism (Wills and Golding, 2016; Brizzolara et al., 2020) and an increase in metabolic rate imbalances the gas exchange process (Mitcham and McDonald, 1993). This is because fruit respiration rate is expedited at high temperatures, leading to an excess O_2 demand and subsequently an internal oxygen deficit (Mitcham and McDonald, 1993; Yearsley et al., 1997). For example, in pears, internal oxygen concentration declined from 16.91 to 4.51% with a rise in temperature from 10 to 40 °C, which was suggested to occur due to reduced oxygen diffusivity (Hansen, 1942).

The respiratory transition between aerobic or anaerobic mechanisms in fruits mainly depends on the in vivo O_2 availability (Ke and Kader, 1992; Ho et al., 2008; Bessemans et al., 2016). A minute depletion of internal O_2 affects the cellular energy status (ATP/ADP ratio) (Geigenberger, 2003; Blanch et al., 2015; Toro and Pinto, 2015; Boeckx et al., 2019). To recover from this deficit in cellular energy and to maintain normal cellular homeostasis, a flux in glycolysis occurs to enhance energy production by conversion of glucose to pyruvate, a process known as the “Pasteur effect” (Bailey-Serres et al., 2012; Boeckx et al., 2019). Under these circumstances, $NADP^+$ and NAD^+ have to be regenerated with limited pyruvate accumulation (Gibbs et al., 2000; Biais et al., 2010; Bailey-Serres et al., 2012; Blanch et al., 2015; Boeckx et al., 2019). Hence, the enhanced glycolytic activity results in fermentation (Boeckx et al., 2019).

In fermentation, pyruvate is converted either to ethanol and CO_2 or directly to lactate (Biais et al., 2010; Boeckx et al., 2019). In the ethanol production pathway, pyruvate is decarboxylated by the enzyme pyruvate decaboxylase (PDC) to acetaldehyde which subsequently gets converted to ethanol by alcohol dehydrogenase (ADH) and finally to ethyl acetate by the enzyme alcohol acyltransferase (AAT) (Botondi et al., 2012; Boeckx et al., 2019). In the lactate pathway, pyruvate directly gets converted to lactate by enzyme lactate dehydrogenase (LDH) (Biais et al., 2010). However, the concentration of lactate production in fruits may be negligible in comparison to that of ethanol (Peppelenbos and Oosterhaven, 1998).

Even though the efficiency of hypoxic ATP production is low compared to aerobic respiration, it facilitates cell survival as long as carbohydrate substrates remain available (Bailey-Serres et al., 2012). A minute concentration of ethanol, acetaldehyde and ethyl acetate are synthesised in fruit and the concentration of these metabolites rises during fruit ripening (Pesis, 2005). Anaerobic conditions result in excessive anaerobic metabolites production within fruit tissue resulting in off-flavours and internal disorders (North, 1971; Peppelenbos and Oosterhaven, 1998; Pedreschi et al., 2009). Further, anaerobic metabolites move out of the cells into the apoplast and diffuse out of the tissue causing depletion of carbon reserves, and also affecting the cellular membrane structure causing complete cellular breakdown (Pedreschi et al., 2009; Blanch et al., 2015; Joseph et al., 2021).

An increase in ethanol and acetaldehyde production at high temperatures (as hot air or hot water treatments) has been reported in apples (Song et al., 2001; Fan et al., 2005), mangoes (Mitcham and McDonald, 1993), peaches (Spadoni et al., 2015) and oranges (Schirra et al., 2005). Moreover, in apples, the severity of flesh browning strongly correlated with the concentrations of ethanol produced as a result of high temperature exposure (Fan et al., 2005).

In previous investigations (Chapters 4 and 6), it was noted that exposure of ‘Hayward’ kiwifruit to high temperatures resulted in higher CO_2 production (Figures 4.2 and 6.3) as well as higher incidence of flesh injury expressed as flesh discolouration and water-soaked symptoms (Figure 6.11). Similar symptoms of flesh discolouration in ‘Hayward’ kiwifruit at high temperatures have been reported by Antunes and Sfakiotakis (2000) which they termed as “cooked kiwifruit” and conceptualised that the incidence was due to heat injury suffered by fruit tissue. As a further investigation, this experiment will aim to understand the influence of high temperatures in inducing anaerobic respiratory metabolism in ‘Hayward’ kiwifruit and also identify whether a relationship exists between the concentrations of anaerobic metabolites and heat injury incidence.

7.2 Material and Methods

7.2.1 Fruit source and storage procedure

Fruit of *Actinidia deliciosa* cv*.* 'Hayward' were sourced from two different grower lines located in the Bay of Plenty region, New Zealand. Fruit were harvested between the 28th-30th of April 2020. Fruit were class-1 grade, count size 33 and transported from commercial cool store to the Massey University postharvest laboratory, Palmerston North under refrigerated condition. Fruit arrived packed within polyliners in 10.5 kg modular bulk (MB) boxes. Quality assessments were conducted upon fruit arrival to the laboratory and before starting of the experiment.

On the day of the experiment, fruit were randomised in coolstore and later transferred to high temperature conditions packed in single-layered polypropylene trays without polyliners. Assessments of physiology (O_2 and CO_2 production), quality (firmness), biochemical analytes (ethanol and acetaldehyde) and incidence of heat injury were conducted after 1, 2, 3, and 5 days of exposure. High-temperature conditions used for the trial were 38 and 40 °C for grower 1 and 36, 38, 40 °C for grower 2 with 20 °C considered as a control for both growers.

This investigation was first conducted for grower 1 and after observing the results, some modifications were adopted for grower 2 in the subsequent investigation. The experimental modifications for grower 2 included an additional storage temperature of 36 °C with assessments extending up to day 7. These changes were made since grower 2 was more susceptible to heat stress (based on higher CO_2 production rates and heat injury incidence) than grower 1 and to gain a better understanding of the relationship between anaerobic metabolites and heat injury incidence. Storage duration at 20 °C was extended to days 9 and 12 for growers 1 and

2, respectively. This storage duration extension at 20 °C was to ensure that the firmness of fruit stored at high temperatures and 20 °C contrasted each other which clarifies whether the rise in ethanol was solely a high temperature effect or was additionally influenced by ripening or senescence processes.

A further mini-trial was conducted for grower 2 which involved exposure of fruit to high temperatures i.e. 0, 20, 30, 33 and 40 °C, and ethanol and acetaldehyde content was estimated when fruit firmness under each temperature declined to ≤ 0.6 kg_f. This was done to verify the relationship between ethanol content and heat injury incidence and to further confirm whether the increased concentration of ethanol in kiwifruit tissue was exclusively a temperature effect or due to ripening or senescence processes.

7.2.2 Fruit physiology measurements

7.2.2.1 O_2 consumption

Oxygen consumption was measured on individual fruit within experimental conditions by enclosing fruit of known weight (ranging 90-110 g) within a 550 mL glass jar for 2 h. A sachet of soda-lime (25 g) was placed inside the jar to avoid CO_2 accumulation. Gas samples were collected immediately after enclosure (considered as initial concentration) and 2 h after enclosure (considered as final concentration) through a rubber septum from the headspace using a 1 mL syringe and injected into a gas analyser fitted with an O_2 infrared transducer (Analytical Development Company, Hoddesdon, UK) that uses O_2-free nitrogen as a carrier gas at a flow rate of 35 mL min^{-1}. The amount of O_2 present in the sample was recorded on an integrator (HP3396A, Hewlett Packard, California USA). Before injecting the sample, the analyser was calibrated with a commercially available O_2 β-standard (BOC Ltd., Auckland, New Zealand) of concentration 21.15 ± 0.10%. A set of 10 fruit were assessed and O_2 consumption was calculated by taking into consideration the weight of fruit, free volume of the glass jar and storage temperature and expressed as nmol kg^{-1} s^{-1}.

7.2.2.2 CO_2 production

The same set of 10 fruit used for O_2 consumption were subsequently measured for CO_2 production. The gas sample collection procedure was similar to that of O_2 consumption measurements with a few exceptions such as the time interval between initial and final sample collection was 15 minutes due to faster CO_2 accumulation rate and exclusion of soda-lime sachet from the jar. The CO_2 gas samples were analysed as described in chapter 4 (Section 4.2.2.1) and the production rates were expressed as nmol kg^{-1} s^{-1}.

7.2.2.3 Respiratory Quotient (RQ)

RQ was estimated by Equation 2.2.

7.2.3 Fruit quality

7.2.3.1 Fruit firmness

Fruit firmness was assessed as described in Chapter 4 (section 4.2.2.3). Fruit (n=10) assessed for O_2 consumption and CO_2 production were subsequently assessed for firmness. Fruit were equilibrated to room temperature by fan cooling for 2 h before firmness assessment.

7.2.3.2 Heat injury incidence

Fruit were cut into halves and assessed for heat injury symptoms. The incidence of heat injury was calculated as the percentage of total fruit population (10 fruit at each time point).

7.2.4 Biochemical analysis

7.2.4.1 Procedures for ethanol and acetaldehyde assessments

Ethanol and acetaldehyde content in fruit was determined using an enzyme assay (Megazyme K-ETOH 02/17 and Megazyme K-ACHYD 06/18, Megazyme, Ireland) following the manual assay procedure as specified below.

7.2.4.1.1 Ethanol content estimation

Kiwifruit juice (10 mL) was extracted (by crushing pulp in a sieve) from each fruit and transferred into centrifuge tubes. Later the juice samples were centrifuged at 13,000 rpm (Sorvall RC6 Plus, Fisher Scientific, Dublin, Ireland) for 30 minutes at 20 °C. Immediately after centrifugation, the juice was filtered through Whatman® qualitative filter paper (125 mm) and collected in Duran® glass bottle. 0.1 mL of the filtered juice sample was pipetted into the cuvettes each of which contained 2 mL distilled water. Later a stepwise procedure as specified in the Megazyme ethanol assay procedure was followed to add assay kit components i.e. 0.2 mL buffer (pH 9), 0.2 mL of β Nicotinamide adenine dinucleotide (β NAD^+) and 0.05 mL aldehyde dehydrogenase (ALDH) into the cuvettes.

At approximately two minutes after addition of these three kit components into each of the cuvette, an initial absorbance reading at 340 nm was recorded using

Pharmacia LKB Biochrom Ultrospec II spectrophotometer. Later, the final kit component i.e. 0.02 mL of alcohol dehydrogenase (ADH) was added into the cuvettes and after 5 minutes, the final absorbance was recorded at 340 nm. A blank sample containing all the assay procedure components except kiwifruit juice was used to eliminate the absorbance readings influenced by kit components during final concentration estimation. The concentration of ethanol content in the sample was estimated using ethanol (K-ETOH) Mega-Calc™ which considers initial and final absorbance values of the blank samples and actual samples containing kiwifruit juice to estimate ethanol content expressed as g/L.

7.2.4.1.1.1 Ethanol measurement precision

Precision in ethanol measurement was determined by preparing 2 separate composite juice samples (each prepared from 10 fruits) and 10 subsamples sampled from each of the two main samples. The standard error of the mean for the determined ethanol content in the sub-sample population (n=10) for both main sample groups ranged 0.006 and 0.02 for samples 1 and 2, respectively. The obtained results (Figure 7.1) suggest that the measurement procedure was precise in estimating ethanol content.

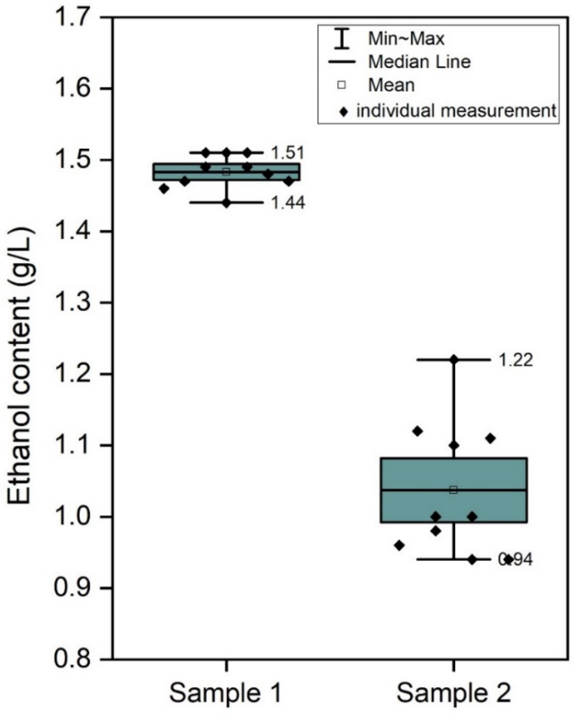


Figure 7.1 Measurement error of two composite juice samples for ethanol content repeatedly measured 10 times.

7.2.4.1.2 Acetaldehyde content estimation

For acetaldehyde assessment, 0.2 mL of the filtered juice sample was pipetted into the cuvettes which contained 2 mL of distilled water. Later a stepwise procedure as specified in the Megazyme acetaldehyde assay procedure was followed to add assay kit components i.e. 0.2 mL buffer (pH 9), 0.2 mL of β Nicotinamide adenine dinucleotide (β NAD^+) and at approximately two minutes after addition of these components into each of the cuvette, an initial absorbance reading at 340 nm was recorded using Pharmacia LKB Biochrom Ultrospec II spectrophotometer. The final kit component i.e. 0.05 mL aldehyde dehydrogenase (ALDH) was added into the cuvettes and after 5 minutes, the final absorbance reading was recorded at 340 nm. A blank sample containing all the assay procedure components except kiwifruit juice was used to eliminate the absorbance readings influenced by kit components during final concentration estimation. The concentration of acetaldehyde content in the sample was estimated using Acetaldehyde (K-ACHYD) Mega-Calc™ which uses initial and final absorbance values of the blank samples and actual samples containing kiwifruit juice to estimate acetaldehyde content which is expressed in g/L.

7.2.5 Data analysis procedure

Effects of treatments on physiology and quality parameters were determined using the General Linear Model (GLM) procedure in Minitab (Minitab Inc., Version 16.1, State College, Pennsylvania, USA) except for heat injury incidence. Data on physiology (O_2 consumption, CO_2 production, RQ) and quality (firmness) for each grower was analysed separately using General Linear Model, considering storage temperature and exposure duration as controlled variables. Once significant differences were determined, Tukey's test at 95 % confidence was used to differentiate treatment means.

Due to larger variability in ethanol and acetaldehyde content between individual fruit, the obtained data was first analysed for normality distribution by Anderson-Darling normality test in Minitab (Minitab Inc., Version 16.1, State College, Pennsylvania, USA). Subsequently, a non-parametric Kruskal-Wallis one-way analysis of variance in Minitab (Minitab Inc., Version 16.1, State College, Pennsylvania, USA) was used to differentiate ethanol and acetaldehyde accumulation between different temperatures and growers. As a post-hoc test for Kruskal Wallis analysis, Dunn-test in R (version 4.1) was used for multiple comparisons for ethanol and acetaldehyde accumulation between temperatures since post-hoc test for Kruskal Wallis analysis was unavailable in Minitab statistical software.

7.3 Results

7.3.1 Initial fruit quality attributes

Fruit of both growers were harvested on similar dates but at harvest quality attributes varied between the growers (Table 7.1). Fruit from grower 2 was softer than grower 1 at harvest and at the start of the experiment. Contrastingly, TSS content was greater in fruit from grower 2 than grower 1. Since the experiments were conducted for grower 1 followed by grower 2, storage duration was the longest for the latter. The presented quality attributes at the start of the experiment (after storage) are for 20 °C since experiments for each of the growers were conducted in ascending order beginning and ending with 20 and 40 °C, respectively.

Table 7.1: Quality attributes of 'Hayward' growers 1 and 2, at-harvest and before exposure to experimental conditions (n=30). Dry matter was assessed only at harvest. Values appended by a different letter in the same row are significantly different (LSD0.05) from each other.

Grower Number		GL1	GL2
Harvest week (ISO)		18	18
Weeks of cool storage		32	36
Firmness (kg_f)	At harvest	5.97^a	5.23^b
	After storage	1.44^a	1.18^b
SSC (° Brix)	At harvest	10.05^b	11.04^a
	After storage	14.6^a	14.85^a
Dry matter (%)	At harvest	17.30^a	17.24^a

7.3.2 O_2 consumption and CO_2 production

As evident in Figure 7.2, O_2 consumption increased with storage temperature, with the consumption under each of the temperatures reaching a maximum on the initial day of exposure. In both growers, at 40 °C, O_2 consumption was highest on the initial day of exposure and dropped to the lowest by day 5 whereas a gradual decline was noted at other temperatures. At 40 °C, O_2 consumption on the initial day reached 580 nmol $kg^{-1}s^{-1}$ and plummeted to 200 nmol $kg^{-1}s^{-1}$ by day 5 in grower 1, whilst it dropped from 600 to 122 nmol $kg^{-1}s^{-1}$ from day 1 to day 5 in grower 2. At 38 °C, O_2 consumption of 480 nmol $kg^{-1}s^{-1}$ was recorded on the initial day and dropped to 425 nmol $kg^{-1}s^{-1}$ by day 5 in grower 1 whereas it declined from 390 to 260 nmol $kg^{-1}s^{-1}$ in grower 2. In grower 2, at 36 °C, O_2 consumption was 400 nmol $kg^{-1}s^{-1}$ on the initial day and reached closer to 240 nmol $kg^{-1}s^{-1}$ by day 7. At 20 °C, O_2 consumption ranged closer to 200 nmol $kg^{-1}s^{-1}$ in both growers throughout the storage period.

Like O_2 consumption, CO_2 production increased with a concomitant rise in temperature in both growers (Figure 7.3). At 40 °C, CO_2 production ascended to a maximum of 800 nmol $kg^{-1}s^{-1}$ in grower 1, whilst a higher CO_2 production of 1300 nmol $kg^{-1}s^{-1}$ was noted in fruit from grower 2 on day 1 of exposure. It was noted in fruit from grower 1 that the CO_2 production rate remained at the peak value until day 2 before subsequently declining to 478 nmol $kg^{-1}s^{-1}$ on day 5 of exposure, whereas, in grower 2, CO_2 production plummeted from the peak value on day 2 and reached 167 nmol $kg^{-1}s^{-1}$ on day 5. In the remaining high temperatures, CO_2 production increased on the initial day of exposure and a slow decline from the peak point was noted during the subsequent days ranging from 750 to 716 nmol $kg^{-1}s^{-1}$ in grower 1 and ranged from 1007 to 540 and 849 to 660 nmol $kg^{-1}s^{-1}$ at 38 and 36 °C in grower 2, respectively. At 20 °C, CO_2 production in both growers was recorded between 180 to 200 nmol $kg^{-1}s^{-1}$ throughout the storage period.

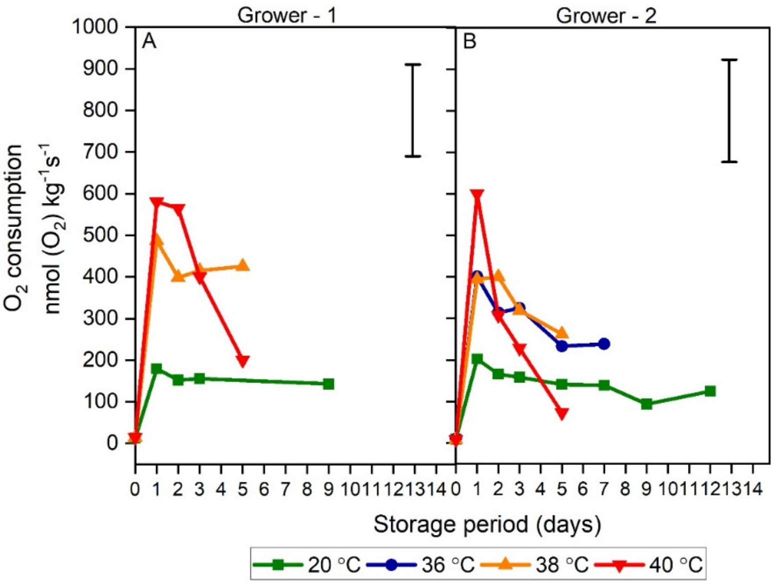


Figure 7.2: O_2 consumption in 'Hayward' kiwifruit at high temperatures (n=10). 36 °C condition was adopted for grower 2 only. The initial value at day 0 represents O_2 consumption measured at 0.5 °C. The error bar represent LSD $_{0.05}$ for the influence of time*temperature interaction on O_2 consumption.

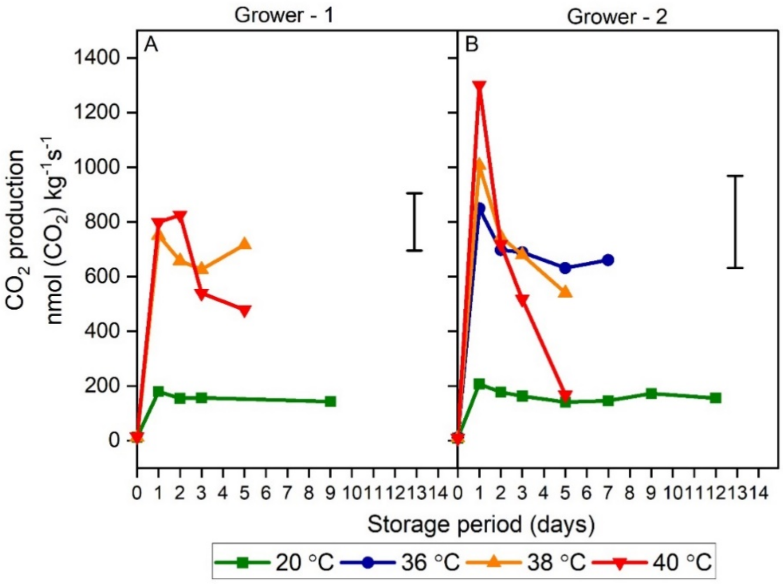


Figure 7.3: CO_2 production in 'Hayward' kiwifruit at high temperatures (n=10). 36 °C condition was adopted for grower 2 only. The initial value at day 0 represents CO_2 production measured at 0 °C. The error bar represent LSD $_{0.05}$ for the influence of time*temperature interaction on CO_2 production.

7.3.3 Respiratory Quotient (RQ)

In both growers, the RQ value remained at or close to 1 at 20 °C. RQ increased at higher temperatures and ranged from 1.5 to 1.7 and 2 to 2.6 at 38 °C for growers 1 and 2, respectively. At 40 °C, the RQ of fruit from grower 1 was closer to that of 38 °C but increased on the final day of exposure reaching a value above 3. In grower 2, a steep rise in RQ above 3 was observed on the initial day of exposure to 40 °C and gradually declined on subsequent days reaching a value of 2 by day 5. At 36 °C (grower 2), the RQ ascended above 2 on the initial day of exposure and later increased closer to 3 on day 5 of exposure.

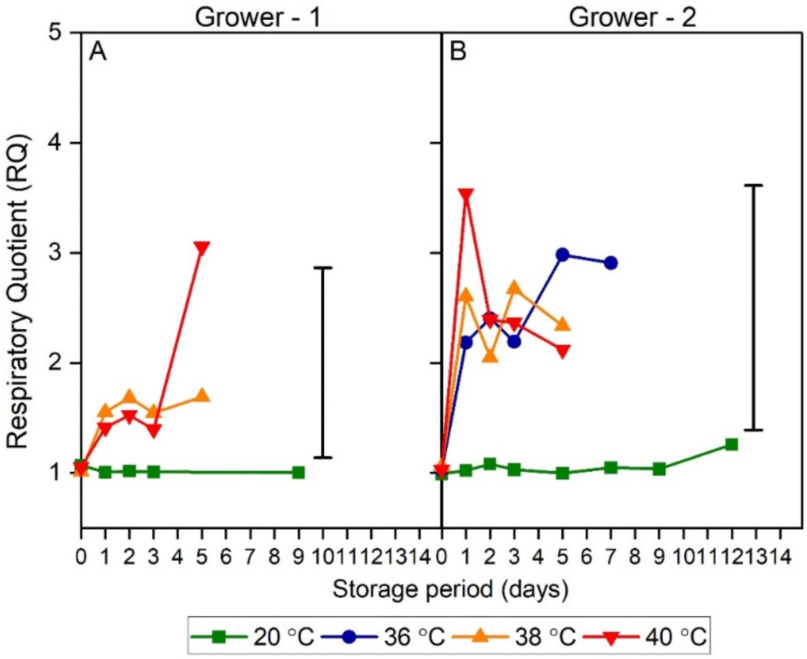


Figure 7.4: Respiratory Quotient (RQ) in 'Hayward' kiwifruit under high temperatures. 36 °C condition was adopted for grower 2 only. Each data point represents an average value of 10 fruit. The initial value at day 0 represents RQ at 0 °C. The error bar represent LSD $_{0.05}$ for the influence of time*temperature interaction on RQ.

7.3.4 Fruit firmness

In grower 1, fruit stored at 38 and 40 °C softened similarly, whereas softening increased with rising temperature for grower 2. Firmness in grower 1 declined from 1.3 kg_f to 0.7 kg_f during 5 days of storage at 38 and 40 °C. In grower 2, firmness declined from 1.1 to 0.4, 0.2 and 0.1 kg_f at 36, 38 and 40 °C, respectively throughout the experiment duration. A slow decline in firmness was noted at 20 °C in both growers reaching approximately 0.7 kg_f by end of storage.

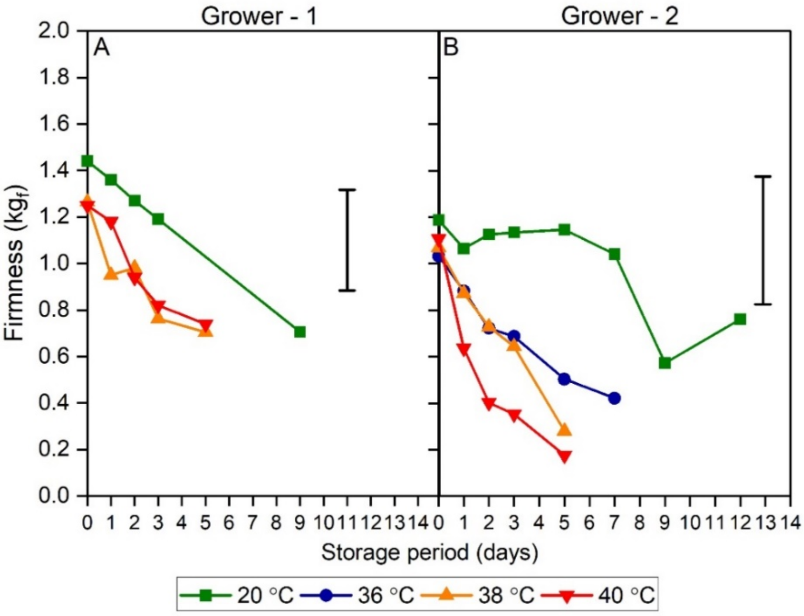


Figure 7.5: Softening in 'Hayward' kiwifruit at high temperatures. 36 °C condition was adopted for grower 2 only. Each data point represents an average value of 10 fruit. The error bar represent LSD $_{0.05}$ for the influence of time*temperature interaction on firmness.

7.3.5 Ethanol content

High-temperature exposure led to an increase in ethanol content over time in both growers. As evident in Figures 7.6-7.7, huge variability in ethanol content after day 2 of exposure existed between individual fruit at high temperatures. For example, in grower 1, on day 5 at 38 °C, ethanol content between 10 fruit ranged between 0.5 to 2.4 g/L. At 20 °C, changes in ethanol content were negligible but increased slightly when firmness dropped to below 0.4 kg_f. Results from the Anderson-Darling normality test indicated that the measured ethanol content between individual fruit is not normally distributed ($P < 0.005$). Non-parametric Kruskal-Wallis test indicates that ethanol content increased with the rise in temperature in both growers (Table 7.2) and the accumulation increased with exposure time at each of the temperatures (Table A.1 and A.2). Results from Post-hoc Dunn-test (Table 7.3) indicate that the ethanol accumulation in grower 1 was significantly different for comparisons between temperatures of 20-38 °C and 20-40 °C and was not significant for 38-40 °C. In grower 2, ethanol accumulation was significantly different when compared between 20-36 °C, 20-38 °C, 20-40 °C, and not significant between 36-38 °C, 36-40 °C and 38-40 °C.

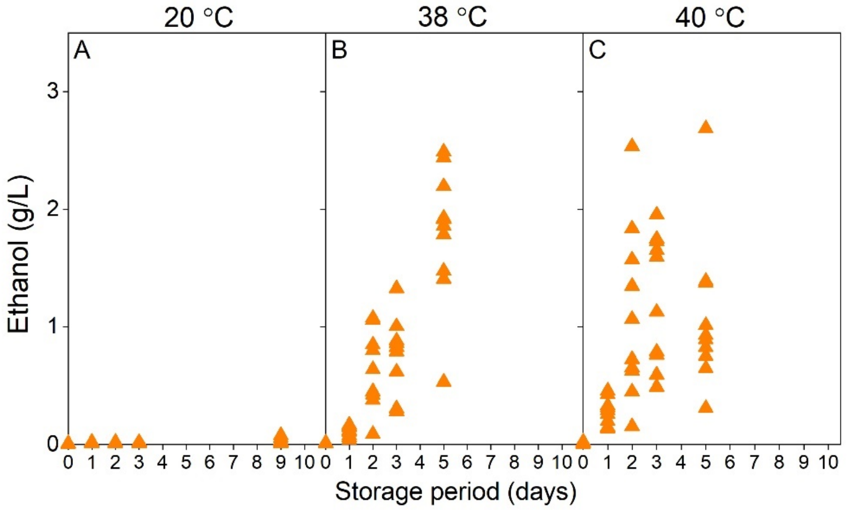


Figure 7.6: Changes in ethanol content in 'Hayward' kiwifruit (grower 1) over time at high temperatures. Each data point represents ethanol content in individual fruit. At each time point, 10 fruit were assessed for ethanol.

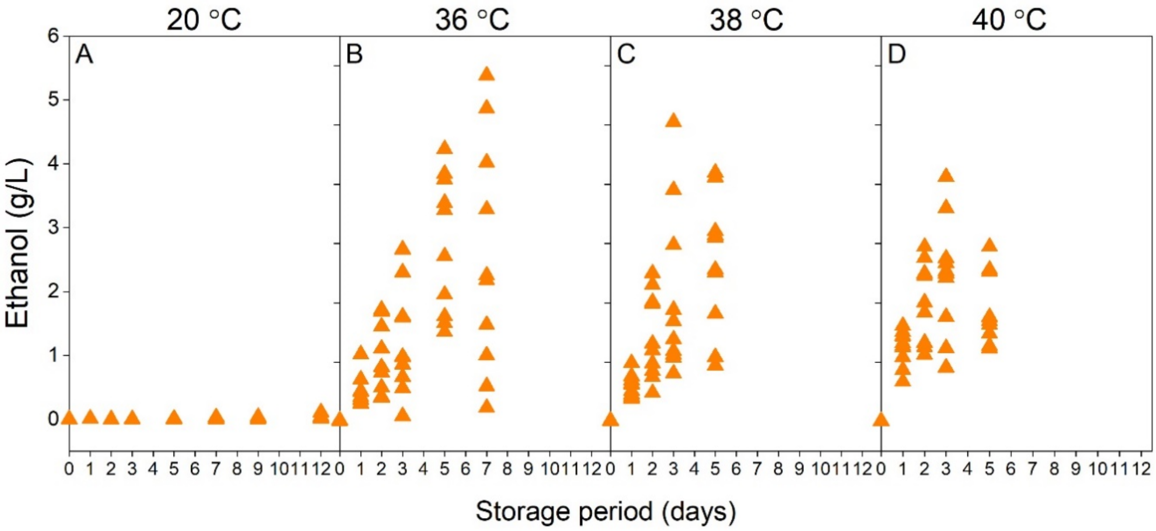


Figure 7.7: Changes in ethanol content in 'Hayward' kiwifruit (grower 2) over time at high temperatures. Each data point represents ethanol content in individual fruit. At each time point, 10 fruit were assessed for ethanol.

Table 7.2: Kruskal-Wallis non-parametric test values for changes in ethanol content at different temperatures. Mean rank represents an average of overall observations within a rank. Z-Value represents absolute value.

Grower	Temperature	Sample size (n)	Median	Mean rank	Z-Value	P-Value
G1	20	50	0.011	36.4	-7.80	0.000
	38	50	0.435	91.7	3.23	0.000
	40	50	0.609	98.4	4.56	0.000
G2	20	80	0.007	47	-11.59	0.000
	36	60	0.944	156.9	4.69	0.000
	38	50	0.985	154	3.83	0.000
	40	50	1.442	160.9	4.62	0.000

Note. Higher the Z-value, the greater the group's average rank from overall average rank. Negative Z-Value = group's average rank is less than overall average rank. Positive Z-Value = group's average rank is greater than overall average rank.

Table 7.3: Pot-hoc Dunn test for multiple comparison for ethanol accumulation between temperatures

Grower	Group comparisons Gp1-Gp2	Sample size (n) Gp1-Gp2	Z-Value	P-Value	Adj P-Value	Adj P-Value significance
G1	20-38 °C	50-50	6.367	$1.92e^{-10}$	$3.83e^{-10}$	****
	20-40 °C	50-50	7.135	$9.64e^{-13}$	$2.89e^{-12}$	****
	38-40 °C	50-50	0.767	0.442	0.442	NS
G2	20-36 °C	80-60	9.267	$1.91e^{-20}$	$1.14e^{-19}$	****
	20-38 °C	80-50	8.544	$1.29e^{-17}$	$5.17e^{-17}$	****
	20-40 °C	80-50	9.097	$9.27e^{-20}$	$4.63e^{-19}$	****
	36-38 °C	60-50	0.221	0.825	0.825	NS
	36-40 °C	60-50	0.299	0.764	0.825	NS
	38-40 °C	50-50	0.498	0.618	0.825	NS

7.3.6 Acetaldehyde content

Minimal changes in acetaldehyde concentration occurred in both growers at high temperatures. Like ethanol, variability existed between individual fruit in acetaldehyde content. In both growers, acetaldehyde concentration increased with storage duration at high temperatures. Results from the Anderson-Darling normality test indicated that the measured acetaldehyde content between individual fruit is normally distributed ($P > 0.005$) in most instances for grower 1 and not normally distributed in most instances for grower 2 ($P < 0.005$). Kruskal-Wallis test indicates that in grower 1, the highest acetaldehyde accumulation occurred at 40 °C followed by 38 and 20 °C and conversely in grower 2, highest acetaldehyde accumulation occurred at 36 °C followed by 38, 40 and 20 °C (Table 7.4). At each temperature, acetaldehyde content increased along with storage duration (Table A.3 and A.4). Results from Post-hoc Dunn-test (Table 7.5) indicate that the acetaldehyde accumulation in grower 1 was significantly different between all temperature comparisons and in grower 2, acetaldehyde accumulation was significantly different when compared between 20-36 °C, 20-38 °C, 20-40 °C, 36-40 °C and not significant between 36-38 °C and 38-40 °C.

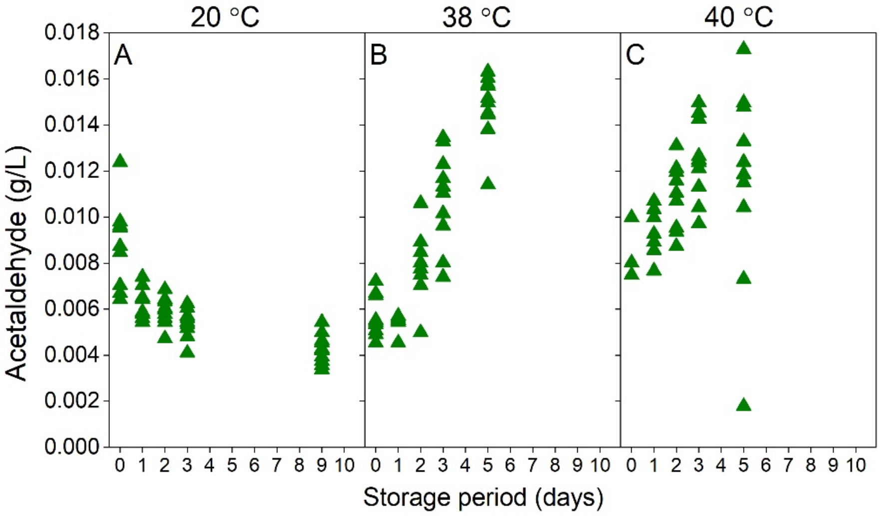


Figure 7.8: Changes in acetaldehyde content in 'Hayward' kiwifruit (grower 1) over time at high temperatures. Each data point represents acetaldehyde content in individual fruit. At each time point, 10 fruit were assessed for acetaldehyde.

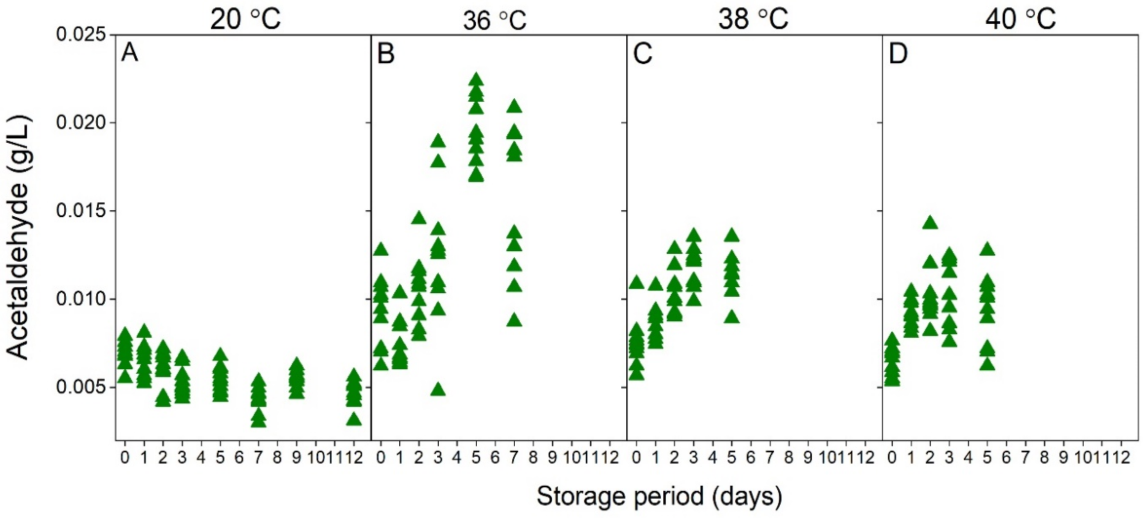


Figure 7.9: Changes in acetaldehyde content in 'Hayward' kiwifruit (grower 2) over time at high temperatures. Each data point represents acetaldehyde content in individual fruit. 10 fruit at each time were assessed for acetaldehyde.

Table 7.4: Kruskal-Wallis non-parametric test results for changes in acetaldehyde content at different temperatures. Mean rank represents an average of overall observations within a rank. Z-Value represents absolute value.

Grower	Temperature	Sample size (n)	Median	Mean rank	Z
G1	20	50	0.005	43.7	-6.33
	38	50	0.007	77.4	0.37
	40	50	0.010	105.4	5.96
G2	20	80	0.005	47.2	-11.57
	36	60	0.010	172.7	6.73
	38	50	0.010	157.4	4.23
	40	50	0.009	138.2	2.03

Note. Higher the Z-value, the greater the group's average rank from overall average rank. Negative Z-Value = group's average rank is less than overall average rank. Positive Z-Value = group's average rank is greater than overall average rank.

Table 7.5: Pot-hoc Dunn test for multiple comparisons for acetaldehyde accumulation between temperatures.

Grower	Group comparisons Gp1-Gp2	Sample size (n) Gp1-Gp2	Z-Value	P-Value	Adj P-Value	Adj P-Value significance
G1	20-38 °C	50-50	3.872	0.000	0.000	***
	20-40 °C	50-50	7.099	$1.25e^{-12}$	$3.76e^{-12}$	****
	38-40 °C	50-50	3.226	0.001	0.001	**
G2	20-36 °C	80-60	10.587	$3.41e^{-26}$	$2.05e^{-25}$	****
	20-38 °C	80-50	8.811	$1.23e^{-18}$	$6.15e^{-18}$	****
	20-40 °C	80-50	7.273	$3.49e^{-13}$	$1.39e^{-12}$	****
	36-38 °C	60-50	1.146	0.251	0.251	NS
	36-40 °C	60-50	2.594	0.0094	0.028	*
	38-40 °C	50-50	1.386	0.165	0.251	NS

7.3.7 Correlation between ethanol content and firmness

An interesting relationship between fruit firmness and ethanol content was observed in this study which was much more evident in grower 2 (Figure 7.11) than in grower 1 (Figure 7.10). In grower 1 at 38 °C, when firmness of the fruit dropped below 1.2 kg_f, ethanol content increased and was greatest in the softest fruit (0.5 to 0.6 kg_f). However, at 40 °C, fruit that had firmness ranging from 0.6 to 1 kg_f had higher ethanol content in comparison to the softest fruit under this temperature. In grower 2, under all higher temperatures, ethanol content surged as firmness dropped below 0.8 $kg_{f.}$ In both growers, ethanol content was observed to be greatest in the softest fruit and in fruit that developed flesh injury symptoms (marked yellow in Figures 7.10C and 7.11B-

D). At 20 °C, it was observed in both growers that the ethanol levels remained at minimal levels and a slight increase was observed when firmness of the fruit dropped to 0.4 kg_f and below.

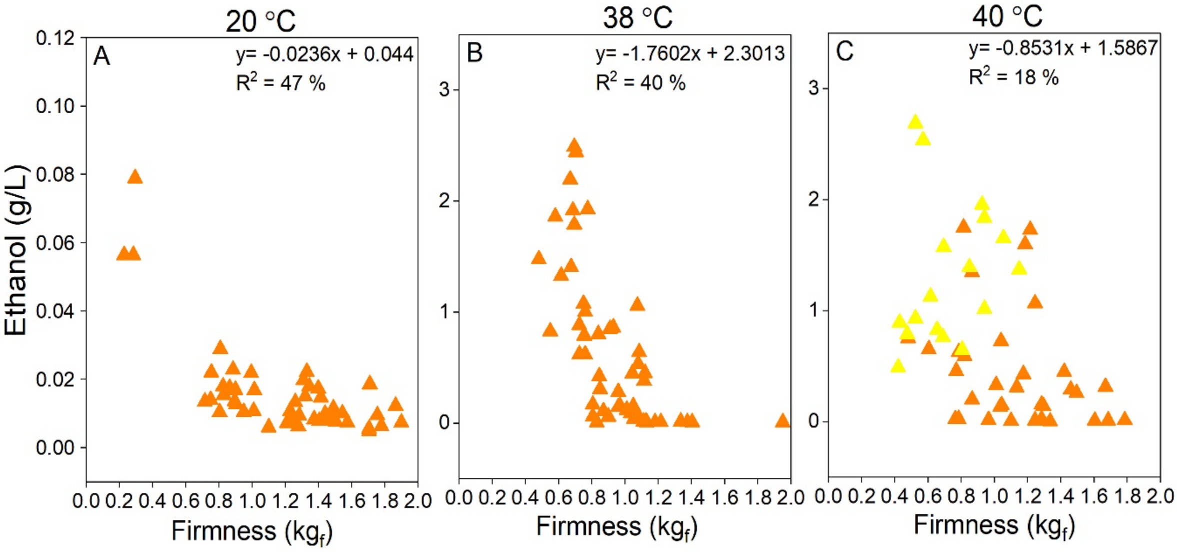


Figure 7.10: Correlation between ethanol content and firmness in 'Hayward' grower 1. Each data point represents ethanol content in individual fruit. Orange and yellow data points represent fruit without heat injury (△ good fruit) and fruit with heat injury (△ fruit with flesh discolouration) respectively. Y scale differs for 20 ° C due to minimal ethanol concentration changes.

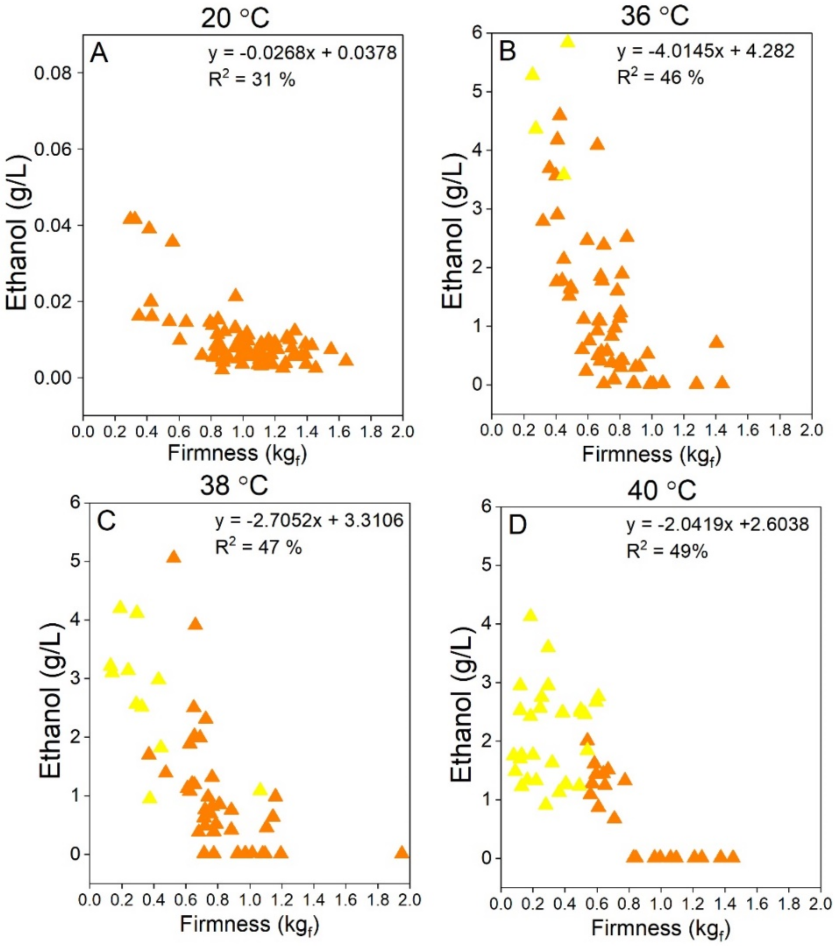


Figure 7.11: Correlation between ethanol content and firmness in 'Hayward' grower 2. Each data point represents ethanol content in individual fruit. Orange and yellow data points represent fruit without heat injury (∆ good fruit) and fruit with heat injury (∆ fruit with flesh discolouration), respectively. Y scale differs for 20 ° C due to minimal ethanol concentration changes.

7.3.8 Correlation between acetaldehyde content and firmness

Acetaldehyde content was higher in fruit which softened below 0.8 kg_f and exhibited flesh injury. In grower 1 (Figure 7.12), a better relationship between firmness and acetaldehyde content was observed in fruit stored at 38 °C followed by 20 °C whilst a poor relationship existed in fruit stored at 40 °C. In grower 2 (Figure 7.13), the relationship between firmness and acetaldehyde was highest in fruit exposed to 36 °C followed by 40 and 38 °C whereas fruit stored at 20 °C had the weakest relationship. Overall, it was noted that the softest fruit contained the highest concentration of acetaldehyde.

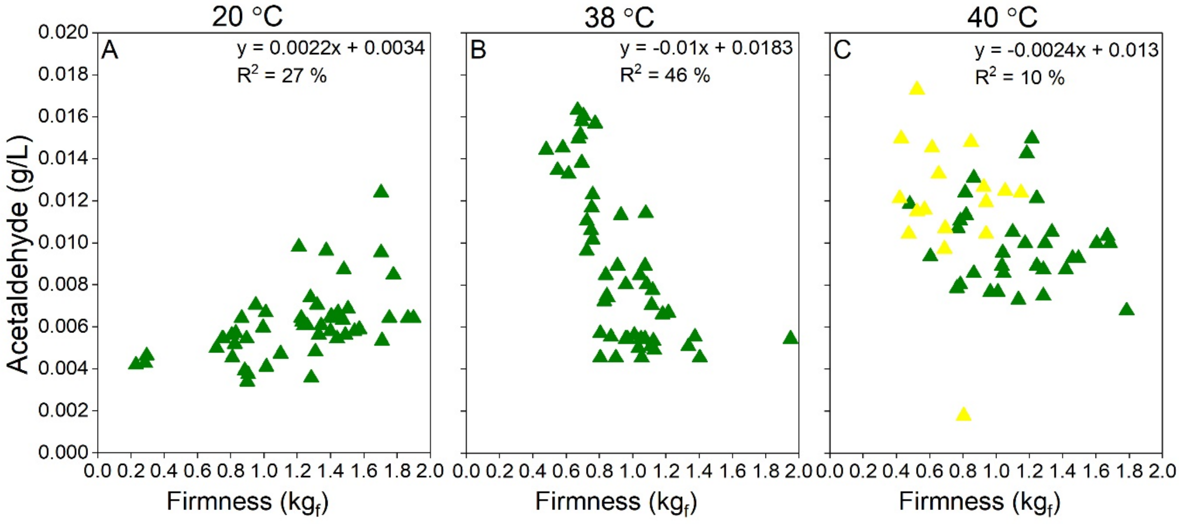


Figure 7.12: Correlation between acetaldehyde content and firmness in 'Hayward' grower 1. Each data point represents acetaldehyde content in individual fruit. Green and yellow data points represent fruit without heat injury (Δ good fruit) and fruit with heat injury (Δ fruit with flesh discolouration), respectively.

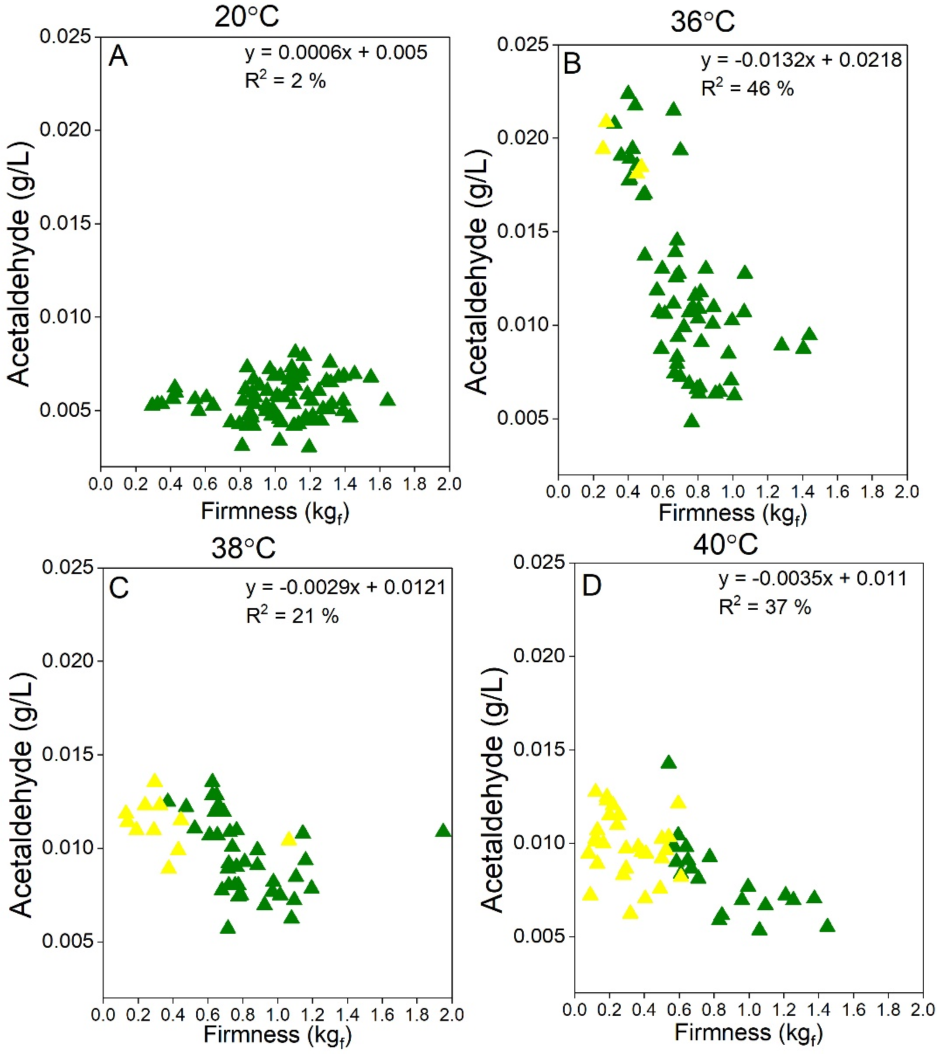


Figure 7.13: Correlation between acetaldehyde content and firmness in 'Hayward' grower 2. Each data point represents acetaldehyde content in individual fruit. Green and yellow data points represent fruit without heat injury (Δ good fruit) and fruit with heat injury (Δ fruit with flesh discolouration), respectively.

7.3.9 Heat injury incidence

Heat injury symptoms were expressed as cavity formation and flesh discolouration (Figure 7.15). The injury was observed to spread from the internal locular region to the peripheral region. Cavity formation was evident closer to the core region. In grower 1, the symptoms became evident only at 40 °C, initially on day 2 of exposure and subsequently increased to 80% on day 5 of exposure. In grower 2, heat injury incidence became evident at all high temperatures with the symptoms appearing on days 1,3 and 5 of exposure to 40, 38 and 36 °C, respectively. In grower 2, at 40 °C, 90 % incidence was noted on day 1 of exposure and was 100% on the remaining days of exposure, whilst at 38 °C, the incidence increased from 20 to 90% from day 3 to day 5 of exposure.

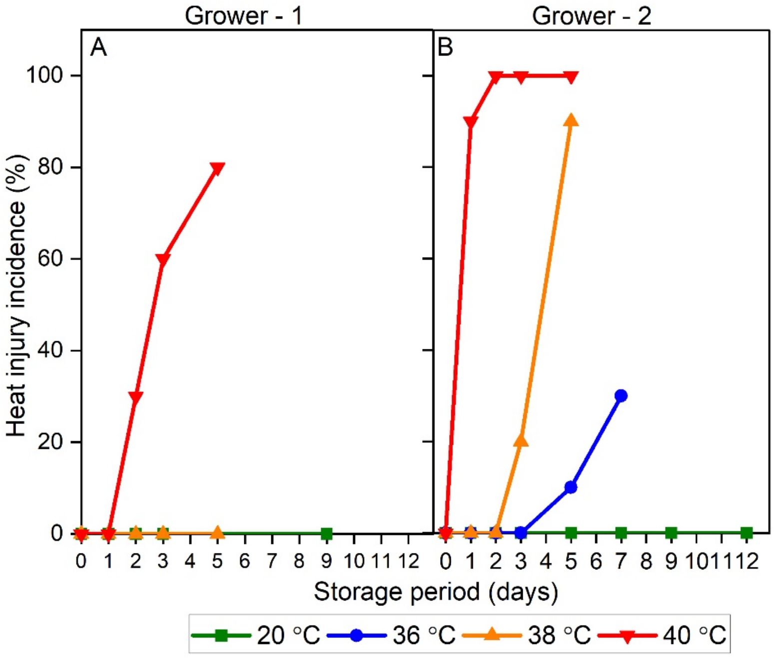


Figure 7.14: Heat injury incidence in 'Hayward' kiwifruit at high-temperatures.

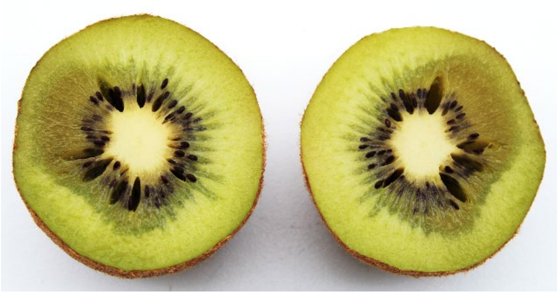


Figure 7.15: Mild (left) and severe (right) heat injury symptoms evident in 'Hayward' grower 1 at 40 °C.

7.3.10 Minitrial- Rise in ethanol and acetaldehyde in over soft kiwifruit

In this additional study, grower 2 fruit with initial firmness of approximately 1 kg_f were exposed to different temperatures i.e. 0, 20, 30, 33 and 40 °C, and were measured for ethanol and acetaldehyde content when firmness under each of the storage temperatures dropped to below 0.6 kg_f. As evident from Figure 7.16A, ethanol content remained minimal at 20 °C even in overripe fruit (< 0.4 kg_f), increased slightly at 30 °C and significantly at 33 and 40 °C. As previously noted, minimal change in acetaldehyde happened with the content being highest in fruit at 40 °C. Heat injury incidence was evident in 33 and 40 °C stored fruit.

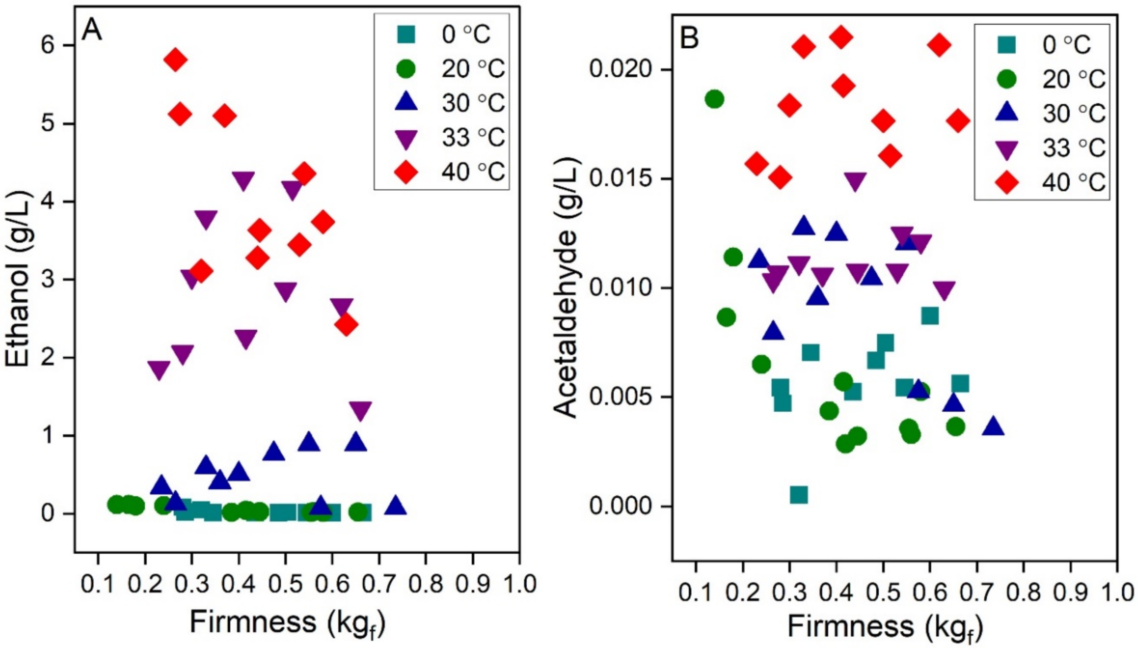


Figure 7.16: Correlation between firmness and ethanol (A), acetaldehyde (B) content in 'Hayward' grower 2 with firmness closer to 0.6 kg_f and below. A set of 10 fruit were exposed to each of the temperatures.

7.4 Discussion

Respiration is a key catabolic process providing energy to the overall cell function (Atkin and Tjoelker, 2003). At the postharvest stage, fruit storage life and respiration rate are contrarily linked wherein lowering respiration extends storage life while an increase in respiration rate shortens storage life due to increased consumption of substrates (Kader and Saltveit, 2003; Bessemans, 2018). In fruits, temperature is the foremost factor affecting the respiration rate followed by O_2 and CO_2 partial pressures (Hertog et al., 1998; Hertog et al., 2001; Lammertyn et al., 2001; Bessemans, 2018). Results from this study suggest that exposing ‘Hayward’ kiwifruit at edible ripeness to high temperatures (> 30 °C) initiates anaerobic respiration as evident from the RQ (Figure 7.4) and ethanol results (Figures 7.6-7.7).

The obtained RQ results although being higher at high temperatures, may still not be solid evidence to indicate the activation of anaerobic respiratory metabolism at high temperatures. This is because large errors were found to exist in the measurements of O_2 consumption rates even after frequent calibration of the O_2 sensor with O_2 β-standard (21.15 ± 0.10%). This was also the case following larger time intervals between the initial and final O_2 concentration sampling. Unlike fruit CO_2 production rate, accurate O_2 consumption measurements are challenging to achieve especially in static respiration assessment methods (Saltveit, 2019). This as suggested by Saltveit (2019) is due to the presence of higher oxygen concentrations in the environment which transforms smaller error percentages to be significant. Additionally, high temperature during enclosure may have increased pressure build up and thus contributed to measurement error.

Despite RQ measurements being unreliable, the rise in ethanol content over time confirms that high temperatures stimulate anaerobic respiratory metabolism in kiwifruit. Minimal increases in ethanol at 20 °C even in senescent fruit indicate that ethanol accumulation was exclusively promoted by high temperatures. Interestingly, ethanol content increased with duration at 38 °C in grower 1 without any symptoms of heat injury. Further, ethanol accumulation between fruit that had developed or not developed heat injury were similar at 40 °C in grower 1 (Figure 7.10C). These observations could be suggesting that the heat injury incidence and ethanol accumulation may not be directly related. Heat injury symptoms being evident in firm fruit suggests that the incidence may not also be due to senescence. This being said, the higher ethanol and acetaldehyde content observed in fruit exhibiting heat injury symptoms, may be a consequence of tissue damage rather than the cause of tissue damage. Since most of the fruit with heat injury incidence were at the senescent stage, senescence could be an additional cause for the higher ethanol and acetaldehyde content in the incidence-prone fruit. The pattern of occurrence of the incidence i.e. spreading from core to outer pericarp as well as cavity formation in the locular region suggests that this incidence is most likely due to CO_2 injury as previously evident in the case of apples (Volz et al., 1998) and pears (Lammertyn et al., 2000).

It is noted that higher CO_2 concentrations within fruit exist in the core region (Schotsmans et al., 2004; Ho et al., 2008) and this region has fewer intercellular spaces than the pericarp region (Reeve, 1953; Burton, 1974). Both of these factors may have influenced the incidence pattern spreading from the center to the peripheral region of the fruit. However, it is quite difficult to elucidate a mechanism by which high CO_2 independently influences tissue injury without the production of anaerobic metabolites. One possibility is the accumulation of succinic acid, a toxic compound known to cause CO_2 core breakdown in apples and pears (Hulme, 1956; Bendall et al., 1960; Williams and Patterson, 1964; Frenkel and Patterson, 1973; Monning, 1983; Rolle, 1987). High CO_2 exposure results in increased accumulation of succinic acid (Ranson, 1953; Williams and Patterson, 1964) and on the other hand suppresses the activity of succinate dehydrogenase enzyme (SDH), which is involved in its oxidation to fumarate in Kreb's cycle (Ranson et al., 1960). Since succinic acid is one of the organic acids present in kiwifruit (Yook, 2009) and was found to rise in kiwifruit upon exposure to high CO_2 concentrations (Lee et al., 1989), its increased accumulation could be one of the possibilities for the occurrence of the heat injury symptoms. There could be other stress-induced mechanisms in influencing this disorder either independently or synergistically but this investigation mainly suggests that the accumulation of anaerobic metabolites may not be the sole cause for the occurrence of heat injury at high temperatures.

The presence of anaerobic metabolites in minute amounts under normal oxygen levels have been reported in kiwifruit (Thomas and Sfakiotakis, 1997; Botondi et al., 2012), apples (Saquet et al., 2000; Boeckx et al., 2019), pears (Boersig et al., 1988), avocados (Ke et al., 1995; Burdon et al., 2007), litchi (Pesis et al., 2002), oranges (Onslow and Barker, 1927), melons (Biais et al., 2010) and bell peppers (Zuckermann et al., 1997). In 'Hayward' kiwifruit, it is observed that little or no changes in ethanol content happen during the ripening transition from eating soft to the overripe stage (Paterson et al., 1991). In contrast to this, Young and Paterson (1985) found minimal levels of ethanol in 'Hayward' kiwifruit above (0.8 to 1 kg_f) or at edible ripeness stage (0.5 to 0.6 kg_f) but noted the accumulation of ethanol increased as fruit approached the senescent stage, an observation which was also reported by López et al. (1999). Similar to these previous reports, a minute level of ethanol was detected in this study at 20 °C with the concentrations slightly elevating in fruit at the senescent stage (firmness < 0.4 kg_f).

With the increase in storage temperatures above 30 °C, the accumulation of ethanol increased linearly with time indicating a considerable switch from the normal aerobic respiratory metabolism. In general, as reported in several fruits, the respiratory switch is mainly influenced by O_2 and CO_2 concentrations within the fruit storage environment (Thomai and Sfakiotakis,1997; Argenta et al., 2002; Blanch et al., 2015). Reducing oxygen concentrations to below lower oxygen limit (LOL) or increasing CO_2 to very high levels both would activate fermentation resulting in off-flavours, abnormal ripening and occurrence of disorders (Ke and Kader, 1992; Ke et al., 1995; Yearsley et al., 1997; Argenta et al., 2002; Nugraha et al., 2019). For example, in a study conducted by Botondi et al. (2012), it was found that storing 'Hayward' kiwifruit under ultra-low (0.25%) and low (1%) levels of oxygen resulted in a significant rise in ethanol and acetaldehyde production after 34 days of cool storage as well as during subsequent shelf-life in comparison to storage at commercial CA conditions (2% O_2 and 5% CO_2). These authors concluded that the rise in ethanol content under these hypoxic conditions was due to increased activity of anaerobiosis-related enzymes such as Pyruvate decarboxylase (PDC), alcohol dehydrogenase (ADH), lactate dehydrogenase (LDH) and glutamate pyruvate transaminase enzymes (GPT). The activities of these anaerobiosis enzymes in influencing ethanol and acetaldehyde accumulation in kiwifruit have recently been confirmed by Ali et al. (2021).

Thomai and Sfakiotakis (1997) observed an increase in ethanol and acetaldehyde content in kiwifruit stored under low oxygen concentration (0.5% O_2 and 99.5% N_2) and noted that the accumulation was higher in late-harvested fruit than in early-harvested fruit. Similarly, López et al. (1999) reported increased ethanol accumulation in kiwifruit as a result of high CO_2 exposure under normal oxygen conditions and speculated that the crabtree effect might have influenced fermentation since ethanol and sugar content in ripe fruit were inversely related. Since increased ethanol production at higher temperatures occurred under normally available oxygen conditions, the possibility for the occurrence of crabtree effect was investigated by establishing a correlation between ethanol and TSS content but it was found that no such relationship exists between these two factors (data not presented). Therefore, this suggests that increased ethanol accumulation as a result of high temperature exposure is mainly due to oxygen deficit within the fruit internal atmosphere, with the RQ results further suggesting the same.

Storing fruit at higher storage temperatures results in increased respiration rate as well as increases fruit resistance to gaseous diffusion (Ke and Kader, 1992). As a result of increased respiratory activity, more demand for O_2 occurs but due to limited diffusion of O_2 within the fruit, an oxygen gradient arises resulting in fermentation. Within fruit, gas transport is mainly influenced by the cellular structure and organisation and is further influenced by the presence of intercellular air spaces (Mendoza et al., 2007; Verboven et al., 2008). During fruit respiration, O_2 first diffuses through the epicarp of the fruit and subsequently transports into the intercellular spaces and enters into the cell through the cell membrane and finally reaches mitochondria wherein it gets utilised for energy synthesis (Ho et al., 2006).

CO_2 travels through a reverse diffusion pathway (Ho et al., 2006). Between O_2 and CO_2, O_2 is known to have reduced diffusive properties in water and lipids as elucidated by Trout et al. (1942) in apples. Due to this, the transport of O_2 is mainly through intercellular spaces while CO_2 transports both by diffusing through the intercellular airspaces as well as through cells (Ho et al., 2014). Therefore, under high temperatures wherein fruit respire at a higher rate, the overall system of gas transport is affected resulting in lower O_2 gradients within the fruit's internal atmosphere.

Further, intercellular spaces act as the main gaseous transport system within the fruit (Ho et al., 2006). As suggested by Burdon et al. (2005), as firmness in kiwifruit drops below 1 kg_f, the intercellular airspaces in the outer pericarp region decline due to liquid logging, restricting O_2 transport and thereby causing fermentation. The decline in intercellular air spaces may not only restricts O_2 transport within the fruit but also affect CO_2 movement out of the fruit (Ben-Yehoshua et al., 1963; Burg and Burg, 1965). As observed in this study, ethanol content increased with advanced softening from an edible ripe to overripe state. Therefore reduced intercellular air spaces with softening advancement may further influence ethanol accumulation other than just high temperatures.

Similar to ethanol, the rise in acetaldehyde concentration in overripe ‘Hayward’ kiwifruit has been reported by Botondi et al. (2012) and Friel et al. (2007). The rise in acetaldehyde at the senescent stage is also observed in pears (Janes, 1978), mangoes (MacLeod and Snyder, 1985) and tomatoes (Gustafson, 1934). The presence of ethanol and acetaldehyde in the fruit is in the ratio of 1:100 (Thomas, 1925). When anaerobic respiration is active, acetaldehyde is converted into ethanol by the action of enzyme alcohol dehydrogenase (ADH) and therefore acetaldehyde concentration is expected to decline or remain at a minimal level with increased production of ethanol as observed in apples (Boeckx et al., 2019) and tomatoes (Gustafson, 1934). However, this may not be the case when ethanol accumulation within the cell reaches a toxic level wherein ADH acts reversely by oxidising ethanol to acetaldehyde (Monk et al., 1987; Zuckermann et al., 1997; Botondi et al., 2012). Minute concentrations of acetaldehyde with very little change over time were observed indicating that it is actively converted into ethanol. Acetaldehyde concentration, similar to ethanol was highest at high temperatures. The obtained acetaldehyde results also confirm the previous reports that the fruit closer to the senescent stage accumulate higher acetaldehyde.

Other than the hypoxic or anoxic conditions, an investigation by Kimmerer and Kozlowski (1982) elucidated that stress could result in the accumulation of anaerobic metabolites in plant tissues. These authors observed that in saplings of red pine and paper birch, the accumulation of ethanol and acetaldehyde increased on exposure to multiple environmental stresses in absence of internal hypoxic conditions. Further, the accumulation of these metabolites continued to rise even when O_2 partial pressure in the plants surrounding atmosphere was increased which confirmed stress regulation on ethanol and acetaldehyde accumulation. It was suggested that stress might have affected O_2 uptake during glycolysis or could have enhanced the activity of the pyruvic decarboxylase enzyme which is involved in fermentation. Although no relatable investigations are available on fruits, it is more likely in the current study that the O_2 deficit could have caused ethanol and acetaldehyde accumulation at high temperatures with stress also having an additional effect on anaerobic metabolites accumulation.

Between the two growers, grower 2 was more sensitive to heat stress in comparison to grower 1 since it exhibited a higher respiration rate and developed heat injury incidence at temperatures wherein no incidence occurred in grower 1. Similarly, the increase in ethanol over time was highest in grower 2 under each high temperature (Table A.2). In apples, it is suggested that maturity affects tolerance to heat stress with more mature fruit being more sensitive to heat exposure due to advancement in the ripening processes (Fan et al., 2011). The two growers used in this study were harvested on similar dates but grower 2 at the time of harvest was more mature than grower 1. Also, since this trial was first conducted for grower 1 and subsequently for grower 2, the durations of cool storage before high temperature exposure were different, being longer for grower 2 than grower 1. To minimise the variability in the ripeness stage between these two growers before exposure, non-destructive firmness measurements by Softness Fruit Sensor (SFS, The New Zealand Institute for Plant and Food Research Limited) were adopted but by the time the trial started for grower 2, the fruit were much softer than grower 1 (Table 7.1). Therefore, differences in the ripeness stage between the growers may have resulted in differences in response to high temperature exposure.

7.5 Conclusion

The influence of high temperatures in activating anaerobic respiratory metabolism in kiwifruit is elucidated. The obtained results suggest that ethanol content increases over time at high temperatures but varies largely between individual fruit. The increase in ethanol in kiwifruit at high temperatures could be an additional risk for quality maintenance in traditional tropical markets. The observed relationship between the accumulation of anaerobic metabolites and the incidence of heat injury suggests that heat injury incidence may not be exclusively influenced by the accumulation of anaerobic metabolites. An investigation aiming to establish a relationship between CO_2 production, succinic acid accumulation and heat injury incidence could be considered as a further approach to gaining an understanding of the incidence of heat injury in kiwifruit. It must be admitted that the differential tolerance observed between the two growers to high temperatures has made it challenging to give a better conclusion for the relationship between ethanol accumulation and heat injury incidence. Hence, growers with consistent responses to high temperatures must be identified through preliminary studies and subsequently used in experiments for the establishment of better conclusions, especially in these kinds of investigations. In Chapter 5, 1-MCP treated ‘Hayward’ kiwifruit had a lower respiration rate in comparison to untreated fruit at 33 °C. Therefore, investigating if 1-MCP treatment minimises ethanol accumulation at high temperatures could be an interesting aspect to be considered for future research.

Chapter 8: Overall discussion and future research recommendations

8.1 Introduction

The majority of the New Zealand grown kiwifruit are destined for sale at international markets either through modern or traditional retailing systems. The offshore success for the New Zealand kiwifruit industry depends upon good consumer satisfaction which may be evident as recurrent purchases (Hashmatt, 2021). A key criterion influencing consumer satisfaction is kiwifruit quality at eating ripe stage (Wright, 2005; Ward and Courtney, 2013). Kiwifruit handled and marketed through traditional retailing systems may have reduced eating quality before reaching final consumers due to insufficient or unavailability of refrigeration (Bellavi Jayashiva, 2012). Reduced fruit quality could result in poor eating experiences affecting fruit marketability as well as consumers perception of New Zealand kiwifruit (Ward and Courtney, 2013).

This study identified in a case study that continuous exposure of kiwifruit (at edible firmness) to temperatures over 30 °C, (and as high as 40 °C) in combination with increased ethylene concentrations (up to 150 nL L^{-1}) to be possible under traditional retailing systems in tropical markets (Chapter 3). These identified conditions were adopted (as storage conditions) in subsequent experiments to gain scientific understanding of the resulting kiwifruit physiology and quality responses to the supply chain potential conditions.

In Chapter 4, it was observed that exposure of kiwifruit (after long term storage and at edible firmness) to 40 °C for a short duration (12 h) resulted in irrecoverable physiological damage expressed as rapid decline in respiration rate (Figure 4.2). It was demonstrated in chapter 6 that kiwifruit after long-term storage (19-21 weeks) could still recover from exposure stress at 38 °C but not at 40 °C (Figure 6.3). These two chapters (Chapters 4 and 6) together conclude that continuous exposure of kiwifruit (after long-term storage) to 40 °C for 12 h results in physiological damage indicating 12 h to be the maximum safest duration of exposure to 40 °C.

No indications of physiological damage (such as rapid CO_2 decline) were evident in 33-38 °C exposed fruit. However, prolonged exposure to 33-38 °C (> 48 h) resulted in the incidence of heat injury expressed as flesh discolouration (in 'Hayward') and water-soaked symptoms. Heat injury incidence at 33-38 °C varied between growers (in both cultivars) and was highest in 'Hayward' (Figure 6.9) than in 'SunGold™' (Figure 6.10). Considering kiwifruit physiological responses and occurrence of heat injury, the safest continuous exposure duration to 33-38 °C could be 48 h. However, if fruit are intended to be further cool stored after exposure to 33-38 °C, exposure should be limited to 24 h since fruit cool stored (for a week at 0.5 °C) beyond 24 h of exposure had developed a 100% incidence of internal breakdown symptoms at these temperature ranges (Figure 6.13). The observed internal breakdown symptoms in kiwifruit cool stored beyond 24 h of exposure to high temperatures (33-40 °C) were like the oxygen deficit induced disorder in apples and pears (Pedreschi et al., 2009).

Findings from Chapter 5 suggest that ethylene significantly advances softening in kiwifruit at temperatures over 30 °C. Inhibiting ethylene perception (by 1-MCP treatment) in soft kiwifruit (firmness ≤ $1kg_f$) resulted in firmness retention throughout 5 days of storage at 33 °C (Figure 5.4). This finding indicates that inhibition of ethylene perception might be a potential strategy to prolong kiwifruit shelflife at traditional retail conditions in tropical regions.

A significant increase in ethanol content developed with time at temperatures over 30 °C (Chapter 7) but not at 20 °C (even in senescent fruit) indicates the activation of anaerobiosis in kiwifruit at high temperatures. The activation of anaerobic metabolism could mainly be due to increased metabolic rate as well as a stress stimulus response. The immediate rise in ethanol content in kiwifruit in the 30-40 °C ranges (Figures 7.6-7.7) suggest the potential risk of off-flavour development even in healthy fruits which do not initially exhibit either physiological or visible symptoms of heat injury. Interestingly, no direct relationship was found to exist between ethanol content and the observed unique high temperature disorder. The mechanisms which could be causing the observed high temperature disorder still needs to be elucidated.

The contributions of the overall experiments in this study to the existing literature on kiwifruit responses to high temperatures, the experimental challenges, and finally, interesting observations which may need further understanding and direct future research opportunities are discussed in detail in the final discussion and conclusion chapter.

8.2 Tropical market environments

Documented information on the environmental conditions prevalent in traditional markets of tropical regions is limited. While a general perception that fresh produce are exposed to high temperatures in traditional marketing systems exists, identifying exposure ranges remains crucial to experimentally simulate the traditional marketing conditions for scientific understanding.

Previously, Bellavi Jayashiva (2012) conducted on spot measurements of fruit core temperature along kiwifruit supply chains in India and identified that at retail, the highest temperature exposure ranging from 19.8-27.4 °C occurred. However, since the key focus of this past study was to understand the influence of supply chain conditions on kiwifruit quality, and not to identify the prevalent environmental conditions, a further study was required to elucidate the potential sale conditions of kiwifruit in regions wherein traditional marketing systems remain dominant.

The findings from the survey (Chapter 3) conducted during a similar (summer) season and within similar focused cities of Bellavi Jayashiva (2012) suggests that kiwifruit are continuously exposed to temperatures of 25-40 °C (varying between cities) at traditional retail stores (Figure 3.4). The mean day temperatures recorded in the current study at Delhi, Mumbai and Bengaluru were 36.1-36.3, 30.7-32.4 and 27.8-28.5 °C, respectively. It is expected that fruit core temperature (not assessed in the survey) remains slightly higher than ambient temperatures (Wang et al., 2001). The temperature recordings obtained from the survey are greater than the previous reporting of Bellavi Jayashiva (2012) or the traditionally adopted ambient conditions (20-25 °C) in postharvest experiments.

A further finding from the survey was the concentrations of ethylene at final retailing conditions in traditional marketing systems (Figure 3.6). The closest previously available information was the ethylene concentrations prevalent in modern fresh produce retailing systems (Warton, 2000; Rees, 2011; Lu 2020). The highest ethylene concentrations recorded at the retail display area in traditional markets were higher than those previously reported in modern retails in the investigations of Lu (2020), Rees (2011) and Warton (2000). This could be due to ethylene measurements being conducted in ex-situ environments at traditional markets. Anthropogenic sources such as vehicle and factory exhausts could be potential sources contributing to increased ambient ethylene concentration at the traditional market vicinity. The obtained data ranges for ethylene and temperatures in the survey (Chapter 3) could be considered as example conditions of traditional marketing systems of tropical regions in future studies which aim to understand fruit postharvest responses to tropical conditions.

8.3 Effect of fruit maturity on high temperature responses

Fruit responses to high temperatures are significantly influenced by the stage of fruit maturity at the time of exposure (Fan et al., 2011). The influence of high temperatures on ripening mechanisms of firm kiwifruit has previously been elucidated (Antunes and Sfakiotakis, 1997; Antunes and Sfakiotakis, 2000). The findings from the case study (Figure 3.8) and of Bellavi Jayashiva (2012) (Figure 2.7) suggest kiwifruit marketed in retail stores (wherein the highest temperature exposure occurs) are at edible firmness (0.4-1.2 kg$_f$) stage. Therefore, in the current study, edible firmness was considered as the stage of fruit maturity exposed to high temperatures.

Antunes and Sfakiotakis (2000) found firm kiwifruit (5.4 kg$_f$) after harvest can recover from exposure stress at 40 °C after 24 h of exposure and exhibited physiological damage symptoms at 45 °C. However, findings from the current study suggest kiwifruit at edible firmness are more prone to not tolerating heat stress than firm fruit as they failed to recover from exposure stress at 40 °C (Figures 4.2 and 6.3). In 'Hayward', if firmness at the time of exposure is > 1 kg$_f$, temperatures over 35 °C reduce softening and conversely if firmness is below 1 kg$_f$, softening increases with a concomitant rise in temperature over 35 °C (Figure 8.1B).

'Hayward' fruit with firmness below 1 kg$_f$ are closer to ethylene autocatalysis (Stec et al., 1989; Ritenour et al., 1999; Schroder and Atkinson, 2006). High temperature exposure may stimulate ethylene production and accelerate softening while a delay in ethylene autocatalysis may occur in fruit of firmness over 1 kg$_f$. This lag phase for ethylene autocatalysis in firm ‘Hayward’ fruit (> 1 kg_f) could plausibly be mediating softening inhibition over 35 °C. Further, although the incidence of heat injury at 40 °C occurred in both firmness ranges (above or below 1 kg_f) after similar exposure duration, the incidence was highest in fruit with initial firmness below 1 kg_f.

Minimal firmness changes occurred in ‘SunGold™’ at 33-38 °C irrespective of varying ranges of initial firmness (at exposure) between growers. At 40 °C, inconsistent softening responses were observed in ‘SunGold™’ between the two investigations (Chapters 4 and 6). In Chapter 6, ‘SunGold™’ fruit with firmness below 1 kg_f softened gradually and retained firmness at eating ripeness even after 5 d at 40 °C (Figure 6.6). Interestingly, in one grower line which had an initial firmness of 1.04 kg_f, no differences in softening rate was observed across the 33-40 °C temperature ranges (Figure 6.6C). However, in another experiment (Chapter 4), wherein fruit had softened more (0.69-0.84 kg_f) due to longer duration of cool storage (22 weeks), fruit firmness declined to overripe stage in just 3 d of exposure to 40 °C (Figure 4.5).

Softening trends observed in ‘Hayward’ and ‘SunGold™’ at temperatures over 30 °C (in Chapters 4 and 6) indicate that if fruit reaches retail with the highest firmness value within the eating firmness range, fruit marketable life could be retained for longer. Having said that, this suggestion remains applicable only to the 30-38 °C ranges under which exposure stress is recoverable (based on CO_2 production trend) but not at 40 °C wherein fruit fail to recover from exposure stress beyond 12 h exposure.

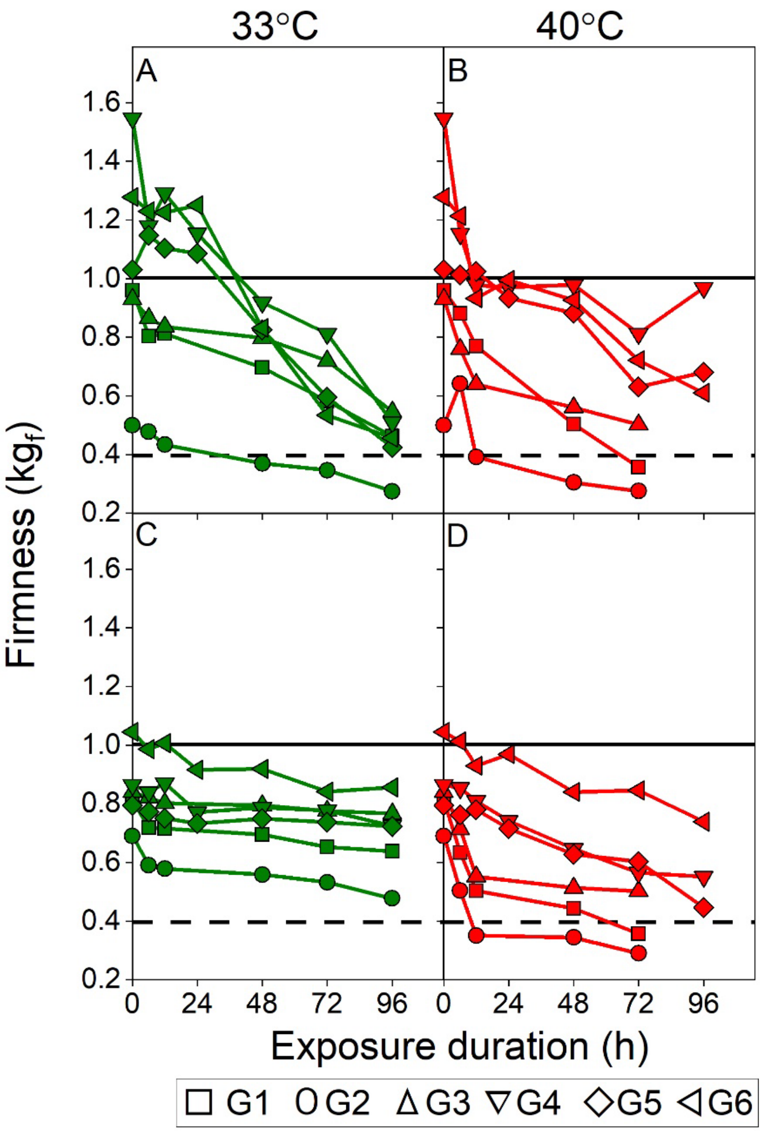


Figure 8.1: Softening observed between the grower lines with varying initial firmness at the point of high temperature exposure in 'Hayward' (A-B) and 'SunGold™' (C-D) at 33 (A and C) and 40 °C (B and D). Each data point represents average value of 30 fruit (n=30). The solid and dashed horizontal lines represent the highest and lowest firmness value of the eating window, respectively.

8.4 Cultivar differences

In 'SunGold™', softening was less accelerated by high temperatures than 'Hayward' (Figure 4.5 and 6.6). The observed differential softening responses between 'Hayward' and 'SunGold™' cultivars at high temperatures may be due to ethylene synthesis and softening mechanisms being differentially influenced by high temperatures in these two cultivars resulting in differences in tolerance as in apples (Johnston et al., 2001). 'Hayward' and 'SunGold™' belong to the genus *Actinidia Lindl* which are known to be highly variable in terms of climatic requirements for growth (Ferguson, 1999) and it should not be unexpected that postharvest performance of these species is influenced by their natural origins (Burdon and Lallu, 2011).

'Hayward' belonging to *Actinidia deliciosa* species requires more chilling periods to successfully bear fruit (Dichio et al., 2015). Conversely, *Actinidia chinensis* cultivars tolerate slightly warm winters (Dichio et al., 2015) and are more sensitive to low storage temperatures than 'Hayward' (Burdon et al., 2014c). These observations suggest that 'Hayward' possesses better tolerance to low temperatures whilst 'SunGold™' may be more tolerant to high temperatures.

8.5 Role of ethylene in tropical conditions

Kiwifruit is highly sensitive to ethylene and even very low concentrations of ethylene (0.005-0.01 $\mu L\ L^{-1}$) in a storage environment has the potential to restrict long-term storage (Pratt and Reid, 1974; Kim, 1999; Wills et al., 2001; Antunes, 2007; Atkinson et al., 2011; Defilippi et al., 2011; Pranamornkith et al., 2012; Jabbar and East, 2016). Preventing ethylene exposure remains a challenge both in modern and traditional fresh produce supply chains but between these two, ethylene exposure under tropical conditions could have more detrimental effects due to high temperature and ethylene exposure interactions. For example, Antunes and Sfakiotakis (2000) observed that at temperatures of 30-34 °C, kiwifruit remained firm (> 4.5 kg_f) throughout 120 h but the presence of propylene (an ethylene analog) at 30-34 °C advanced softening to 0.5 kg_f.

In this study, fruit of both ‘Hayward’ and ‘SunGold™’ cultivars were at edible firmness (≤ 1 kg_f) at the time of exposure to ethylene (150 nL L^{-1}) at 33 °C. No softening changes in 1-MCP treated fruit (inhibiting ethylene perception) and softening changes in untreated fruit (exposed to either ethylene or not) suggest ethylene significantly advanced softening at temperatures over 30 °C (Figure 5.4). On the other hand, if ethylene further advanced softening at high temperatures, untreated fruit exposed to ethylene should have softened faster than those stored in air. However, softening in both untreated fruit categories (i.e. fruit exposed to either ethylene or not) occurred almost similarly in ‘Hayward’.

An explanation for the observed similar softening response in ‘Hayward’ could be due to an increase in endogenous ethylene concentration immediately upon high temperature exposure resulting in the application of exogenous ethylene being redundant. The initiation of autocatalytic ethylene production in ‘Hayward’ was confirmed by the measurement of ethylene concentrations from the outflow of the barrels which reached 1000 nL L^{-1} on day 2 at 33 °C. Conversely, maximum ethylene concentration of 25 nL L^{-1} was recorded in 1-MCP treated ‘Hayward’ (stored in air) fruit barrel indicating minimal ethylene production happened.

The general concept of plant sensitivity towards a hormone (through a dose-response curve) has been elucidated (Firn et al., 1986). When endogenous hormone levels are high, the exogenous application invokes minimal changes (Firn et al., 1986; Tongonya et al., 2021). For example, in apples, exogenous ethylene application did not further accelerate softening after internal ethylene concentration had reached saturation point (Johnston et al., 2009). This saturation point for ethylene response occurs at concentrations of 10,000 nL L^{-1} in apples and 1000 nL L^{-1} in kiwifruit (Tongonya et al., 2021) (Figure 8.2).

Figure 8.2: Response induced by different concentrations of exogenous ethylene in apples and kiwifruit (representation from Tongonya et al., 2021).

In 'SunGold™', which exhibits minimal softening at high temperature, ethylene influence on softening was not substantial since only a slight acceleration in softening occurred in the presence of ethylene at 33 °C during 7 d storage (Figure 5.4C). However, at 20 °C, ethylene significantly accelerated softening in 'SunGold™' (Figure 5.5C) suggesting that the ethylene perception mechanism in 'SunGold™' is more active at 20 °C than at 33 °C. This observation could be indicating that the ethylene sensing mechanism in 'SunGold™' is inhibited at high temperatures which may be a physiological reason for minimal softening changes at high temperatures.

8.6 1-MCP treatment efficacy

The two main findings from this study on 1-MCP treatment efficacy are that a) the treatment could still be effective in inhibiting ethylene perception and delaying softening in kiwifruit of edible firmness after long-term storage and b) the treatment remains functional and persistent at shelflife temperatures over 30 °C. Additionally, the 1-MCP treatment being effective on soft kiwifruit in the current study may also be indicating that 'System 2' ethylene production may have not initiated at the point of 1-MCP application.

The previous longest storage duration after which 1-MCP application was found to be effective in delaying softening in kiwifruit under ambient conditions was 120 days (Ilina et al., 2010). The findings in the current study support the previous knowledge that kiwifruit still elicits a response to 1-MCP (at 750 nL L^{-1} for 24 h at 4 °C) after 24-28 weeks of cool storage even at firmness ≤ 1 kg_f. Soft kiwifruit responding to 1-MCP treatment leads to speculation that 1-MCP treatment any time before autocatalytic ethylene initiation may be effective in delaying kiwifruit softening.

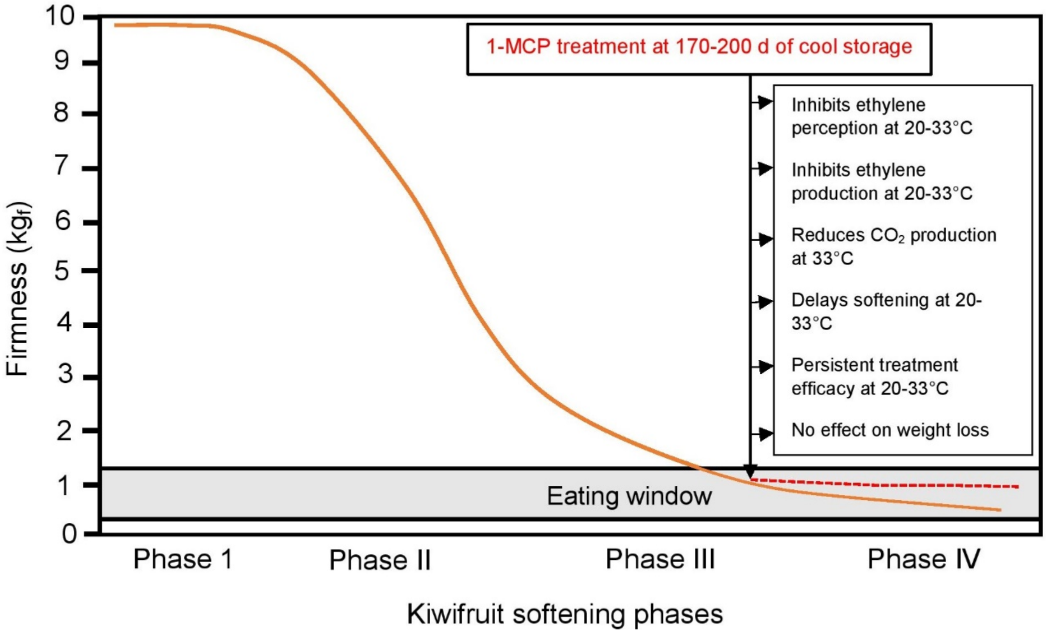


Figure 8.3: Softening changes in kiwifruit as influenced by 1-MCP treatment (750 nL L^{-1} for 24 h at 4 °C) at Phase III (eating window). Orange solid line indicate the normal softening pattern and red dashed line indicate softening due to 1-MCP treatment (modified from Atkinson et al., 2011).

Key unknown information which may serve as a challenge for 1-MCP application is its effect on kiwifruit respiration. While it was observed that 1-MCP treated kiwifruit (Hayward) had a reduced respiration rate than untreated fruit at 33 °C (Figure 5.2), respiration rate in 1-MCP treated fruit remained higher than untreated fruit at 20 °C. There is a possibility that higher respiration rates could affect fruit quality attributes, especially on the ones contributing towards taste. A sensory evaluation on 1-MCP treated kiwifruit stored at high temperature may be an option to identify whether fruit that retained firmness (due to 1-MCP treatment) may or may not taste well at high temperatures.

An additional issue pertaining to 1-MCP treatment on kiwifruit is the incidence of a disorder termed 'hardcore'. Zaffoli et al. (2016) observed 1-MCP treatment (1000 nL L^{-1} for 24 h) on firm (6.98-7.85 kg_f) kiwifruit resulted in the lack of synchronised softening (i.e. core region to soften less in comparison to other tissue regions) upon fruit transfer from coolstorage (60, 90, 120 d) to 20 °C. The presence of hard core in ripe kiwifruit is generally unnoticeable at the point of fruit purchase and is known later, which may affect consumer perception of the overall quality of the fruit (Li et al., 2016; Gong et al., 2021). However, the incidence of hardcore may not be of a risk if 1-MCP application is done on soft kiwifruit (≤ 1 kg_f), since all tissues regions at this stage are soft with minimal differences in firmness existing between different tissue regions (Gong et al., 2021).

8.7 Industrial applicability

The possible way to market kiwifruit at its best quality to final consumers under traditional retail conditions is by limiting fruit exposure to high temperatures and elevated ambient ethylene concentrations. However, since avoiding both these remains unlikely under traditional retailing systems which generally contribute to maximum fruit sales in tropical regions, the next available option would be by reducing the impact of high temperatures and ethylene exposure on kiwifruit. While the safe durations of exposure for kiwifruit to high temperatures (30-40 °C) are identified in this study, recommendations based on this could be developed and extended to the traditional retailers in tropical markets. However, this leads to a question as to how safe duration exposure recommendation would work out in the traditional supply chain systems wherein refrigeration is improbable and what would the retailers do if fruit exposure to high temperatures goes beyond the recommended safe exposure durations. If fruit are soft or have any visible symptoms of heat injury, it is obvious that the fruit are discarded but if fruit doesn’t exhibit any visible symptoms of heat injury but still are exposed to beyond safe durations, it is likely that the fruit are marketed to the consumers as the retailers do not want to suffer losses.

There are a few options that could be adopted in the earlier part of the supply chain which may minimise the impact of high temperatures on fruit quality at the retail. For example, it was observed in this study that the firmer the fruit are, the better they retain firmness and at high temperatures (Figure 8.1). Hence, supplying the firmest available fruit to tropical markets could minimise fruit losses at the retailer’s end. There are also possibilities that some growers may possess better tolerance to high temperatures than others. Therefore, identifying growers which possess better tolerance to high temperatures (through trials) and exporting the fruit of these growers to tropical markets could reduce losses. It is a positive sign that ‘SunGold™’ possesses better tolerance to high temperature since the demand for this cultivar is high in Asia and the Middle East (H. Arora, personal communication, March 30, 2020).

A future quality loss control strategy in tropical markets would be by enhancing thermotolerance in kiwifruit through breeding techniques. In apples, a hot-dry climate resilient cultivar ‘HOT84A1’ has already been developed and is ready for commercial cultivation (Ghahremani, 2020). It is expected that the resilience of this apple cultivar is retained after harvest resulting in a better postharvest performance at high temperatures. Hence, programs aiming to develop high temperature resilient kiwifruit cultivars are prudent for tackling the issues of postharvest losses, especially in regions where cool chain adoption is limited.

The obtained results from Chapter 5 indicate 1-MCP as a potential kiwifruit quality maintenance tool in tropical markets. The best suitable point within the supply chain for 1-MCP application is a day (24 h) before fruit exits the importers cool store to wholesale markets where fruit are then sold to the retailers. 1-MCP treatment earlier either during shipping or during storage at the importers cool store might result in diminished treatment effect since a further duration of cool storage after treatment could result in the synthesis of new ethylene receptors (Kim et al., 1999) which later become susceptible to ambient ethylene at the retailer’s store.

The 1-MCP treatment being effective on edible ripe kiwifruit (Chapter 5) suggest that the delayed application may not be of an issue with efficacy and is still effective in preventing ethylene perception subsequently resulting in firmness retention. However, firmness is not the only quality parameter that influences the eating quality of kiwifruit and firm fruit that doesn't taste good is still an issue. Hence there is a need for organoleptic trials to identify whether the quality attributes pertaining to taste are retained and not impacted either by 1-MCP treatment or high temperature exposure. A major drawback that makes it challenging for the use of 1-MCP on kiwifruit could be the consumer’s negative perception over the use of chemicals on fruit despite the chemicals being scientifically proven as safe and are commercially approved for use.

8.8 Future research opportunities

8.8.1 Mechanism of programmed cell death (PCD)

Programmed cell death (PCD) is a genetically controlled protective mechanism adopted by plants to eliminate redundant, injured and infected cells and facilitate normal growth and developmental processes (Chichkova et al., 2004; Lord et al., 2013; Kacprzyk et al., 2021). Additionally, PCD is activated in response to various biotic and abiotic stresses (Cai et al., 2014; van Aken and van Breusegem, 2015). Under biotic stresses such as pathogen infestation, PCD is activated in infected cells causing cell suicide and preventing disease spread to neighbouring healthy cells (Greenberg, 1996). However, under abiotic stresses such as heat, PCD activation may be the consequence of excess ROS generation (Vacca et al., 2006).

An investigation by Qu et al. (2009) elucidates the activation of apoptotic-like PCD in tomato fruit under mild heat stress conditions of 45 °C for 20 minutes. These authors detected intrinsic PCD linked events such as DNA damage, release of cytochrome-c from the mitochondria and the activation of caspase-9 and caspase-3 like proteins. These caspase-like proteins are involved in activation of proteases and nucleases enzymes involved in executing cellular destruction mechanisms by cleaving of DNA, causing protoplast to shrink and blebbing of the cell membrane (Brentnall et al., 2013). PCD activation in response to heat stress has been confirmed in other plants such as in cucumber (Balk et al., 1999) and in tobacco (Vacca et al., 2006).

Early activation of PCD at 40 °C may be a reason for the observed significant physiological changes in kiwifruit within a short time (< 24 h). Conversely, at temperatures in which exposure stress was recoverable (30-38 °C), there might either be an absence or delay in the activation of PCD. Further, the decline in fruit tolerance to heat stress with advancement in ripening could be due to PCD mechanism being more active in soft fruit than in firm fruit. Therefore, investigating PCD mechanism in kiwifruit (at edible firmness) at 30-40 °C ranges along with different fruit maturity may provide better evidence for two key observations in the current experiment i.e. a) physiological response differences between 33-38 °C and 40 °C and b) decline in heat tolerance in kiwifruit with advancement in ripeness.

8.8.2 Physiological mechanisms controlling differential softening responses between kiwifruit cultivars at high temperatures

The observed differential softening responses between 'Hayward' and 'SunGold™' at high temperatures (30-40 °C) in the current study could be either due to varying inherent tolerance between these two cultivars to high temperatures or due to ethylene perception and softening mechanisms being differentially influenced by high temperatures. Ethylene accelerated softening in 'SunGold™' at 20 °C but not at 33 °C and 'Hayward' softening similarly in the presence or absence of exogenous ethylene at 33 °C. These responses are evidence that suggests ethylene perception and response mechanisms are differentially influenced between these two cultivars at high temperatures.

It is possible that high temperature inhibits ethylene perception and synthesis in 'SunGold™' resulting in minimal softening changes and conversely accelerating ethylene production in 'Hayward' resulting in drastic firmness decline. In apples, the differential softening response between cultivars at high temperatures was due to varying internal ethylene concentrations (Johnston et al., 2001). At 30-35 °C, no firmness changes occurred in apple cultivars in which ethylene production was inhibited while softening was accelerated in cultivars that produced ethylene (Johnston et al., 2001).

To identify ethylene's role in influencing differential softening responses in kiwifruit cultivars at high temperatures, the best way is to first establish a relationship between ethylene production and softening in kiwifruit at high temperatures. This could be achieved by monitoring ethylene production and softening of individual kiwifruit (at edible firmness) of both 'Hayward' and 'SunGold™'cultivars upon exposure to high temperatures.

8.8.3 Kiwifruit responses to ethylene exposure at high temperatures

In Chapter 5, it was observed that softening in 'Hayward' occurred similarly either in the presence or absence of exogenous ethylene at 33 °C. As this is an interesting observation, the proposed possibility of immediate ethylene autocatalysis resulting in tissue ethylene saturation and exogenous ethylene not further accelerating softening could be investigated. This hypothesis can be tested by exposing soft (firmness < 1 kg_f) 'Hayward' kiwifruit to different concentrations of ethylene (ranging from low to high) at a particular high temperature (> 30 °C). A similar flow-through barrel setup as adopted in Chapter 5 could be used for the experimental setup.

If tissue ethylene saturation occurs within the initial hours of exposure to high temperatures, then no significant differences in softening can be expected between different concentrations of ethylene. An alternative method to capture ethylene production data could be the use of propylene (an ethylene analogue) instead of ethylene as propylene induces a similar effect as that of ethylene and facilitates detection of ethylene produced from the fruit. This study could be further extended to understand ethylene exposure responses in post-climacteric stage kiwifruit.

8.8.4 Investigating ethylene ethanol relationship in kiwifruit

Increased volatile production in climacteric fruits such as kiwifruit and apple occur during ‘System 2’ ethylene production in an ethylene-dependent pathway (Johnston et al., 2009; Atkinson et al., 2011). Since ethanol is an aromatic volatile compound synthesised in fruit at lower concentrations during natural ripening (Pesis, 2005), there might be a relationship between the rise in ethanol and ethylene production at high temperatures. Increased ethanol accumulation at high temperatures may be strongly dependent on ‘System 2’ ethylene or may be partially dependent on ethylene and strongly influenced by anaerobiosis and stress mechanisms. A recent study by Ali et al. (2021) suggests ethanol accumulation in ‘Bruno’ kiwifruit is reduced by 1-MCP treatment at room temperature.

A good approach to investigate the ethylene ethanol relationship at high temperature is to differentiate ethanol content in fruit inhibited (by 1-MCP treatment) or not inhibited for ethylene perception. If ethanol accumulation is strongly influenced by ethylene, then fruit inhibited for ethylene production may accumulate less ethanol than the fruit not inhibited for ethylene production. This understanding of ethylene ethanol relationship will give a better clarity for the observed ethanol increase results in chapter 7. Hence, an ethylene ethanol relationship will provide benefits in identifying if 1-MCP treatment reduces ethanol accumulation at high temperatures.

8.8.5 A broader understanding of 1-MCP efficacy on kiwifruit

The effectiveness of 1-MCP in delaying softening in eating ripe kiwifruit at temperatures over 30 °C is a finding that may direct several future research opportunities. This includes investigating 1-MCP efficacy on kiwifruit over a wider range of high temperatures (35-40 °C). At 33 °C, 1-MCP treatment remained effective on kiwifruit and showed no signs of decline either in the presence or absence of ethylene through the storage period. However, whether similar effectiveness, as well as consistency in 1-MCP treatment on kiwifruit is retained at temperatures > 35 °C could be a key consideration in future studies.

The duration of storage before 1-MCP application on kiwifruit could be further extended beyond 200 days to identify a storage duration limit beyond which 1-MCP efficacy diminishes on kiwifruit. Further, to mimic the onshore 1-MCP application strategy, further additional weeks of storage after 1-MCP treatment (to simulate shipping conditions to a country) before exposure to high temperatures could be investigated.

8.9 Conclusion

This research initially elucidates the potential sale conditions of kiwifruit in traditional markets of tropical regions. The subsequent investigations attempted to develop an understanding of the influence of potential tropical market conditions on kiwifruit physiology and quality. High temperature ranges at which kiwifruit (at edible firmness) recover or fail to recover from exposure stress have been identified. Based on the physiological observations, the safest exposure duration for kiwifruit is 12 h at 40 °C and 48 h at 33-38 °C. Further, the tolerable duration of exposure to high temperature (33-40 °C) for kiwifruit (after long-term cool storage) before return to cool storage is 24 h.

The observed differential postharvest responses between cultivars to high temperatures indicate ‘SunGold™’ to be more resilient to high temperatures than ‘Hayward’. Fruit physiological mechanisms which could be controlling the differential cultivar responses to high temperatures need further investigation. The role of ethylene in influencing kiwifruit softening at temperatures over 30 °C is elucidated. The findings suggest ethylene significantly advances kiwifruit softening at temperatures over 30 °C. Since the understanding of ethylene’s influence on kiwifruit was confined to a temperature (33 °C), further investigations considering wider high temperature ranges are essential for broader understanding. The 1-MCP application being effective at 33 °C at 750 nL L^{-1} suggests 1-MCP treatment is an effective technology to prevent fruit losses in tropical regions. However, there remain questions with regards to 1-MCP efficacy and consistency over a wider range of tropical temperatures as well as 1-MCP action on ethanol accumulation in kiwifruit that need further investigation.

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Appendices

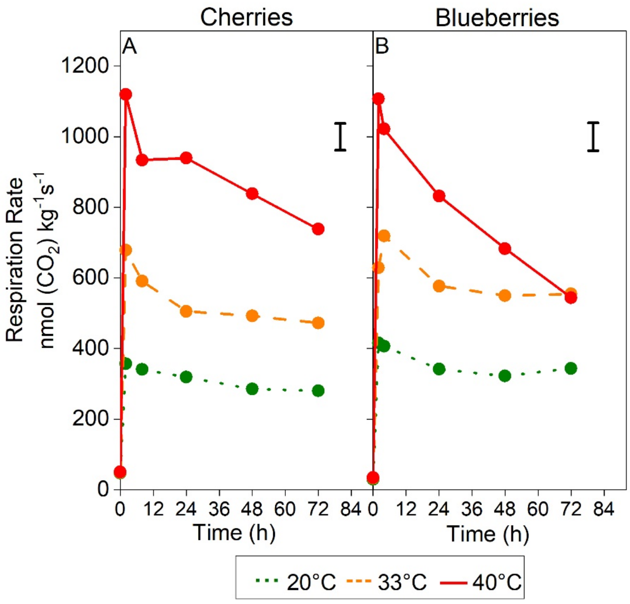

Figure A.1: CO$_2$ production of cherries (A) and blueberries (B) at different tropical storage conditions. Each data point represents average CO$_2$ production values of 10 composite replicates. Initial value at 0 h represents CO$_2$ production at 4 °C. Error bar displayed represents LSD$_{0.05}$ for the influence of temperature*time interaction on CO$_2$ production.

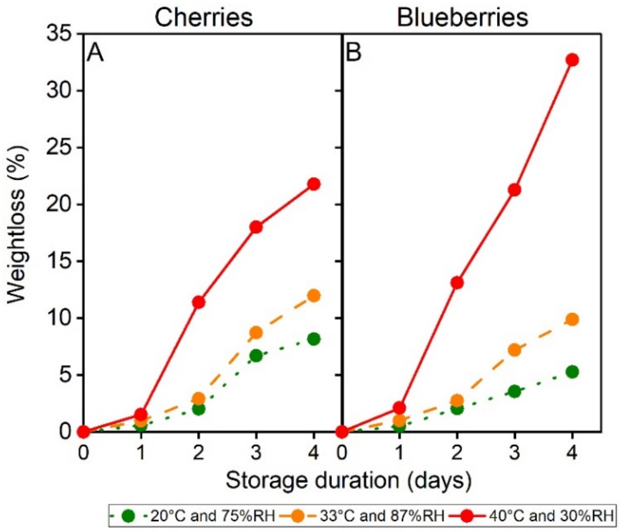

Figure A.2: Weight loss (%) of cherries and blueberries at different tropical storage conditions.

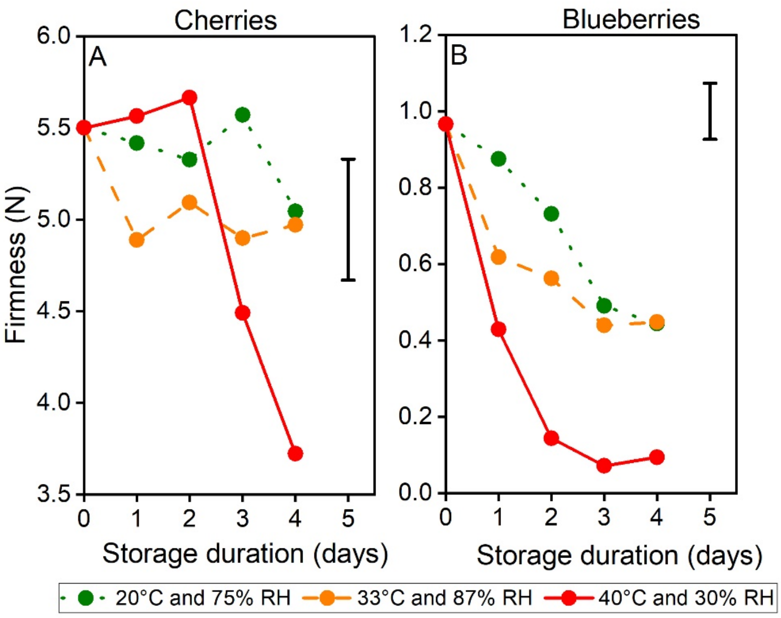

Figure A.3: Firmness of cherries (A) and blueberries (B) at different tropical storage conditions. Each data point represents average firmness value of 5 replicates (50 cherries/blueberries in total). Error bar displayed represents LSD$_{0.05}$ for the influence of temperature*storage duration interaction on firmness.

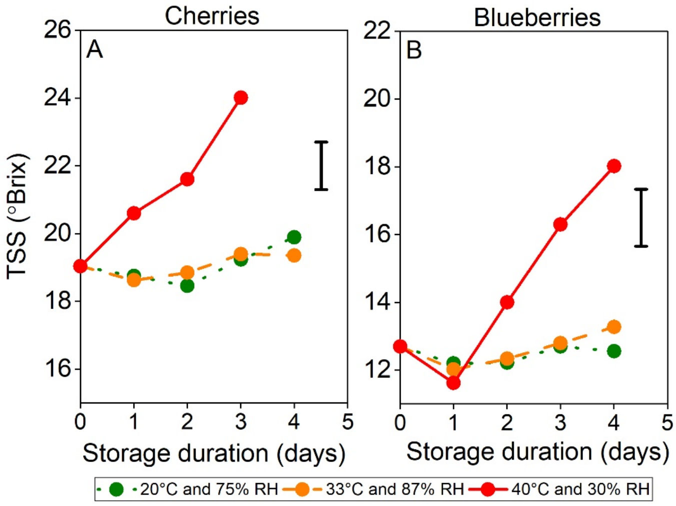

Figure A.4: TSS (°Brix) in cherries (A) and blueberries (B) at different tropical storage conditions. Each data point represents average value of 10 replicates (50 cherries/blueberries in total). Error bar displayed represents LSD$_{0.05}$ for the influence of temperature*storage duration interaction on TSS changes.

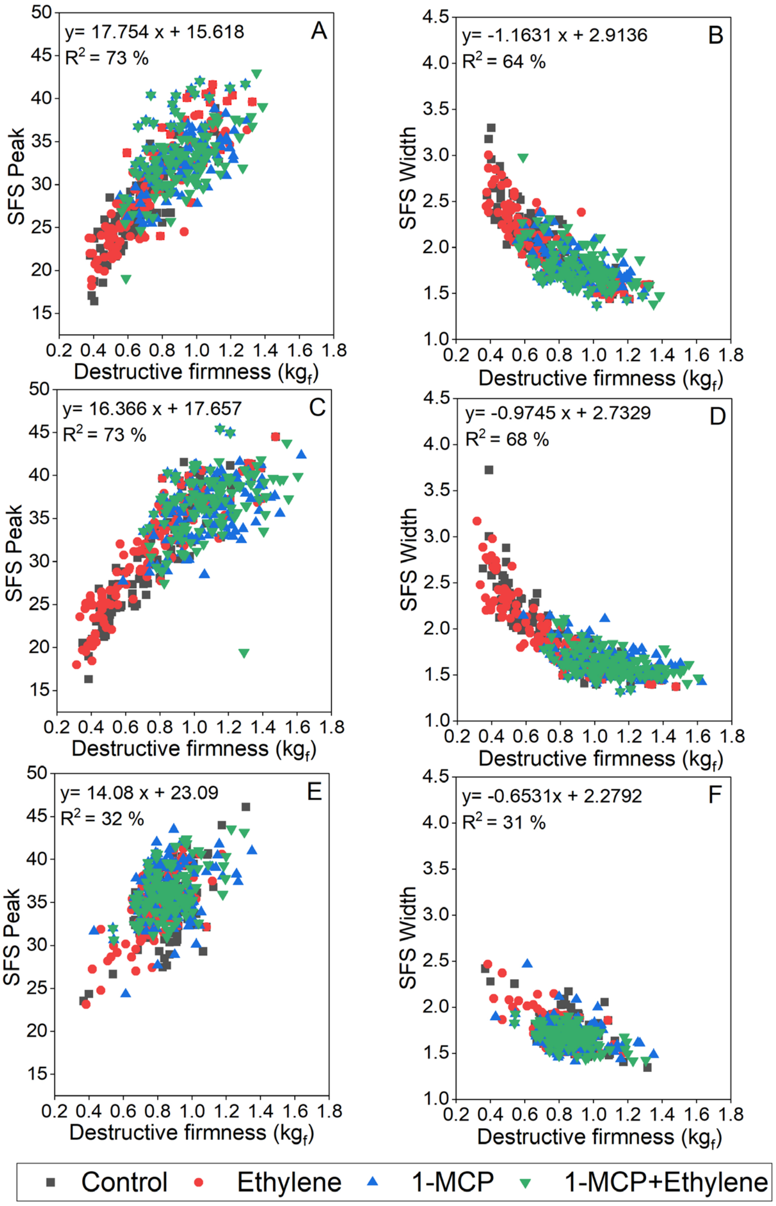

Figure A.5: Correlation between destructive firmness and Non-destructive firmness (Soft Fruit Sensor peak and width values) in Hayward grower 1 (A-B), Hayward grower 2 (C-D), and SunGold™ (E-F) at 33 °C and 95% RH storage conditions. Each plot contains data points obtained from overall experimental duration.

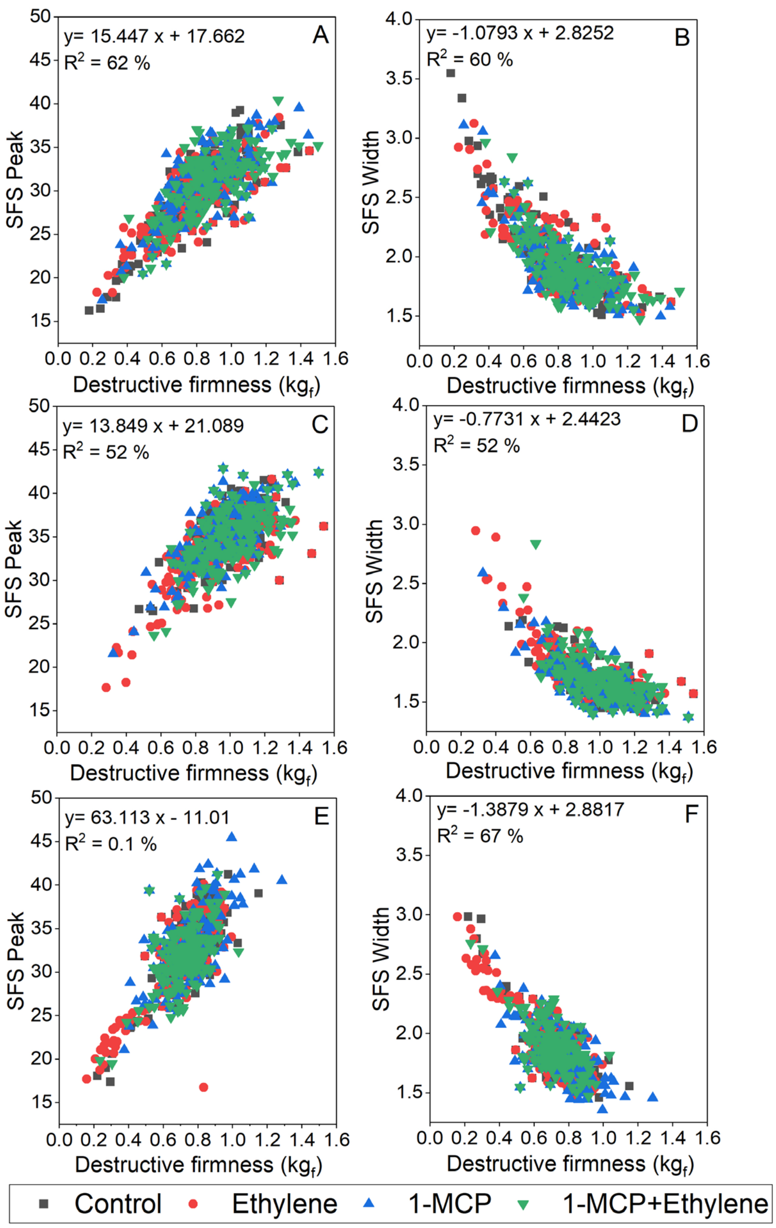

Figure A.6: Co-relation between destructive firmness and Non-destructive firmness (Soft Fruit Sensor peak and width values) in Hayward grower 1 (A-B), Hayward grower 2 (C-D), and SunGold™ (E-F) at 20 °C and 95% RH storage conditions. Each plot contains data points obtained from overall experimental duration.

Table A.1: Kruskal-Wallis non-parametric test values for changes in ethanol content over time at different temperatures in 'Hayward' grower 1. Mean rank represents an average of overall observations within a rank. Z-Value represents absolute value.

Temperature	Day	Sample size (n)	Median	Mean rank	Z	P-Value
20 °C	0	10	0.0081	11.6	-3.37	0.000
	1	10	0.0135	25.2	-0.07	0.000
	2	10	0.0094	19	-1.58	0.000
	3	10	0.0161	33.7	1.99	0.000
	9	10	0.0198	38	3.03	0.000
38 °C	0	10	0.0098	5.5	-4.85	0.000
	1	10	0.1137	16.1	-2.2B	0.000
	2	10	0.5459	29.5	0.97	0.000
	3	10	0.8081	32.2	1.62	0.000
	5	10	1.8887	44.2	4.54	0.000
40 °C	0	10	0.0120	5.5	-4.85	0.000
	1	10	0.2743	16.7	-2.13	0.000
	2	10	0.8955	33.3	1.89	0.000
	3	10	1.3625	37.6	2.93	0.000
	5	10	0.9111	34.4	2.16	0.000

Note. Higher the Z-value, the greater the group's average rank from overall average rank. Negative Z-Value = group's average rank is less than overall average rank. Positive Z-Value = group's average rank is greater than overall average rank.

Table A.2: Kruskal-Wallis non-parametric test values for changes in ethanol content over time at different temperatures in 'Hayward' grower 2. Mean rank represents an average of overall observations within a rank. Z-Value represents absolute value.

Temperature	Day	Sample size (n)	Median	Mean rank	Z
20 °C	0	10	0.004	14.1	-3.84
	1	10	0.010	58.5	2.62
	2	10	0.003	7.8	-4.76
	3	10	0.006	32.1	-1.22
	5	10	0.007	44.0	0.50
	7	10	0.007	39.5	-0.15
	9	10	0.015	60.1	2.85
	12	10	0.014	68.0	3.99
36 °C	0	10	0.017	5.5	-4.96
	1	10	0.398	20.3	-2.02
	2	10	0.974	31.2	0.14
	3	10	1.033	33.1	0.53
	5	10	1.710	39.1	1.71
	7	10	3.890	53.8	4.61
38 °C	0	10	0.012	5.5	-4.85
	1	10	0.573	16.7	-2.13
	2	10	1.260	30.0	1.09
	3	10	1.292	34.5	2.18
	5	10	2.833	40.8	3.71
	0	10	0.000	5.5	-4.85

40 °C	1	10	0.130	20.6	-1.19
	2	10	0.215	32.6	1.72
	3	10	0.248	36.6	2.70
	5	10	0.172	32.1	1.61

Note. Higher the Z-value, the greater the group's average rank from overall average rank. Negative Z-Value = group's average rank is less than overall average rank. Positive Z-Value = group's average rank is greater than overall average rank.

Table A.3: Kruskal-Wallis non-parametric test values for changes in acetaldehyde content over time at different temperatures in 'Hayward' grower 1. Mean rank represents an average of overall observations within a rank. Z-Value represents absolute value.

Temperature	Day	Sample size (n)	Median	Mean rank	Z
20 °C	0	10	0.008	43.9	4.46
	1	10	0.006	31.6	1.48
	2	10	0.006	26.4	0.22
	3	10	0.005	18.8	-1.64
	9	10	0.004	6.8	-4.52
38 °C	0	10	0.005	12.0	-3.27
	1	10	0.005	10.6	-3.61
	2	10	0.008	25.4	-0.01
	3	10	0.011	34.4	2.15
	5	10	0.015	45.1	4.75
40 °C	0	10	0.008	13.6	-2.90
	1	10	0.009	16.8	-2.11
	2	10	0.010	26.9	0.34

	3	10	0.012	37.6	2.93
	5	10	0.012	32.6	1.73

Note. Higher the Z-value, the greater the group's average rank from overall average rank. Negative Z-Value = group's average rank is less than overall average rank. Positive Z-Value = group's average rank is greater than overall average rank.

Table A.4: Kruskal-Wallis non-parametric test values for changes in acetaldehyde content over time at different temperatures in 'Hayward' grower 2. Mean rank represents an average of overall observations within a rank. Z-Value represents absolute value.

Temperature	Day	Sample size (n)	Median	Mean rank	Z
20 °C	0	10	0.006	67.3	3.89
	1	10	0.006	60.0	2.84
	2	10	0.006	51.0	1.53
	3	10	0.005	34.9	-0.81
	5	10	0.005	37.8	-0.39
	7	10	0.004	12.8	-4.04
	9	10	0.005	39.2	-0.19
	12	10	0.004	21.0	-2.84
36 °C	0	10	0.009	19.8	-2.12
	1	10	0.006	9.8	-4.12
	2	10	0.010	25.4	-1.02
	3	10	0.011	31.1	0.11
	5	10	0.017	43.0	2.48
	7	10	0.020	54.0	4.67
	0	10	0.007	8.4	-4.15

38 °C	1	10	0.008	15.3	-2.47
	2	10	0.010	29.2	0.90
	3	10	0.011	36.9	2.76
	5	10	0.011	37.7	2.96
40 °C	0	10	0.006	6.5	-4.60
	1	10	0.009	26.1	0.15
	2	10	0.009	30.4	1.19
	3	10	0.011	36.5	2.67
	5	10	0.009	27.9	0.59

Note. Higher the Z-value, the greater the group’s average rank from overall average rank. Negative Z-Value = group’s average rank is less than overall average rank. Positive Z-Value = group’s average rank is greater than overall average rank.

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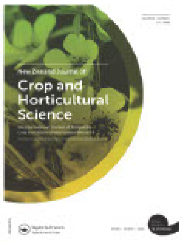

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Postharvest physiology of kiwifruit in tropical environments

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Abstract

New Zealand's kiwifruit export supply chain includes distribution to tropical climates. Notably, the Middle East and southeast Asian countries represent large developing markets with substantially higher ambient temperature and relative humidity conditions. Fruit sales in these regions can be dominated by wet markets causing fruit exposure to extreme environmental conditions before consumer purchase. There is a general paucity of data on how temperate fresh produce respond to tropical environmental conditions postharvest at the end of the supply chain. The objective of this study was to compare shelf-life performance for kiwifruit (*Actinidia* sp.) exposed to regional extremes i.e., hot/humid: 33°C and 87% RH and hot/dry: 40°C and 30% RH conditions, with typically studied shelf-life conditions (20°C and 75% RH). The influence of packing with a layer of polyethylene in these conditions was also studied. Respiration rate and fruit quality parameters (weight loss, firmness, total soluble solids and titratable acidity) were monitored for 5 days. As expected, fruit stored at 40°C conditions had the highest rate of respiration, softening and weight loss followed by 33 and 20°C. An approximate 6-fold rise in respiration rate (when compared to 20°C peak range) was observed in the initial 12 h of exposure to 40°C which later plummeted to less than 20% of the peak 2 days later. In contrast at 33°C, the respiration rate was found to remain within 80% of the peak range during the entire storage period. It appears that 40°C and 30% RH led to significant changes in fruit physiology within less than 1 d that may result in fruit damage as evidenced by rapid respiratory decline. This result raises the question of what combination of conditions (temperature and time of exposure) will cause damage to kiwifruit in these potential end of market scenarios.

Keywords: *Actinidia,* high temperature, shelf life, respiration, firmness

INTRODUCTION

Kiwifruit (*Actinidia* sp.) is New Zealand's major contributor to the fresh produce export earnings and accounted for NZ$ 3.1 billion in 2019 (Aitken and Warrington, 2019). ZESPRI®, New Zealand's kiwifruit growers marketing co-operative, have been successful in expanding sales to nearly 60 countries worldwide (Bollen et al., 2015).

With the rise in production volume, market expansion has been one of the major goals for the New Zealand kiwifruit industry. In developed countries dominated by modern retail, market establishment or expansion may not be very strenuous since fruit quality is managed in a consistent cool chain through to the consumer and hence expected to reach consumers in a state of high quality (Porat et al., 2018). However, in other regions, traditional retail conditions (e.g., wet markets) continue to have a considerable share of fruit sales and make the process of quality product delivery more challenging (Punter et al., 2016). The limited adoption or availability of refrigeration and the relatively high ambient temperature conditions have the potential to present a considerable challenge in maintaining product quality under traditional retail conditions.

Antunes and Sfakiotakis (2000) studied the influence of elevated storage temperatures (30-45°C) on physiological and ripening mechanisms of 'Hayward' kiwifruit and observed

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