










Dynamic controlled atmosphere: A review of methods for monitoring fruit responses to low oxygen

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Abstract

The storage of fruit at minimum oxygen condition is crucial for optimal fruit quality maintenance. However, the optimal oxygen partial pressure of fruit varies according to several factors such as species, cultivar, harvest maturity, temperature, growing season and storage period. Based on these factors, storage technologies were developed that allow for the detection of the lower oxygen limit (LOL) and the storage of fruit under the lowest optimal oxygen partial pressure. One emerging technology is known as dynamic controlled atmosphere (DCA). Commercially, there are four DCA systems used: [1] DCA based on ethanol production and accumulation (DCA-Eth); [2] DCA based on chlorophyll fluorescence (DCA-CF); DCA based on the respiratory quotient (DCA-RQ) and [4] DCA based solely on CO₂ production (DCA-CD). This reviews highlights the recent developments of these DCA systems and their effect on fruit quality. Generally, the storage of fruit under DCA has a positive effect on the overall fruit quality, with regards to reduced physiological disorders and higher flesh firmness maintenance, when compared to controlled atmosphere (CA). Evidence also shows that storing fruit under DCA-RQ and DCA-CD allowed higher volatile compound emission and concentration, which can contribute positively to fruit flavor. The DCA systems are “green storage technologies” because the system enables the increase of storage temperature, thereby saving electrical energy. Storage of apples under DCA maintains an overall fruit quality similar to CA combined with the ripening inhibitor 1-Methylcyclopropene (1-MCP), which is an interesting option for organic fruit storage. Dynamic controlled atmosphere is a recently developed storage technique and is in constant improvement. The latest developed DCA techniques (DCA-RQ and DCA-CD), in contrast to DCA-CF, allow the use of extremely low oxygen levels. In the future, new and multi-sensor DCA systems are under development, which might not just control O₂ partial pressure but also temperature and other parameters to allow for more energy efficient but high quality fruit storage systems.

Keywords: Anaerobic metabolism; Ethanol; Chlorophyll fluorescence; Respiratory quotient; 1-Methylcyclopropene (1-MCP); CO₂ production

Introduction

Several fruit species have a harvest window that is concentrated over a short period of the year. This makes it necessary to store a portion of the production to supply fruit over the production season. Storage is generally performed under temperatures as low as possible to reduce fruit metabolism to a minimum and to extend postharvest life (Steffens et al., 2007; Brackmann et al., 2008).

A controlled atmosphere system (CA) for fruit storage is associated with low temperatures, where the oxygen partial pressure (pO₂) is reduced and carbon dioxide partial pressure (pCO₂) is increased (Brackmann et al., 2008; Weber et al., 2011; Both et al., 2014; Kitemann et al., 2015; Bekele et al., 2016). However, the oxygen and carbon dioxide partial pressures defined for fruit crops in previous studies (Thewes et al., 2015; Weber et al., 2015; Both et al., 2017) the variation in fruit metabolism

as dependent on harvest maturity, fruit temperature, growing season and storage period. Thewes et al. (2020b) demonstrated that fruit metabolism is affected by such factors, which can affect the optimal pO₂ conditions during controlled atmosphere storage (Figure 1 and 7).

Over the past 25 years, several technologies have been developed to determine the optimum pO₂ by monitoring fruit metabolism in real time during CA storage. These technologies allow for the dynamic adjustment of the pO₂ according to the fruit requirements (Figure 1), known as dynamic controlled atmosphere, DCA (Weber et al., 2015; Mdilshwa et al., 2018; Prange, 2018). Currently, there are four DCA systems used in commercial fruit storage rooms: [1] monitoring fruit responses to low oxygen based on anaerobic metabolism compounds (Figure 1) such as ethanol (DCA-Eth) (Schouten et al., 1998; Veltman et al., 2003); [2] monitoring chlorophyll fluorescence (DCA-CF) (Prange, 2018; Wright et al., 2011);

[3] determining the respiratory quotient (DCA-RQ) (Gasser et al., 2008; Weber et al., 2015; Bessemans et al., 2016), and [4] monitoring fruit responses to low oxygen based on CO₂ production (DCA-CD) (Thewes et al., 2020b). These four DCA technologies allow fruit to be stored at the lowest oxygen limit (LOL), without compromising the fruit quality (Figure 1). The objective of this review was to compare DCA technologies that are available commercially and examine the effect of such systems on the overall quality of fruit.

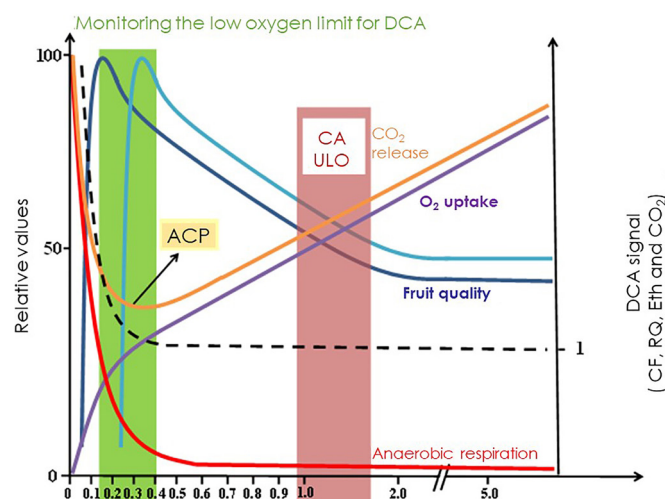


Figure 1. Schematic representation of fruit metabolism and fruit quality responses to oxygen partial pressure (pO_2) of the storage atmosphere. The lowest oxygen limit (LOL) is determined by monitoring one of four different DCA methods: chlorophyll fluorescence (CF), respiration quotient (RQ), ethanol (Eth) production and CO₂ (CD) production. ACP means the anaerobic compensation point (Neuwald et al., 2019 adapted from Boersing et al., 1988 and Hoehn et al., 2009).

Dynamic controlled atmosphere system based on Chlorophyll fluorescence (DCA-CF)

The DCA-CF system uses chlorophyll fluorescence as the fruit response to low oxygen and is the most studied and commercially used DCA system worldwide (Figure 2). During DCA-CF storage, the oxygen partial pressure is lowered in the storage room and the chlorophyll fluorescence of the fruit is periodically monitored. The oxygen partial pressure at which the sensor software detects a spike in chlorophyll fluorescence is considered the LOL (Prange et al., 2003, 2015; Wright et al., 2015, 2011; Zanella and Stürz, 2015; Prange, 2018). Generally, fruit are stored at an oxygen partial pressure just above the LOL. The recommended oxygen partial pressure for fruit is 0.2 kPa above the partial pressure at which the spike in chlorophyll fluorescence was detected but is never below 0.4 kPa O₂.

Chlorophyll fluorescence occurs as a response to stress, which reduces the excitation energy transfer to the reaction centers of the photosystems (Taiz and Zeiger, 2017). Several stresses can cause chlorophyll fluorescence

such as high temperature, excess of radiation, drought (Taiz and Zeiger, 2017) and low oxygen during storage (Prange et al., 2003; Wright et al., 2012, 2011; Prange, 2018;). However, it is not physiologically clear how the low oxygen affects chlorophyll fluorescence.

In the literature, four main models attempt to explain how low oxygen during fruit storage induces chlorophyll fluorescence:

1. Reducing oxygen to extremely low partial pressures result in acetaldehyde, ethanol, and ethyl acetate accumulation. The increase of these compounds can alter cell membranes and organelles such as the photosystem II in the chloroplast, affecting energy transfer (quenching) and thus increasing chlorophyll fluorescence (Maxwell and Johnson, 2000);
2. Low oxygen causes acidosis of cells and organelles (Ke et al., 1994), which can modify the photosystem II and in turn increase chlorophyll fluorescence (Prange et al., 2005);
3. Storage under extremely low oxygen increases the pool of reduced compounds in the cytosol. These reduced compounds are transported to the chloroplast where they are used to reduce the plastoquinone pool, a process known as 'chlorofermentation'. Chlorofermentation reduces the quenching in photosystem II and increases chlorophyll fluorescence (Wright et al., 2015, 2011);
4. Chlorophyll fluorescence is linked to xanthophylls, especially to zeaxanthin, which mediates the dissipation of an excess of excitation energy in the antenna chlorophyll of the photochemical apparatus. While zeaxanthin is converted to antheraxanthin by the enzyme zeaxanthin epoxidase in normal atmospheric conditions (Wright et al., 2011), this conversion is reduced when oxygen is lowered, allowing zeaxanthin to dissipate excess energy through chlorophyll fluorescence.

In practical terms, to measure chlorophyll fluorescence, fruit samples are put into plastic baskets with a Fluorescence Interactive Response Monitor (FIRM) sensor on its upper side (Figure 3). Together with the FIRM, a light emitting diode (LED) is installed, which is the light source of the system. The number of sensors installed in each storage room depends on the room size and can be modified according to the experience of the operator.

DCA-CF is used globally and is available in two

commercial systems: HarvestWatch™ and FruitObserver®, which are produced by the companies Isolcell and Besseling, respectively (Prange, 2018). The company Walz GmbH (Effeltrich, Germany) has developed a Pulse Amplitude Modulation (PAM) system, known as Apple – PAM

that is used to measure chlorophyll fluorescence of individual fruit. Schlie et al. (2019) evaluated Apple-PAM on 'Elstar PCP' apples and found that both harvest date and fruit firmness can influence the fermentation behavior of 'Elstar PCP'.

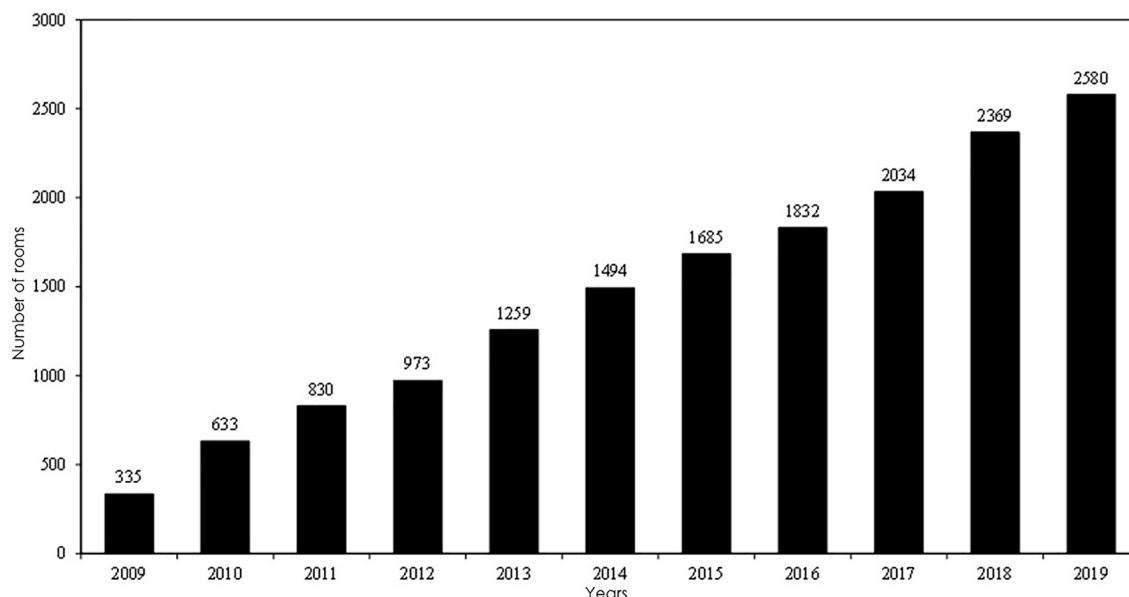


Figure 2. Number of rooms equipped with DCA-CF (HarvestWatch™) over ten years Worldwide (Adapted from Isolcell, 2020).

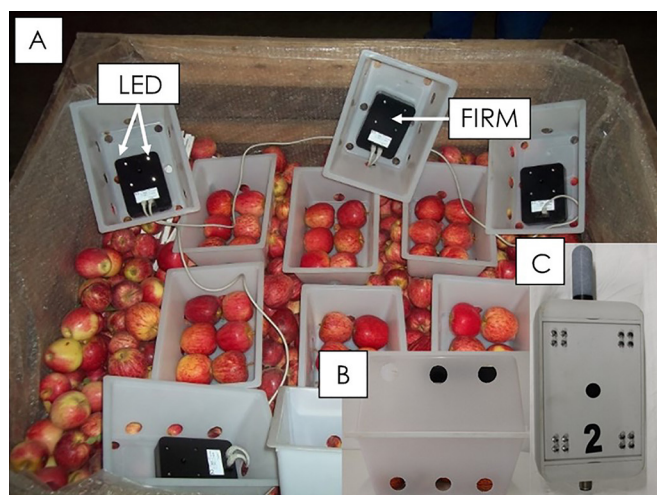


Figure 3. Picture of the installation of chlorophyll fluorescence sensors in a commercial room of 'Galaxy' apples. A: Shows the sensors HarvestWatch™ with Light emitting diode (LED) and Fluorescence Interactive Response Monitor (FIRM). B: sensors after closing. C: shows the sensor from FruitObserver®.

The DCA-CF system allows fruit to be stored a little above the LOL, reducing fruit metabolism and maintaining higher overall quality compared to CA (Prange et al., 2005; Zanella et al., 2005, 2008; Hennecke et al., 2008; Köpcke, 2015; Wright et al., 2011; Thewes et al., 2015). With the DCA-CF system, the oxygen partial pressures vary more at the beginning of the storage period, where the chlorophyll fluorescence is detected

(Thewes et al., 2015).

Several studies have evaluated the effect of DCA-CF on fruit quality maintenance and compared it to fruit stored under CA and ultralow oxygen (ULO). Storage under DCA-CF generally reduced the incidence of physiological disorders such as superficial scald (Zanella et al., 2005; Prange et al., 2015; Eren et al., 2015; Mditshwa et al., 2017a, 2017b, 2018), flesh breakdown (Köpcke, 2015; Rizzolo et al., 2015; Thewes et al., 2015; Deuchande et al., 2016; Both et al., 2017), skin spots (Hennecke et al., 2008; Köpcke, 2015; Rizzolo et al., 2015), and fruit maintained a higher flesh firmness (Gabioud Rebeaud and Gasser, 2015; Köpcke, 2015; Rizzolo et al., 2015), and fruit maintained a higher flesh firmness (Gabioud Rebeaud and Gasser, 2015; Köpcke, 2015; Thewes et al., 2015; Tran et al., 2015; Both et al., 2017; Weber et al., 2019, 2020) when compared to fruit stored under CA. However, the storage of apples under DCA-CF, with the recommendation to increase the pO_2 to 0.2 kPa above the LOL, resulted in fruit with lower volatile compounds concentrations and emissions, especially esters, when compared to CA (Aubert et al., 2015; Thewes et al., 2017b, 2017c; Both et al., 2017; Donadel et al., 2019). A reduction in volatile emissions can have a negative influence on fruit taste, causing off-flavor and reducing aroma (Aubert et al., 2015; Tran et al., 2015). A recent study demonstrated that apple fruit stored under DCA-CF had a lower ester concentration when compared to

CA because of a lower gene expression of lipoxygenase *MdLOX1* and alcohol acyl-transferase *MdAAT1* as well as lower concentrations of precursors for the related enzyme (Thewes et al., 2020a). The authors attributed their findings to the reduction in aerobic metabolism to a minimum without inducing anaerobic metabolism.

In fruit, chlorophyll is present in higher concentration in the skin cells. Thus, the LOL detection by chlorophyll fluorescence will represent a stress situation of the most outer cells of the fruit (Wright et al., 2015). However, Ho et al. (2013) reported that oxygen is less available at the core (inner flesh cells) due to the diffusion resistance. Therefore, when the skin cells are under low oxygen stress, the cells of the core likely stay under anaerobic metabolism, which can damage the

inner fruit quality. Studies evaluating apples of the 'Gala' group have demonstrated that when chlorophyll spikes, the respiratory quotient (ratio between CO₂ release and O₂ uptake) is higher than 10, indicating a high anaerobic metabolism rate (Figure 4). Another problem that can occur when DCA-CF is used for determining the LOL is that the magnitude of the chlorophyll fluorescence signal reduces over the storage period, because the photosystem II, which is mainly responsible for chlorophyll fluorescence, continuously adapts to new conditions such as the fruit tolerating lower levels of oxygen. Furthermore, chlorophyll degradation and corresponding lower fluorescence emission occurs as normal process of fruit ripening.

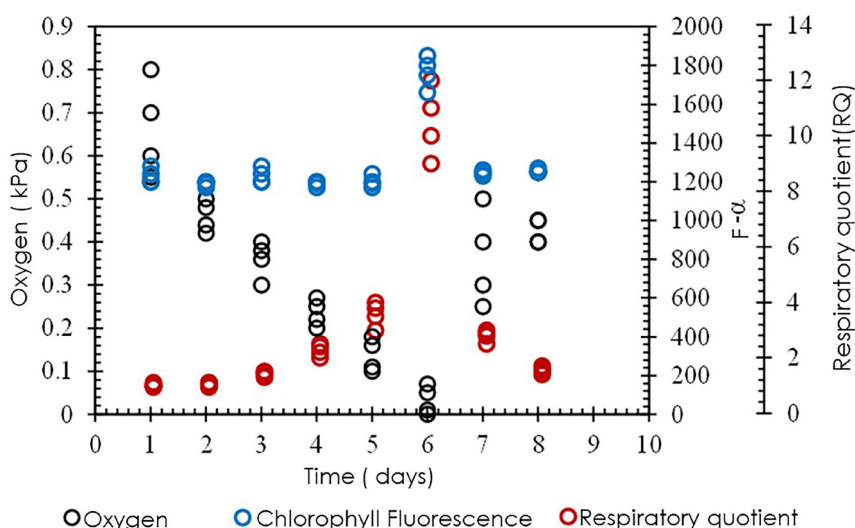


Figure 4. Relationship between oxygen in the storage room, chlorophyll fluorescence and respiratory quotient in 'Galaxy' apples at a temperature of 2.0 °C.

Dynamic controlled atmosphere system based on ethanol (DCA-Eth)

The principle of DCA is to store the fruit with an oxygen partial pressure as low as possible, the so-called LOL. It is necessary to monitor fruit metabolism periodically over the whole storage period to store fruit at the LOL. If fruit are stored below the LOL, anaerobic metabolism can occur which can damage fruit due to the excessive accumulation of anaerobic metabolism compounds such as acetaldehyde, ethanol and ethyl acetate (Pesis, 2005; Wright et al., 2015; Saltveit, 2019). The increase in ethanol concentration due to anaerobic metabolism is the basis for the DCA-Eth system.

DCA-Eth was the first DCA system developed and monitors the fruit response to the oxygen variation in the storage room. DCA-Eth is performed by gradually lowering the oxygen partial pressure and determining the ethanol concentration periodically (Schouten et al., 1998;

Veltman et al., 2003). Oxygen is lowered until an increase in ethanol concentration is detected. There are two main locations and forms where ethanol can be determined; in the room headspace or juice obtained from fruit.

DCS® (Dynamic controlled system) is a commercially available DCA-Eth system, which determines the ethanol concentration in the chamber headspace. DCS® was developed in the Netherlands and is marketed by the company Storex (Figure 5). Another DCA-Eth system, which determines the ethanol concentration in the fruit juice is ILOS-Plus® and is marked by company Marvil, Italy. In Germany, a DCA-Eth system was developed where fruit are stored for 21 days at 1.4 kPa O₂ before the O₂ is decreased in intervals. Following 21 days, O₂ is decreased to 1.1 kPa O₂ for seven days and then decreased to 0.8 kPa for another seven days. A fruit sample should be taken at each interval and evaluated for anaerobic metabolism compounds. If the levels of

anaerobic compounds exceed a limit, the fruit need to be stored at the next higher O_2 interval before another sample is taken (Hennecke et al., 2008; Köpcke, 2014). Köpcke (2014) reported an increased risk of low oxygen damage when apple fruit were stored below 0.8 kPa O_2 .

The storage of 'Elstar' apples under DCA-Eth reduced the incidence of superficial scald, maintained a higher flesh firmness and greener skin color compared to fruit stored under controlled atmosphere (Schouten et al., 1998; Veltman et al., 2003). According to these same authors, DCA-Eth allowed 'Elstar' apples to be stored in oxygen partial pressures ranging between 0.1 and 0.7 kPa. Another study applying DCA-Eth on 'Rocha' pears, found high acetaldehyde and ethanol accumulation in fruit pulp, resulting in a higher incidence of flesh breakdown and thus damaged fruit (Deuchande et al., 2016). These reports are the main studies evaluating the effect of DCA-Eth on fruit quality and the results are inconclusive (Schouten et al., 1998; Veltman et al., 2003; Deuchande et al., 2016), as suggested by an earlier review of DCA technologies (Mdithwa et al., 2018).

One problem that can occur when the LOL is determined by DCA-Eth is that the accumulated ethanol can metabolize into other compounds. As fruits are living products, the ethanol produced during anaerobic metabolism is rapidly converted into other compounds, such as ethyl esters (Lee et al., 2012; Both et al., 2017; Thewes et al., 2017b, 2020a, Donadel et al., 2019; Anese et al., 2020). Therefore, if ethanol is monitored alone, a sub-estimation of the LOL can occur, which can induce damage to fruit flesh as observed in 'Rocha' pears (Deuchande et al., 2016).

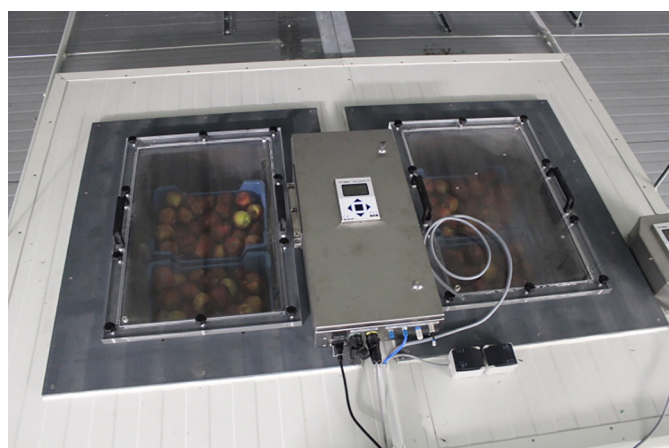


Figure 5. Picture of the installation of DCS sensors in a commercial room of apples.

Dynamic controlled atmosphere system based on Respiratory quotient (DCA-RQ)

The storage of fruit under DCA-RQ is based on the principle that the ratio between CO_2 release and O_2

uptake during fruit respiration is near one. The CO_2 to O_2 ratio is close to one under normoxic conditions, where the oxygen supplementation to the fruit for respiration is adequate. However, even under normoxic conditions, the RQ value can vary a little above and below one, and is exactly one when the substrate of respiration are sugars (Goyette et al., 2012). Delele et al. (2019) reported that RQ values lower than one could be a function of CO_2 solubilization in the cellular juice, while Patel and Bhardwaj (2019) stated it could also occur when lipids are used as respiration substrates (Patel and Bhardwaj, 2019). However, the factor that affects RQ variation most during storage is the O_2 partial pressure of the storage room.

Based on RQ variation over the storage period it is possible to estimate the LOL (Gasser et al., 2008; Van Schaik et al., 2015; Weber et al., 2015; Bessemans et al., 2016). RQ levels above one indicate that anaerobic metabolism is occurring in fruit cells. Compounds produced during anaerobic metabolism can have a positive effect on fruit maturity and ripening, such as ethanol, while other compounds have no effect. At low concentrations, ethanol can be beneficial to fruit quality maintenance (Asoda et al., 2009; Liu et al., 2012; Jin et al., 2013; Weber et al., 2016, 2020). In contrast, when the concentration of anaerobic metabolism compounds are too high, the formation of off-flavors can occur (Wright et al., 2015) and internal damages in the fruit may be noticed (Weber et al., 2015; Deuchande et al., 2016).

Several studies have used DCA-RQ to detect the LOL and have compared the fruit quality to CA and DCA-CF. Promising results using DCA-RQ have been observed in Brazil (Brackmann et al., 2015; Weber et al., 2015, 2017; Both et al., 2017; Thewes et al., 2017c, 2017b; Donadel et al., 2019) and Europe (Gasser et al., 2008; Van Schaik et al., 2015; Bessemans et al., 2016, 2018; Delele et al., 2019; Thewes et al., 2019; Weber et al., 2019, 2020). These researches demonstrated that storage under DCA-RQ resulted in apples with lower superficial scald (Bessemans et al., 2016), flesh breakdown and higher flesh firmness when compared to CA (Weber et al., 2015, 2019, 2020; Both et al., 2017; Thewes et al., 2017a).

The optimal RQ level for apple storage is well defined and ranges between 1.3 and 1.5 (Brackmann et al., 2015; Bessemans et al., 2016; Both et al., 2017; Thewes et al., 2017a, 2017a; Weber et al., 2017, 2020; Anese et al., 2020). In general, storing fruit with a RQ of 1.3 results in fruit with better maintenance of flesh firmness and reduced incidence of physiological disorders and decay (Weber et al., 2015, 2020; Thewes et al., 2017a, 2019, 2020b; Both et al., 2017; de Oliveira Anese et al., 2019; Anese et al.,

2020). In contrast, storing fruit with a RQ of 1.5 results in fruit with higher volatile compound emissions, especially esters and alcohols (Both et al., 2017; Thewes et al., 2017c, 2017b, 2020a; Donadel et al., 2019; Schmidt et al., 2020), which can improve fruit flavor. According to Thewes et al. (2020a), the higher ester accumulation in fruit stored with DCA-RQ 1.5 is due to the higher precursor availability and a higher level of *MdAAT1* enzyme expression.

The storage under DCA-RQ allows for the initiation of anaerobic metabolism in fruit to occur at safe levels (Weber et al., 2017, 2017). Anaerobic metabolism induces the accumulation of ethanol in fruit flesh, a metabolite that helps fruit metabolism inhibition (Asoda et al., 2009; Jin et al., 2013; Weber et al., 2016, 2020). Based on the strong metabolism reduction by DCA-RQ, several studies have demonstrated that it is possible to increase the storage temperature in a range between 1° and 3 °C above the standard storage temperature (Both et al., 2018; de Oliveira Anese et al., 2019; Weber et al., 2019, 2020). Increasing the storage temperature above the standard will save energy and reduce storage costs. Additionally, storage under DCA-RQ maintains a fruit quality similar to CA + 1-MCP (Thewes et al., 2017a, 2020a.; Weber et al., 2017; de Oliveira Anese et al., 2019; Anese et al., 2020). However, volatile compounds related to aroma are drastically increased when compared to CA + 1-MCP (Thewes et al., 2017c, 2020a; Anese et al., 2020; Schmidt et al., 2020).

In DCA - RQ storage, the pO_2 may be reduced to extremely low levels (<0.3 kPa), depending on the apple cultivar and storage time (Both et al., 2018; Donadel et al., 2019; Thewes et al., 2019; Schmidt et al., 2020; Thewes et al., 2020b). However, this can only occur if the pCO_2 is adjusted correctly in the storage room. A general recommendation for DCA is to keep the same O_2 and CO_2 ratio that is used in CA storage (Zanella et al., 2008), which could result in very low levels of CO_2 in DCA - RQ storage rooms. In experimental evaluations, the pCO_2 is typically adjusted to 1.2 kPa or below, depending on the apple cultivar (Thewes et al., 2020b). It is accepted that as the pCO_2 is lowered in the storage room, the CO_2 adsorber efficiency is also lowered. Currently, there is a research gap for the appropriate CO_2 partial pressure, which improves the CO_2 adsorber use without causing high CO_2 damage in fruit. In 'Galaxy' apples, fruit quality was better maintained at 2.0 kPa CO_2 in CA storage, compared to 1.2 and 1.6 kPa CO_2 . However, the higher pCO_2 in DCA-RQ 1.5 conditions resulted in a lower percentage of healthy fruit after 9 months of storage plus 7 d shelf life (Brackmann et al., 2015). The authors

concluded that pCO_2 should not be above 1.6 kPa for 'Galaxy' apple storage under DCA-RQ. Beyond the need of elucidating the best pCO_2 for each apple cultivar in DCA storage, different CO_2 concentration inside the storage room may also influence the LOL for DCA. Different CO_2 levels inside the room may influence fruit respiration and, consequently, the rate of CO_2 production and accumulation in the room. Therefore, CO_2 should also receive higher attention in future investigations in DCA storage.

One advantage of DCA-RQ is the direct determination of LOL based on the ratio between CO_2 release and O_2 uptake, while the DCA-Eth and DCA-CF have a mechanism to detect the LOL based on a secondary event and not directly from the respiration. Figure 4 shows that the RQ level increased above one at an pO_2 of 0.3 to 0.4 kPa, which was much higher than the pO_2 that caused the spike in chlorophyll fluorescence (≤ 0.1 kPa). The earlier detection of oxygen stress by DCA - RQ compared to DCA-CF is that it monitors respiration rate directly. At ≤ 0.1 kPa O_2 , when the chlorophyll fluorescence spiked, the RQ is very high (≈ 10). However, in practical terms, it is very difficult to determine the oxygen uptake of fruit in commercial rooms because of room leakage (Bessemans et al., 2018).

Currently, there are three main systems to determine the RQ that are commercially available. The DCA-RQ system named Advanced Control Respiration (ACR) - My Fruit Dynamic, from the company Van Amerongen CA Technology, is based on RQ determination of the whole storage room. With ACR, all machinery is turned off during the RQ determination to avoid errors, and the internal room pressure is maintained by nitrogen injection (Veltmann, 2013). Creating a small overpressure in the storage room reduces the influx of oxygen from the external atmosphere to the room atmosphere, reducing the error of O_2 uptake measurement. Studies performed using this DCA - RQ system found satisfactory results for the LOL estimation for 'Elstar' apples (Van Schaik et al., 2015).

The other two main DCA-RQ systems use a small chamber that is placed inside commercial rooms for determination of the RQ. Inside this small chamber is a fruit sample that is representative of the entire commercial room. These two DCA-RQ systems are commercially available as Safepod® and RQ - StoreFresh by Storage Control System Inc. (Sparta, MI, USA) and Isolcell (Italy), respectively. The Safepod® system is based on the RQ measurement in a small chamber allocated in the storage room (Schaefer and Bishop, 2012). The RQ-

StoreFresh system, developed by the Federal University of Santa Maria, Brazil, is based on the installation of two RQ measurement chambers with one fruit chamber and one gas reservoir chamber (Brackmann, 2015). The main advantages of these two systems is a more precise RQ determination because there is no influx of oxygen from the external atmosphere into the small chamber placed inside the commercial room. Another advantage is that no machinery is turned off during RQ determination, thus temperature and pressure inside the room are maintained.

Recently, a DCA-RQ system for commercial purposes was developed, which allows for the estimate of the correct O_2 uptake based on mathematical modeling, using inputs from the chamber leakage and atmosphere pressure variation (Bessemans et al., 2018, 2016). This system was tested for apples (Bessemans et al., 2018, 2016) and pears (Delele et al., 2019), showing promising results on fruit quality maintenance. However, the room leakage can vary over the storage period, which can influence the mathematical model and consequently, the RQ estimation.

More recently, a modular sensor system in combination with a respirometer for in-situ real-time measurement of respiration rate and RQ was developed by Keshri et al. (2019) (Figure 6). The Respiration Measuring Sphere (RMS88) is a compact spherical shaped (D- 88 mm) sensor system that houses a fluorescence based O_2 sensor (measuring range 0 kPa to 25 kPa) and a non-dispersive infrared CO_2 sensor (measuring range 0 ppm to 200000 ppm). Additionally, the CO_2 sensor measures relative humidity and temperature. This compact system was tested at lab scale as well in a commercial CA storage facility for the measurement of in-situ real-time respiration rate and RQ of strawberries and 'Pinova' apples, respectively (Keshri, Truppel et al. 2020). The mobile, leak-proof, and modular design of the system allows wireless monitoring of the start of anaerobic activity in real-time. The modular respirometer showed potential for its adoption and integration into existing CA facilities as well as in an advanced DCA monitoring and control system.

Dynamic controlled atmosphere system based on carbon dioxide production (DCA-CD)

It is necessary to monitor fruit metabolism in real time over the whole storage period to determine the LOL. One of the main methods to determine the overall fruit metabolism is by measuring the CO_2 production rate (Steffens et al., 2007; Saltveit, 2019). The CO_2 production rate reduces as the oxygen partial pressure is lowered in

the storage room until a particular oxygen partial pressure, where the CO_2 production then begins to increase because of anaerobic metabolism (Figure 7). Figure 7 demonstrates that fruit at the start of the storage have a relatively low tolerance to low pO_2 and have a higher LOL (blue line). With storage time the fruit adapt (yellow line) and at the end of the storage, before the senescence, fruit have the highest tolerance to the low oxygen conditions (red line). Based on the response of CO_2 production to oxygen variation, it is possible to monitor the LOL of fruit based solely on the CO_2 measurement (Thewes, 2019).

A DCA- CD system was also developed recently in the Postharvest Center of the Federal University of Santa Maria, Brazil (Thewes, 2019; Thewes et al., 2020b). This system was able to estimate the LOL accurately for several apple cultivars (Thewes et al., 2020b). According to this study, fruit stored under DCA-CD resulted in an apple quality maintenance comparative to fruit stored under DCA-RQ and had a better quality than fruit stored under CA-ULO. Another study that evaluated the DCA-CD system in commercial storage rooms verified an accurate LOL estimation, allowing the storage of 'Shalimar' apples under pO_2 , ranging between 0.2 and 0.8 kPa (Neuwald et al., 2020). This study also showed that fruit treated with or without 1-MCP maintained a similar flesh firmness after 6 months of storage plus 7 days at 20 °C when stored under DCA-CD (Neuwald et al., 2020).



Figure 6. Modular sensor system RMS88 and respirometer installed in a commercial storage facility of apples to measure in-situ real-time respiration rate and RQ.

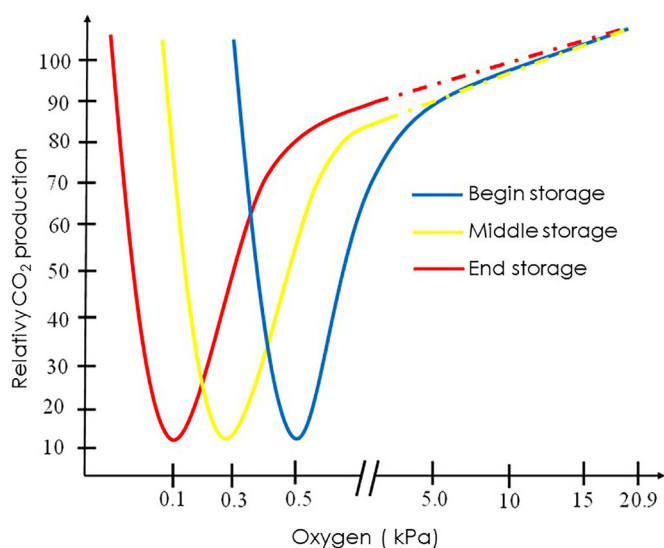


Figure 7. Relationship between oxygen in the storage room and relative CO₂ production of fruits over the storage period. Different colors represent variation as a function of the variety and/or storage duration.

The main advantage of the DCA-CD system is that the LOL estimation does not require the measurement of oxygen uptake (Thewes et al., 2020b). The measurement of oxygen uptake is the main challenge in commercial rooms because of room leakage (Bessemans et al., 2016, 2018). Thus, the DCA-CD system is easier to apply in commercial rooms because only the CO₂ production is used as an input for the LOL estimation. According to Bessemans et al. (2018), the measurement of CO₂ production in storage rooms is less influenced by the external ambient atmosphere than O₂ uptake.

Thewes et al. (2020b) reported that the DCA-CD system allows for the induction of anaerobic metabolism at safe levels, which can help fruit to maintain quality. The apple cultivar 'Elstar' stored under DCA-CD maintained higher concentrations of volatile compounds, especially esters, when compared to CA and DCA-CF, had similar concentrations to fruit stored under DCA-RQ (Thewes, 2019). This study also suggests that apples stored under DCA-CD maintain a similar overall fruit quality with higher concentrations of volatile compounds when compared to CA + 1-MCP. Commercially, the DCA-CD system is named FruitAtmo® by company Frigotec, Germany.

LOL variation over different seasons

Fruit metabolism is affected by several factors such as storage temperature, harvest maturity, cultivar and growing season (Steffens et al., 2007; Thewes et al., 2017a; Saltveit, 2019). Figure 8 shows the LOL variation for 'Gala' and 'Fuji' apples over five consecutive seasons. It is clearly presented that there are significant differences among years. Therefore, it is necessary to monitor the LOL

every year, as it is not possible to use the estimated value from past seasons and apply the previous LOL to the current season. This suggests that, regardless of the DCA system, the LOL should be determined in each season and each individual storage room to avoid losses due to inadequate oxygen partial pressure during storage.

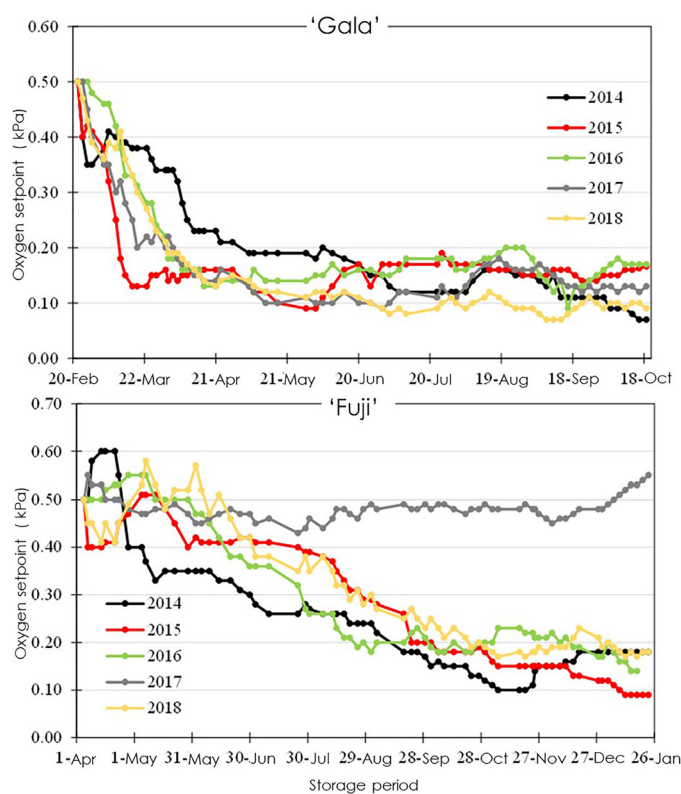


Figure 8. Lower oxygen limit (LOL) variation for 'Gala' and 'Fuji' apples based on DCA-RQ 1.3 over a period of 5 consecutive years (Thewes et al., 2019).

Future prospects of DCA systems

The storage under dynamic controlled atmosphere is constantly changing. Thus, in the near future, there will be a need to develop DCA systems that allow for more atmosphere changes to be made than just the O₂ partial pressure. One important factor that can be varied according to fruit metabolism is the storage temperature. DCA storage significantly reduces fruit respiration, which allows fruit to be stored at higher temperatures, thus saving energy. Recent results show that DCA with temperature control significantly reduced energy consumption, between 15 % and up to 50 %. With the increasing demand for more sustainable food, DCA systems show the potential of being the future of more sustainable fruit storage.

Another factor that can be varied according to fruit metabolism is the storage rooms CO₂ partial pressure. Altering the pCO₂ according to fruit metabolism can increase the efficiency of CO₂ scrubbers and help with fruit quality maintenance. There is also a system being

developed to monitor eight fruit volatile compounds in real time (periodically) over the storage period using a low-cost portable and a fully integrated gas sensor. According to the Newsletter of the Interreg North-West Europe, with this system, it will be possible to control the room atmosphere according to fruit metabolism. The system will also be able to detect in advance the occurrence of problems with fruit quality such as decay incidence and some physiological disorders, and consequently avoiding fruit losses, by scaling the storage room opening.

Dynamic storage facilities are always computer controlled. Future innovations of DCA systems may include automatic decision support systems that sense and respond to variations in gas concentrations. Furthermore, automatic decision support could also respond to temperature variations based on the fresh produce species being stored, the variety, pre-harvest conditions and maturity. Additionally, such systems could support the warehouse operator in making the correct decision in real-time. Research is being conducted on upgrading the existing DCA systems to incorporate new technologies for collecting data on additional quality parameters such as color and firmness of stored produce. The use of multi-sensor technology could also be incorporated into DCA storage rooms for better monitoring of quality during storage. Data from different imaging technologies and other systems such as an electronic nose (E-nose) are processed using sensor fusion (soft sensors). Soft sensors process multiple sensor information for identified quality classifiers and the development of warning systems, for instance, the decline in quality (Onwude et al., 2020). Such information will assist growers in decision making at the right time before the stored produce is spoiled. The more information on the stored produce physiology will lead to better fruit quality maintenance and thereby reduce fruit losses. Application of DCA systems to other pome fruit varieties and other fresh produce such as kiwifruit is an area that needs to be explored. The biggest challenge for the post-harvest storage industry is that each year several new varieties and species of fresh fruit come into the market. More research is needed to understand the dynamic physiological responses of fresh produce to CA in order to determine the optimal conditions for each cultivar and scenario. Recent trends in sensor and electronics miniaturization and new material development suggest a bright future for smarter, more versatile food storage systems.

Conclusions

This review has shown that there are four main

DCA technologies available for commercial storage rooms. This review also detailed new concepts of DCA that are in development, especially with regards to a DCA system that allows more than one factor variation and monitors several fruit volatile compounds. It is highlighted that the storage of fruit under DCA reduces the quality losses when compared to CA, especially the incidence of physiological disorders like superficial scald and flesh breakdown. Also, DCA can maintain fruit with a higher flesh firmness. Furthermore, it was shown that the storage of fruit under DCA-RQ and DCA-CD allowed for higher volatile compound emissions and concentrations, which can contribute positively to fruit flavor. It is also suggested that the DCA-CD system is easier to apply in commercial rooms because the CO₂ measurement is used solely to determine the LOL.

The DCA systems are clean and green storage technologies, which can enable the increase of storage temperature, saving electrical energy, and reducing fruit damage from low temperatures. Storage of apples under DCA maintains an overall fruit quality similar to CA + 1-MCP. Since 1-MCP is not allowed to be used for organic fruit production, DCA is the only highly efficient storage alternative for long stored organic apples.

References

- Anese, R. de O., Brackmann, A., Thewes, F.R., Schultz, E.E., Ludwig, V., Wendt, L.M., Wagner, R., Klein, B., 2020. Impact of dynamic controlled atmosphere storage and 1-methylcyclopropene treatment on quality and volatile organic compounds profile of 'Galaxy' apple. *Food Packaging and Shelf Life* 23, 100443. <https://doi.org/10.1016/j.fpsl.2019.100443>
- Asoda, T., Terai, H., Kato, M., Suzuki, Y., 2009. Effects of postharvest ethanol vapor treatment on ethylene responsiveness in broccoli. *Postharvest Biology and Technology* 52, 216–220. <https://doi.org/10.1016/j.postharvbio.2008.09.015>
- Aubert, C., Mathieu-Hurtiger, V., Vaysse, P., 2015. Effects of dynamic atmosphere on volatile compounds, polyphenolic content, overall fruit quality, and sensory evaluation of "pink lady®" apples. *Acta Horticulturae*. 275–280. <https://doi.org/10.17660/ActaHortic.2015.1071.34>
- Bekele, E.A., Ampofo-Asiama, J., Alis, R.R., Hertog, M.L.A.T.M., Nicolai, B.M., Geeraerd, A.H., 2016. Dynamics of metabolic adaptation during initiation of controlled atmosphere storage of 'Jonagold' apple: Effects of storage gas concentrations and conditioning. *Postharvest Biology and Technology* 117, 9–20. <https://doi.org/10.1016/j.postharvbio.2016.02.003>
- Bessemans, N., Verboven, P., Verlinden, B.E., Nicolai, B.M., 2018. Model based leak correction of real-time RQ measurement for dynamic controlled atmosphere storage. *Postharvest Biology and Technology* 136, 31–41.

<https://doi.org/10.1016/j.postharvbio.2017.09.011>

Bessemans, N., Verboven, P., Verlinden, B.E., Nicolai, B.M., 2016. A novel type of dynamic controlled atmosphere storage based on the respiratory quotient (RQ-DCA). *Postharvest Biology and Technology* 115, 91–102. <https://doi.org/10.1016/j.postharvbio.2015.12.019>

Boersing, M. R., Kader, A. A., Romani, R.J. 1988. Aerobic-Abaerobic respiratory transition in pear fruit and cultured pear fruit cells. *Journal of the American Society for horticultural Science*, v. 113, n. 6, p. 869-873.

Both, V., Brackmann, A., Thewes, F.R., Ferreira, D. de F., Wagner, R., 2014. Effect of storage under extremely low oxygen on the volatile composition of 'Royal Gala' apples. *Food Chemistry* 156, 50–57. <https://doi.org/10.1016/j.foodchem.2014.01.094>

Both, V., Brackmann, A., Thewes, F.R., Weber, A., Schultz, E.E., Ludwig, V., 2018. The influence of temperature and 1-MCP on quality attributes of 'Galaxy' apples stored in controlled atmosphere and dynamic controlled atmosphere. *Food Packaging and Shelf Life* 16, 168–177. <https://doi.org/10.1016/j.foodchem.2018.03.010>

Both, V., Thewes, F.R., Brackmann, A., de Oliveira Anese, R., de Freitas Ferreira, D., Wagner, R., 2017. Effects of dynamic controlled atmosphere by respiratory quotient on some quality parameters and volatile profile of 'Royal Gala' apple after long-term storage. *Food Chemistry* 215, 483–492. <https://doi.org/10.1016/j.foodchem.2016.08.009>

Brackmann, A. Control apparatus for controlled atmosphere cells for storing perishable items. U.S. Patent, n.US/2015/0257401, 2015.

Brackmann, A., Weber, A., Both, V., 2015. CO₂ partial pressure for respiratory quotient and harvest watch dynamic controlled atmosphere for "galaxy" apples storage. *Acta Horticulturae*. 435–440. <https://doi.org/10.17660/ActaHortic.2015.1079.56>

Brackmann, A., Weber, A., Pinto, J.A.V., Neuwald, D.A., Steffens, C.A., 2008. Manutenção da qualidade pós-colheita de maçãs "Royal Gala" e "Galaxy" sob armazenamento em atmosfera controlada. *Ciência Rural* 38, 2478–2484. <https://doi.org/10.1590/S0103-84782008000900010>

de Oliveira Anese, R., Brackmann, A., Wendt, L.M., Thewes, F.R., Schultz, E.E., Ludwig, V., Berghetti, M.R.P., 2019. Interaction of 1-methylcyclopropene, temperature and dynamic controlled atmosphere by respiratory quotient on 'Galaxy' apples storage. *Food Packaging and Shelf Life* 20, 100246. <https://doi.org/10.1016/j.foodchem.2018.07.004>

Delele, M. A. et al. Storage of respiratory produce. European patent. Publication number EP2547213 B1, 2015.

Delele, M.A., Bessemans, N., Gruyters, W., Rogge, S., Janssen, S., Verlinden, B.E., Smeets, B., Ramon, H., Verboven, P., Nicolai, B.M., 2019. Spatial distribution of gas concentrations and RQ in a controlled atmosphere storage container with pear fruit in very low oxygen conditions. *Postharvest Biology and Technology* 156, 110903. <https://doi.org/10.1016/j.postharvbio.2019.05.004>

Deuchande, T., Carvalho, S.M.P., Guterres, U., Fidalgo, F., Isidoro, N., Larrigaudière, C., Vasconcelos, M.W., 2016. Dynamic controlled atmosphere for prevention of internal browning disorders in 'Rocha' pear. *LWT - Food Science and Technology* 65, 725–730. <https://doi.org/10.1016/j.lwt.2015.08.075>

Donadel, J.Z., Thewes, F.R., de Oliveira Anese, R., Schultz, E.E., Berghetti, M.R.P., Ludwig, V., Klein, B., Cichoski, A.J., Barin, J.S., Both, V., Brackmann, A., Wagner, R., 2019. Key volatile compounds of 'Fuji Kiku' apples as affected by the storage conditions and shelf life: Correlation between volatile emission by intact fruit and juice extracted from the fruit. *Food Research International* 108625. <https://doi.org/10.1016/j.foodres.2019.108625>

Eren, I., Çalhan, O., Onursal, C.E., Güneçli, A., 2015. Effects of controlled atmosphere, dynamic controlled atmosphere and 1-mcp on quality of "granny smith" apples. *Acta Horticulturae* 495–502. <https://doi.org/10.17660/ActaHortic.2015.1071.64>

Gabioud Rebeaud, S., Gasser, F., 2015. Fruit quality as affected by 1-MCP treatment and DCA storage - a comparison of the two methods. *European Journal of Horticultural Science* 80, 18–24. <https://doi.org/10.17660/eJHS.2015/80.1.3>

Gasser, F., Eppler, T., Naunheim, W., Gabioud, S., Hoehn, E., 2008. Control of the critical oxygen level during dynamic ca storage of apples by monitoring respiration as well as chlorophyll fluorescence. *Acta Horticulturae* 69–76. <https://doi.org/10.17660/ActaHortic.2008.796.6>

Goyette, B., Vigneault, C., Raghavan, V., Charles, M.-T., 2012. Hyperbaric Treatment on Respiration Rate and Respiratory Quotient of Tomato. *Food Bioprocess Technol* 5, 3066–3074. <https://doi.org/10.1007/s11947-011-0671-y>

Hennecke, C., Köpcke, D., Dierend, W., 2008. Dynamische Absenkung des Sauerstoffgehaltes bei der Lagerung von Äpfeln. *Erwerbs-Obstbau* 50, 19–29. <https://doi.org/10.1007/s10341-007-0055-7>

Ho, Q.T., Verboven, P., Verlinden, B.E., Schenk, A., Nicolai, B.M., 2013. Controlled atmosphere storage may lead to local ATP deficiency in apple. *Postharvest Biology and Technology* 78, 103–112. <https://doi.org/10.1016/j.postharvbio.2012.12.014>

Hoehn, E., Prange, R. K., Vigneault, C. 2009. Storage Technology and Applications. In: Yahia, E. M. Ed. Modified and controlled atmospheres for storage, transportation, and packaging of horticultural commodities. *CRC Press Taylor Francis Group* : Boca Raton, p. 17-50.

Jin, Y.Z., Lv, D.Q., Liu, W.W., Qi, H.Y., Bai, X.H., 2013. Ethanol vapor treatment maintains postharvest storage quality and inhibits internal ethylene biosynthesis during storage of oriental sweet melons. *Postharvest Biology and Technology* 86, 372–380. <https://doi.org/10.1016/j.postharvbio.2013.07.019>

Ke, D., Yahia, E., Mateos, M., Kader, A.A., 1994. Ethanolic Fermentation of 'Bartlett' Pears as Influenced by Ripening Stage and Atmospheric Composition. *Journal of the*

- American Society for Horticultural Science 119, 976–982. <https://doi.org/10.21273/JASHS.119.5.976>
- Kittemann, D., Neuwald, D.A., Streif, J., 2015. Internal browning in “kanzi®” apples - reasons and possibilities to reduce the disorder. *Acta Horticulturae* 409–414. <https://doi.org/10.17660/ActaHortic.2015.1079.52>
- Köpcke, D., 2015. 1-Methylcyclopropene (1-MCP) and dynamic controlled atmosphere (DCA) applications under elevated storage temperatures: Effects on fruit quality of “Elstar”, “Jonagold” and “Gloster” apple (*Malus domestica* Borkh.). *European Journal of Horticultural Science* 80, 25–32. <https://doi.org/10.17660/eJHS.2015/80.1.4>
- Köpcke, D., 2014. Neue Entwicklungen in der DCA-Lagerung nach eine Vortrag auf den Norddeutschen Obstbautagen in Jork 2014 *Mitteilungen OVR*. 69 (6), 156–160.
- Lee, J., Rudell, D.R., Davies, P.J., Watkins, C.B., 2012. Metabolic changes in 1-methylcyclopropene (1-MCP)-treated ‘Empire’ apple fruit during storage. *Metabolomics* 8, 742–753. <https://doi.org/10.1007/s11306-011-0373-5>
- Liu, W.W., Qi, H.Y., Xu, B.H., Li, Y., Tian, X.B., Jiang, Y.Y., Xu, X.F., Lv, D.Q., 2012. Ethanol treatment inhibits internal ethylene concentrations and enhances ethyl ester production during storage of oriental sweet melons (*Cucumis melo* var. *makuwa* Makino). *Postharvest Biology and Technology* 67, 75–83. <https://doi.org/10.1016/j.postharvbio.2011.12.015>
- Maxwell, K., Johnson, G.N., 2000. Chlorophyll fluorescence—a practical guide. *Journal of Experimental Botany* 51, 659–668. <https://doi.org/10.1093/jexbot/51.345.659>
- Mditshwa, A., Fawole, O.A., Opara, U.L., 2018. Recent developments on dynamic controlled atmosphere storage of apples—A review. *Food Packaging and Shelf Life* 16, 59–68. <https://doi.org/10.1016/j.foodpack.2018.01.011>
- Mditshwa, A., Fawole, O.A., Vries, F., van der Merwe, K., Crouch, E., Opara, U.L., 2017a. Minimum exposure period for dynamic controlled atmospheres to control superficial scald in ‘Granny Smith’ apples for long distance supply chains. *Postharvest Biology and Technology* 127, 27–34. <https://doi.org/10.1016/j.postharvbio.2016.12.009>
- Mditshwa, A., Fawole, O.A., Vries, F., van der Merwe, K., Crouch, E., Opara, U.L., 2017b. Repeated application of dynamic controlled atmospheres reduced superficial scald incidence in ‘Granny Smith’ apples. *Scientia Horticulturae* 220, 168–175. <https://doi.org/10.1016/j.scienta.2017.04.003>
- Neuwald, D. A., Saquet, A. A., Klein, N., Disorders during storage of fruits and vegetables. In Tonetto de Freitas, S., and Pareek, S., *Postharvest physiological disorders in fruits and vegetables*. CRC Press Taylor Francis Group : Boca Raton, p 89 - 110. <https://doi.org/10.1201/b22001-5>
- Neuwald, D.A., Büchele, F., Thewes, F.R., Brackmann, A., Wirth, R. 2020. Erste Ergebnisse mit FruitAtmo aus der Praxis: Autonome Kontrolle der Lagerbedingung sichert Fruchtqualität. *Besseres Obst*, 2, 30 - 32.
- Patel, H., Bhardwaj, A., 2019. Physiology, Respiratory Quotient, in: StatPearls. StatPearls Publishing, Treasure Island (FL).
- Pesis, E., 2005. The role of the anaerobic metabolites, acetaldehyde and ethanol, in fruit ripening, enhancement of fruit quality and fruit deterioration. *Postharvest Biology and Technology* 37, 1–19. <https://doi.org/10.1016/j.postharvbio.2005.03.001>
- Prange, R.K., 2018. Dynamic Controlled Atmosphere (DCA) Storage of Fruits and Vegetables, in: *Reference Module in Food Science*. Elsevier, p. B9780081005965214000. <https://doi.org/10.1016/B978-0-08-100596-5.21349-8>
- Prange, R.K., DeLong, J.M., Harrison, P.A., 2005. Quality management through respiration control: is there a relationship between lowest acceptable respiration, chlorophyll fluorescence and cytoplasmic acidosis? *Acta Horticulturae* 823–830. <https://doi.org/10.17660/ActaHortic.2005.682.107>
- Prange, R.K., DeLong, J.M., Harrison, P.A., Leyte, J.C., McLean, S.D., 2003. Oxygen Concentration Affects Chlorophyll Fluorescence in Chlorophyll-containing Fruit and Vegetables. *Journal of the American Society for Horticultural Science* 128, 603–607. <https://doi.org/10.21273/JASHS.128.4.0603>
- Prange, R.K., Wright, A.H., DeLong, J.M., Zanella, A., 2015. A review on the successful adoption of dynamic controlled-atmosphere (dca) storage as a replacement for diphenylamine (dpa), the chemical used for control of superficial scald in apples and pears. *Acta Horticulturae* 389–396. <https://doi.org/10.17660/ActaHortic.2015.1071.50>
- Rizzolo, A., Buccheri, M., Bianchi, G., Grassi, M., Vanoli, M., 2015. Quality of “conference” pears as affected by initial low oxygen stress, dynamically controlled atmosphere and 1-mcp treatment. *Acta Horticulturae* 343–350. <https://doi.org/10.17660/ActaHortic.2015.1079.43>
- Saltveit, M.E., 2019. Respiratory Metabolism, in: *Postharvest Physiology and Biochemistry of Fruits and Vegetables*. Elsevier, pp. 73–91. <https://doi.org/10.1016/B978-0-12-813278-4.00004-X>
- Schaefer, J.C.; Bishop, D.J. Dynamic control system and method for controlled atmosphere room. Publication number US 2012/0097050 A1, 2012.
- Schlie, T. P., Köpcke, D., Rath, T., Dierend, W., 2019. Importance of individual apple fruit characteristics for DCA-CF Storage on the variety ‘Elstar PCP’. *Erwerb-Obstbau*. <https://doi.org/10.1007/s10341-019-00463-z>
- Schmidt, S.F.P., Schultz, E.E., Ludwig, V., Berghetti, M.R.P., Thewes, F.R., Anese, R. de O., Both, V., Brackmann, A., 2020. Volatile compounds and overall quality of ‘Braeburn’ apples after long-term storage: Interaction of innovative storage technologies and 1-MCP treatment. *Scientia Horticulturae* 262, 109039. <https://doi.org/10.1016/j.scienta.2019.109039>

- Schouten, S.P., Prange, R.K., Verschoor, J., Lammers, T.R., Oosterhaven, J., 1998. Improvement of Quality of Elstar Apples by Dynamic Control of ULO Conditions. *IFAC Proceedings Volumes* 31, 25–29. [https://doi.org/10.1016/S1474-6670\(17\)44023-7](https://doi.org/10.1016/S1474-6670(17)44023-7)
- Steffens, C.A., Brackmann, A., Pinto, J.A.V., Eisermann, A.C., 2007. Taxa respiratória de frutas de clima temperado. *Pesquisa agropecuária brasileira* 42, 313–321. <https://doi.org/10.1590/S0100-204X2007000300003>
- Thewes, Fabio Rodrigo, Anese, R.O., Thewes, Flavio Roberto, Ludwig, V., Klein, B., Wagner, R., Nora, F.R., Rombaldi, C.V., Brackmann, A., 2020a. Dynamic controlled atmosphere (DCA) and 1-MCP: Impact on volatile esters synthesis and overall quality of 'Galaxy' apples. *Food Packaging and Shelf Life* 26, 100563. <https://doi.org/10.1016/j.foodpack.2020.100563>
- Thewes, Fabio Rodrigo, Brackmann, A., Both, V., Anese, R. de O., Schultz, E.E., Ludwig, V., Wendt, L.M., Berghetti, M.R.P., Thewes, Flavio Roberto, 2020b. Dynamic controlled atmosphere based on carbon dioxide production (DCA-CD): Lower oxygen limit establishment, metabolism and overall quality of apples after long-term storage. *Postharvest Biology and Technology* 168, 111285. <https://doi.org/10.1016/j.postharvbio.2020.111285>
- Thewes, F.R., Both, V., Brackmann, A., Weber, A., de Oliveira Anese, R., 2015. Dynamic controlled atmosphere and ultralow oxygen storage on 'Gala' mutants quality maintenance. *Food Chemistry* 188, 62–70. <https://doi.org/10.1016/j.foodchem.2015.04.128>
- Thewes, F.R., Brackmann, A., Anese, R. de O., Ludwig, V., Schultz, E.E., dos Santos, L.F., Wendt, L.M., 2017a. Effect of dynamic controlled atmosphere monitored by respiratory quotient and 1-methylcyclopropene on the metabolism and quality of 'Galaxy' apple harvested at three maturity stages. *Food Chemistry* 222, 84–93. <https://doi.org/10.1016/j.foodchem.2016.12.009>
- Thewes, F.R., Brackmann, A., Both, V., Weber, A., Anese, R. de O., Ferrão, T. dos S., Wagner, R., 2017b. The different impacts of dynamic controlled atmosphere and controlled atmosphere storage in the quality attributes of 'Fuji Suprema' apples. *Postharvest Biology and Technology* 130, 7–20. <https://doi.org/10.1016/j.postharvbio.2017.04.003>
- Thewes, F.R., 2019. Dynamic controlled atmosphere methods × 1-MCP: Metabolism and quality of stored apples. Ph.D Thesis. Federal University of Santa Maria, Santa Maria, Brazil. 239p.
- Thewes, F.R., Brackmann, A., de Oliveira Anese, R., Bronzatto, E.S., Schultz, E.E., Wagner, R., 2017c. Dynamic controlled atmosphere storage suppresses metabolism and enhances volatile concentrations of 'Galaxy' apple harvested at three maturity stages. *Postharvest Biology and Technology* 127, 1–13. <https://doi.org/10.1016/j.postharvbio.2017.01.002>
- Thewes, F.R., Brackmann, A., Neuwald, D.A., 2019. Dynamics of sugars, anaerobic metabolism enzymes and metabolites in apples stored under dynamic controlled atmosphere. *Scientia Horticulturae* 255, 145–152. <https://doi.org/10.1016/j.scienta.2019.05.027>
- Tran, D.T., Verlinden, B.E., Hertog, M., Nicolai, B.M., 2015. Monitoring of extremely low oxygen control atmosphere storage of 'Greenstar' apples using chlorophyll fluorescence. *Scientia Horticulturae* 184, 18–22. <https://doi.org/10.1016/j.scienta.2014.11.014>
- Van Schaik, A.C.R., Van de Geijn, F.G., Verschoor, J.A., Veltman, R.H., 2015. A new interactive storage concept: dynamic control of respiration. *Acta Horticulturae* 245–251. <https://doi.org/10.17660/ActaHortic.2015.1071.29>
- Veltman, R.H., Verschoor, J.A., van Dugteren, J.H.R., 2003. Dynamic control system (DCS) for apples (*Malus domestica* Borkh. cv 'Elstar'): optimal quality through storage based on product response. *Postharvest Biology and Technology* 27, 79–86. [https://doi.org/10.1016/S0925-5214\(02\)00186-2](https://doi.org/10.1016/S0925-5214(02)00186-2)
- Veltman, R.H. Method and apparatus for controlling the atmosphere in a space filled with agricultural or horticultural products. Publication number WO 2013125944 A1, 2013.
- Weber, A., Brackmann, A., Anese, R. de O., Both, V., Pavanello, E.P., 2011. "Royal Gala" apple quality stored under ultralow oxygen concentration and low temperature conditions. *Pesquisa agropecuária brasileira* 46, 1597–1602. <https://doi.org/10.1590/S0100-204X2011001200003>
- Weber, A., Brackmann, A., Both, V., Pavanello, E.P., Anese, R. de O., Thewes, F.R., 2015. Respiratory quotient: innovative method for monitoring 'Royal Gala' apple storage in a dynamic controlled atmosphere. *Scientia agricola* (Piracicaba, Braz.) 72, 28–33. <https://doi.org/10.1590/0103-9016-2013-0429>
- Weber, A., Brackmann, A., Both, V., Pavanello, E.P., Anese, R.O., Schorr, M.R.W., 2016. Ethanol reduces ripening of "Royal Gala" apples stored in controlled atmosphere. *Anais da Academia Brasileira de Ciências* 88, 403–410. <https://doi.org/10.1590/0001-3765201620140181>
- Weber, A., Neuwald, D.A., Kitemann, D., Thewes, F.R., Both, V., Brackmann, A., 2020. Influence of respiratory quotient dynamic controlled atmosphere (DCA-RQ) and ethanol application on softening of Braeburn apples. *Food Chemistry* 303, 125346. <https://doi.org/10.1016/j.foodchem.2019.125346>
- Weber, A., Thewes, F.R., Anese, R. de O., Both, V., Pavanello, E.P., Brackmann, A., 2017. Dynamic controlled atmosphere (DCA): interaction between DCA methods and 1-methylcyclopropene on 'Fuji Suprema' apple quality. *Food Chemistry* 235, 136–144. <https://doi.org/10.1016/j.foodchem.2017.05.047>
- Weber, A., Thewes, F.R., Sellwig, M., Brackmann, A., Wünsche, J.N., Kitemann, D., Neuwald, D.A., 2019. Dynamic controlled atmosphere: Impact of elevated storage temperature on anaerobic metabolism and quality of 'Nicoter' apples. *Food Chemistry* 298, 125017. <https://doi.org/10.1016/j.foodchem.2019.125017>

Wright, A.H., DeLong, J.M., Arul, J., Prange, R.K., 2015. The trend toward lower oxygen levels during apple (*Malus × domestica* Borkh) storage – A review. *Journal of Horticultural Science & Biotechnology* 90, 14. <https://doi.org/10.1080/14620316.2015.11513146>

Wright, A.H., DeLong, J.M., Gunawardena, A.H.L.A.N., Prange, R.K., 2012. Dynamic controlled atmosphere (DCA): Does fluorescence reflect physiology in storage? *Postharvest Biology and Technology* 64, 19–30. <https://doi.org/10.1016/j.postharvbio.2011.09.015>

Wright, A.H., DeLong, J.M., Gunawardena, A.H.L.A.N., Prange, R.K., 2011. The interrelationship between the lower oxygen limit, chlorophyll fluorescence and the xanthophyll cycle in plants. *Photosynth Res* 107, 223–235. <https://doi.org/10.1007/s11120-011-9621-9>

Zanella, A., Cazzanelli, P., Panarese, A., Coser, M., Chistè, C., Zeni, F., 2005. Fruit fluorescence response to low oxygen stress: modern storage technologies compared to 1-mcp treatment of apple. *Acta Horticulturae* 1535–1542. <https://doi.org/10.17660/ActaHortic.2005.682.204>

Zanella, A., Cazzanelli, P., Rossi, O., 2008. Dynamic controlled atmosphere (dca) storage by the means of chlorophyll fluorescence response for firmness retention in apple. *Acta Horticulturae* 77–82. <https://doi.org/10.17660/ActaHortic.2008.796.7>

Zanella, A., Stürz, S., 2015. Optimizing postharvest life of horticultural products by means of dynamic ca: fruit physiology controls atmosphere composition during storage. *Acta Horticulturae* 59–68. <https://doi.org/10.17660/ActaHortic.2015.1071.4>

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