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Review article

Modelling respiration rate of fresh fruits and vegetables for modified atmosphere packages: a review

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Abstract

Respiration rate and gas exchange through the package material are the processes involved in creating a modified atmosphere inside a package that will extend shelf life of fresh fruits and vegetables. Thus, modelling respiration rate of the selected produce is crucial to the design of a successful modified atmosphere packaging (MAP) system. In this paper, general aspects of the respiration process are presented. The major methods for measuring respiration rates, along with their advantages and limitations are discussed. Factors affecting the respiration rate and respiratory quotient are outlined, stressing the importance of temperature, O_2 and CO_2 concentrations, and storage time. Respiration rate models in the literature are also reviewed. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: CO_2 production; Gas composition effects; O_2 consumption; Respiratory quotient; Temperature effects

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1. Introduction

Quality optimisation and loss reduction in the postharvest chain of fresh fruits and vegetables are the main objectives of postharvest technology. Temperature

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Nomenclature

A	surface area, m^2
E	activation energy, Pa m^3 mol^{-1}
F	flow rate, m^3 s^{-1}
L	thickness, m
M	mass, kg
m_M	molar mass, g mol^{-1}
P	permeability coefficient, m^2 s^{-1}
p_T	total pressure, Pa
R	respiration (consumption/production) rate, m^3 kg^{-1} s^{-1}
R_c	universal gas constant, Pa m^3 mol^{-1} K^{-1}
T	temperature, °C or K
t	time, s
V	free volume, m^3
y	volumetric concentration, % v/v
$\alpha, \phi, \gamma, \delta$	model parameters

Superscripts

e	external
in	inlet
out	outlet

Subscripts

c	competitive
f	final
i	initial
n	non-competitive
ref	reference
u	uncompetitive

control and modification of atmosphere are two important factors in prolonging shelf life.

Modified atmosphere packaging (MAP) of fresh produce relies on modification of the atmosphere inside the package, achieved by the natural interplay between two processes, the respiration of the product and the transfer of gases through the packaging, that leads to an atmosphere richer in CO_2 and poorer in O_2. This atmosphere can potentially reduce respiration rate, ethylene sensitivity and production, decay and physiological changes, namely, oxidation (Gorris & Tauscher, 1999; Kader, Zagory, & Kerbel, 1989; Saltveit, 1997).

MA packages should be carefully designed, as a system incorrectly designed may be ineffective or even shorten the shelf life of the product. The design should take into consideration not only steady-state conditions, but also the dynamic process, because if the product is exposed for a long time to unsuitable gas composition before reaching the adequate atmosphere, the package may have no benefit. The design of an MA package depends on a number of variables: the characteristics of the product, its mass, the recommend atmosphere composition, the permeability of the packaging materials to gases and its dependence on temperature and the respiration rate of the product as affected by different gas composition and temperature. Thus, respiration rate modelling is central to the design of MAP for fresh fruits and vegetables.

The main objective of this paper is to present in a systematic way information available in the literature regarding mathematical modelling of respiration rate of fresh and fresh-cut produce, focusing particularly on:

(i) general aspects of the respiration process,
(ii) usual methods of measuring respiration rates,
(iii) factors affecting the respiration rate and
(iv) respiration rate models reported in the literature.

2. Plant metabolism

Respiration is a metabolic process that provides the energy for plant biochemical processes. Various substrates used in important synthetic metabolic pathways in the plant are formed during respiration (Meyer, Anderson, Bohling, & Fratianne, 1973). Aerobic respiration (for the sake of simplicity, the word respiration will be used throughout this paper to designate aerobic respiration) consists of oxidative breakdown of organic reserves to simpler molecules, including CO_2 and water, with release of energy. The organic substrates broken down in this process may include carbohydrates, lipids, and organic acids. The process consumes O_2 in a series of enzymatic reactions. Glycolysis, the tricarboxilic acid cycle, and the electron transport system are the metabolic pathways of aerobic respiration.

The ratio of CO_2 produced to O_2 consumed, known as the respiratory quotient (RQ), is normally assumed to be equal to 1.0 if the metabolic substrates are carbohydrates. The total oxidation of 1 mol of hexose consumes 6 mol of O_2 and produces 6 mol of CO_2. If the substrate is a lipid, the RQ is always lower than unity, because the ratio between C and O in lipids is lower than the ratio in carbohydrates. If the substrate is an acid, the RQ is higher than unity. Therefore, normal RQ values in the literature are reported as ranging from 0.7 to 1.3 (Kader, 1987). Renault, Houal, Jacquemin, and Chambroy (1994) justified an RQ value of 1.0 for strawberries, presumably reflecting rich glycosidic reserves. Beaudry, Cameron, Shirazi, and Dostal-Lange (1992) explained an observed RQ of 1.3 for blueberries by their high content of citric acid and sugars. The RQ is much greater than 1.0 when anaerobic respiration takes place. In fermentative metabolism, ethanol production involves decarboxylation of pyruvate to CO_2 without O_2 uptake. Various MAP studies have reported values of

RQ indicative of anaerobic respiration (Beaudry et al., 1992; Beit-Halachmy & Mannheim, 1992; Carlin, Nguyen-the, Hilbert, & Chambroy, 1990; Joles, Cameron, Shirazi, Petracek, & Beaudry, 1994; Jurin & Karel, 1963). The RQ value for apples at 20 °C remained relatively constant down to 3.5% O_2, at which point it increased rapidly (Jurin & Karel, 1963). Carlin et al. (1990) obtained an RQ of 6 for grated carrots packed in low permeability films. Beit-Halachmy and Mannheim (1992) found an RQ of approximately 1 for mushrooms at 20 °C and at O_2 levels greater than 1.5–2%; below this O2 level, RQ increased rapidly to a value higher than 6.

3. Respiration rate measurement

The respiration rate of fresh produce can be expressed as O_2 consumption rate and/or CO_2 production rate. The usual methods of respiration rate determination are:

(i) the closed or static system,
(ii) the flowing or flushed system and
(iii) the permeable system.

In the closed system, a gas-tight container of known volume is filled with product and the container, containing ambient air as the initial atmosphere, is closed (Cameron, Boylan-Pett, & Lee, 1989; Fishman, Rodov, & Ben-Yehoshua, 1996; Gong & Corey, 1994; Haggar, Lee, & Yam, 1992; Henig & Gilbert, 1975; Jacxsens, Devlieghhere, & Debevere, 1999; Maneerat, Tongta, Kanlayanarat, & Wongs-Aree, 1997; Ratti, Raghavan, & Gariépy, 1996; Song, Kim, & Yam, 1992). Changes in the concentration of O_2 and CO_2 over a certain period of time are measured and used to estimate respiration rates (Eqs. (1) and (2)). In the flow through system, the product is enclosed in an impermeable container through which a gas mixture flows at a constant rate (Fidler & North, 1967; Lee, Haggar, Lee, & Yam, 1991; McLaughlin & O'Beirne, 1999; Smyth, Song, & Cameron, 1998; Talasila, Chau, & Brecht, 1992). The respiration rates are calculated from the absolute differences in gas concentrations between the outlet and the inlet (Eqs. (3) and (4)) when the system reaches steady state. In the permeable system, a package of known dimensions and film permeability is filled with product (Beaudry, 1993; Beaudry et al., 1992; Joles et al., 1994; Lakakul, Beaudry, & Hernandez, 1999; Lee, Song, & Yam, 1996; Piergiovanni, Fava, & Ceriani, 1999; Smyth et al., 1998; Talasila, Cameron, & Joles, 1994). The steady-state concentrations of O_2 and CO_2 are determined and a mass balance is performed on the system in order to estimate the respiration rates (Eqs. (5) and (6)):

$$R_{O_2} = \frac{\left(y_{O_2}^{t_i} - y_{O_2}^{t_f}\right) \times V}{100 \times M \times (t_f - t_i)}, \tag{1}$$

$$R_{CO_2} = \frac{\left(y_{CO_2}^{t_f} - y_{CO_2}^{t_i}\right) \times V}{100 \times M \times (t_f - t_i)}, \tag{2}$$

$$R_{O_2} = \frac{\left(y_{O_2}^{in} - y_{O_2}^{out}\right) \times F}{100 \times M}, \tag{3}$$

$$R_{CO_2} = \frac{\left(y_{CO_2}^{out} - y_{CO_2}^{in}\right) \times F}{100 \times M}, \tag{4}$$

$$R_{O_2} = \frac{P_{O_2} \times A}{100 \times L \times M} \times \left(y_{O_2}^{e} - y_{O_2}\right), \tag{5}$$

$$R_{CO_2} = \frac{P_{CO_2} \times A}{100 \times L \times M} \times \left(y_{CO_2} - y_{CO_2}^{e}\right). \tag{6}$$

Limitations exist for all of these methods (Beaudry, 1993; Cameron, Talasila, & Joles, 1995; Emond, 1992; Emond, Chau, & Brecht, 1993; Lee et al., 1996). In the static system, it is difficult to accurately estimate the gas volume (or free volume). Also, the O_2 depletion and CO_2 production that take place during measurement may affect the respiration rate. In order to determine the period of time between sampling, two aspects have to be considered. On the one hand, the difference of concentrations has to be sufficient to guarantee a noticeable modification of the atmosphere; on the other hand, the modification of concentrations has to be minimal in order to avoid affecting the respiration rate. Talasila (1992) proposed a method to determine the period of time based on the accuracy of the gas measuring equipment. In order to model the influence of gas concentrations on respiration rate, the gas concentrations normally associated with the respiration rate measured are the initial values or the average values between the initial and final measurements. An alternative method employed to avoid this problem is to use automated systems for respiration rate measurement that include measuring instruments such as gas chromatographs or O_2 probes (Cameron et al., 1989). Another important limitation of the closed system is that it does not allow respiration rates to be measured for any combination of gases.

Estimation of gas flow rate is often difficult in the flow through system. In addition, flow rates have to be carefully chosen in order to accurately measure the difference in gas concentrations between the inlet and the outlet. Thus, an estimation of the expected respiration rate needs to be known beforehand. The flow through system has the great limitation of not being sufficiently accurate to determine low respiration rates. Normally, in respiration rate experiments with low respiring produce, at low temperatures, and/or at low O_2 levels, respiration rates cannot be determined with this method.

The permeable system is the least accurate method because the determination of more variables is involved: these include the package dimensions (free volume, surface area, and thickness of the gas exchange material) as well as its permeability characteristics. Determination

Table 1
Main characteristics of the three methods of respiration rate measurement

Characteristics	System		
	Closed	Flow through	Permeable
Non-destructive	√	√	√
Time and labour consuming	√	√	√
Complexity of experimental set-up	Simple	Complex	Complex
Ability to test different combinations of gases	√	√	×
Concentration is kept approximately constant during the experiment	×	√ [a]	√ [a]
Suitable for low respiring products	√	×	√
Suitable for high respiring products	×	√	√
Accuracy is very sensitive to determination of	Free volume	Flow-rate	Permeability package dimensions, steady-state concentrations

[a] If only the steady-state conditions are used in the calculations.

of the free volume in a flexible package may be very difficult. The permeable system is not so flexible as the flow through system with regard to utilisation of any combination of gases desired. Gas concentrations in the permeable system depend on package permeability characteristics, package dimensions and product mass. Time to achieve equilibrium may be seen as a limitation of this method. For example, Beaudry et al. (1992) used the permeable system to measure blueberry respiration, and found that it took from 2 days at 25 °C to 14 days at 0 °C to achieve equilibrium. Lakakul et al. (1999) reported periods to achieve equilibrium for 3–12 days in LDPE packages with apple slices at 15 and 0 °C, respectively. Definition of the steady-state concentration values is another difficulty of the permeable method.

All of these experimental methods for measuring respiration are time and labour intensive. The advantages and limitations of the different methods are summarised in Table 1. None of methods is clearly preferable over the others. When choosing the respiration rate determination method for a specific study, the benefits and limitations of each method should be taken into consideration.

To overcome the limitations of the closed and permeable system methods, modifications have been introduced. Variations on the closed system are:

(i) flushing with a known gas mixture and immediately closing the container (Jacxsens et al., 1999; Jurin & Karel, 1963; Makino, Iwasaki, & Hirata, 1996; Yang & Chinnan, 1988); and

(ii) flushing with a known gas mixture during a certain period of time in order to equilibrate with that atmosphere (Andrich, Fiorentini, Tuci, Zinnai, & Sommovigo, 1991; Emond et al., 1993; Lebermann, Nelson, & Steinberg, 1968; Peppelenbos & Leven, 1996; Peppelenbos, van't Leven, van Zwol, & Tijskens, 1993; Talasila, 1992).

After closing the container, one measurement of respiration rate may be determined (Andrich et al., 1991; Emond et al., 1993; Lebermann et al., 1968; Makino et al., 1996; Peppelenbos & Leven, 1996; Peppelenbos et al., 1993; Talasila, 1992) or measurements of O_2 depletion and CO_2 accumulation over time may be performed (Cameron et al., 1989; Fishman et al., 1996; Gong & Corey, 1994; Haggar et al., 1992; Henig & Gilbert, 1975; Jurin & Karel, 1963; Yang & Chinnan, 1988). This procedure has the limitation of only providing sets of concentrations, from high O_2/low CO_2 to low O_2/high CO_2 concentrations. Haggar et al. (1992) and Gong and Corey (1994) determined the respiration rate expression by derivation of the best-fitted equation of O_2 and CO_2 concentrations as a function of time. Emond et al. (1993) used only combinations of O_2 and CO_2 that would occur in a perforation-mediated MAP. But, in both cases, the individual effects of O_2 and CO_2 could not be analysed.

Modifications of the permeable system include:

(i) use of gas concentrations outside the package different from ambient air and

(ii) use of the non-steady-state part of the process.

Beaudry (1993) used the package in chambers flushed with a known gas mixture in order to obtain more combinations of steady-state O_2 and CO_2 in the package. Lee et al. (1996) measured O_2 and CO_2 evolution and empirically fitted a curve to the data.

Invariably in these methods, the respiration rate determination takes into account not only the cellular respiration process but also the gas exchange process (the skin resistance to gas diffusion, the solubility of the gases, and the diffusion of gases inside the product) because it is the atmosphere surrounding the product that is measured. In a more detailed description, O_2 and CO_2 movement entails the following steps:

(i) O_2 diffusion in the gas phase through the dermal system (stomata, lenticels or breaks in the dermal system);

(ii) exchange of O_2 through the intercellular atmosphere and the cellular solution;

(iii) solubilisation and diffusion of O_2 in solution within the cell to the mitochondrial membrane;

(iv) O_2 consumption in the mitochondrial membrane;

(v) CO_2 production in the mitochondrial matrix;

(vi) diffusion of CO_2 in the mitochondrial matrix to the cellular solution;

(vii) exchange of CO_2 through the cellular solution and the intercellular atmosphere;

(viii) diffusion of CO_2 in the gas phase through the dermal system openings to the surrounding atmosphere (Andrich et al., 1991; Kader, 1987).

The respiration of microorganisms as well as any other plant physiological processes that occur involving O_2 and CO_2 (synthesis of plant hormones, oxidation reactions, and photosynthesis) are also included in the determination. Because these processes are in series, the slowest one determines the overall rate. The resistance to gas diffusion varies among crops and may influence the internal O_2 and CO_2 levels (Banks, Hewett, Rajapakse, Austin, & Stewart, 1989; Dadzie, Banks, Cleland, & Hewett, 1996). Andrich, Zinnai, Balzini, Silvestri, and Fiorentini (1998) considered that, in the case of the apple, the resistance to gas diffusion was located in the skin. In leafy vegetables or in products with large surface area to volume ratios, gas diffusion may be considered to contribute negligible resistance. Furthermore, Cameron et al. (1989) verified that, even in tomatoes, skin resistance is not the limiting step in the process. Only a few workers have related respiration rate and internal O_2 concentrations indirectly via mathematical models (Andrich et al., 1991; Andrich et al., 1998). Dadzie et al. (1996) modelled respiration rate of apples in response to internal O_2 pressure and developed a relationship between internal and external O_2 pressure. Modelling of all these processes individually is very difficult. For MAP applications, the global process may be described in a single equation that simplifies the mathematical modelling of the system.

4. Factors affecting respiration rate and respiratory quotient

The internal factors affecting respiration are type and maturity stage of the commodity. Vegetables include a great diversity of plant organs (roots, tubers, seeds, bulbs, fruits, sprouts, stems and leaves) that have different metabolic activities and consequently different respiration rates. Even different varieties of the same product can exhibit different respiration rates (Fidler & North, 1967; Gran & Beaudry, 1992; Song et al., 1992). In general, non-climacteric commodities have higher respiration rates in the early stages of development that steadily decline during maturation (Lopez-Galvez, El-Bassuoni, Nie, & Cantwell, 1997). Respiration rates of climacteric commodities also are high early in development and decline until a rise occurs that coincides with ripening or senescence. Lopez-Galvez et al. (1997) reported higher respiration rates for slices of immature peppers than mature-green, turning, and red ripe fruit. Climacteric products do not follow this pattern. Climacteric products exhibit a peak of respiration and ethylene (C_2H_4) production associated with senescence or ripening. However, this does not imply that the respiratory response to MA or controlled atmospheres (CA) necessarily changes during the climacteric period. For example, Cameron et al. (1989) observed no influence of maturity or ripeness stage of tomatoes on O_2 uptake as a function of O_2 concentration.

Care is necessary when packing in MAP due to alterations of respiration rate over time that are not normally considered in MAP design. The storage time period after harvest may influence the respiration curve due to:

(i) the normal deterioration of the product with ageing,

(ii) ripening of climacteric products and

(iii) wound metabolism in fresh-cut products.

In the senescent stage of climacteric plant organ development there is a rise in respiration, presumably in order to obtain more energy for metabolic processes. In non-climacteric tissues and climacteric tissues in the post-climacteric stage, increased respiration after some period of time in storage may be caused by the onset of decay by microorganisms. For example, Woodward and Topping (1972) analysed the respiration rate of strawberries in long-term storage (30 days) at 3 °C in air and in CA. The pattern was the same for all experiments: an initial decrease and then an increase due to rotting. The same pattern of respiration was observed for strawberries by El-Kazzaz, Sommer, and Fortlage (1983). In contrast, Andrich et al. (1991) did not observe variations in respiration rate at 20.5 °C for apples previously stored at 3–4 °C for different periods ranging from 11 to 19 weeks. Products in MAP are usually in short-term storage (distribution and retailing), thus, the influence of storage time due to senescence may be considered negligible.

Normally, climacteric changes are considered important only in long term and not relevant to MAP (Fishman et al., 1996). MA conditions may control the timing of the climacteric rise as well as the magnitude of the peak. Young, Romani, and Biale (1962) observed a delay in the climacteric rise in avocados and bananas due to elevated CO_2 levels, but only a reduction of O_2 uptake at the climacteric peak in avocados. Fidler and North (1967) observed a delay in the onset of the climacteric rise in apples due to reduced O_2 levels. The respiration curve of cherimoyas in air at 10 °C exhibited

a climacteric rise 15 days after harvest, while in 15% or 10% O_2 the rise was delayed by 5 or 10 days, respectively, and at 5% O_2 the climacteric was not observed during the 40-day period of the experiment (Palma, Stanley, Aguilera, & Zoffoli, 1993).

Wounding plant cells and tissues causes the respiration rate to increase. Wounding induces elevated C_2H_4 production rates, that may stimulate respiration and consequently accelerate deterioration and senescence in vegetative tissues and promote ripening of climacteric fruit (Brecht, 1995). The wounding may be due to mechanical damage or cutting of the product. The respiration rate may gradually increase over time until a maximum value is reached and then start decreasing again to either the value before the wounding or to a higher value. For example, the respiratory rate of apple slices was about 2–3 times that of the whole fruit (Lakakul et al., 1999). Smyth et al. (1998) reported a rapid decrease of respiration rate over time for cut iceberg lettuce at 5 °C in CO_2-scrubbed air. In contrast to senescent or climacteric products, where changes may occur after MAP, in fresh-cut or damaged products these changes in respiration rate may occur just after or even before packaging.

Temperature has been identified as the most important external factor influencing respiration. Biological reactions generally increase two or three-fold for every 10 °C rise in temperature within the range of temperatures normally encountered in the distribution and marketing chain (Burzo, 1980; Zagory & Kader, 1988). At higher temperatures, enzymatic denaturation may occur and reduce respiration rates. If temperatures are too low, physiological injury may occur, which may lead to an increase in respiration rate (Fidler & North, 1967).

Other external factors are O_2 and CO_2 concentrations. Respiration is widely assumed to be slowed down by decreasing available O_2 as a consequence of reduction of overall metabolic activity (Isenberg, 1979; Kader, 1987; Smock, 1979; Solomos & Kanellis, 1989). The reduction of respiration rate in response to low O_2 levels is not the result of the cytochrome oxidase activity, which has great affinity to O_2, but due to a decrease in the activity of other oxidases, such as polyphenoloxidase, ascorbic acid oxidase and glycolic acid oxidase, whose affinity is much lower (Kader, 1986). The influence of CO_2 is not so clear in the process, and depends on type and developmental stage of the commodity, CO_2 concentrations and time of exposure. Tables 2, 3 and 4 provide examples from the literature where commodities were exposed to CO_2-enriched atmospheres which had no effect, reduced or stimulated respiration rate, respectively. Variable patterns of respiratory response to elevated CO_2 were also observed. Carrots exhibited a decrease in respiration rate at 10% CO_2 and an increase at 30% CO_2 (Pal & Buescher, 1993). Different durations of product exposure to the specified atmosphere can cause different results regarding the influence of CO_2 on the commodity (Peppelenbos & Leven, 1996). The idea of respiratory inhibition by CO_2 was first supported by simple explanations, i.e., that CO_2 was a product of the respiration process and, caused simple feedback inhibition (Herner, 1987; Wolfe, 1980). Another hypothesis considered that CO_2 had a strong controlling effect on mitochondrial activity, including citrate and succinate oxidation. Kader (1989) considered that elevated CO_2 might affect the Krebs cycle intermediates and enzymes. Others considered that CO_2 might inhibit C_2H_4 production rather than having a direct effect on the respiration process. This would explain, for example, the reported influence of CO_2 only on products producing C_2H_4 (Kubo et al., 1989). The respiration rate increase may be explained in terms of CO_2 injury of tissues with a concomitant increase in C_2H_4 production. Some varieties of lettuce are very sensitive to CO_2, and brown stain (browning of the epidermal tissue near the midrib) is a common CO_2 injury when the product is exposed to levels above its tolerance limit (Kader et al., 1989; Ke & Saltveit, 1989;

Table 2
Products in which CO_2 concentration had no influence on respiration rate[a]

Product	CA/MA conditions	Exposure period	References
Preclimacteric avocados and bananas	10% or 21% O_2 plus 0–10% CO_2 (CA)	21–50 days	Young et al. (1962)
'Cox's orange pippin', 'Tydeman's late orange', 'Jonathan', 'Sturmer', 'Newton' and 'Blenheim' apples	1.5–10% O_2 plus 0–10% CO_2 (CA)	30–200 days	Fidler and North (1967)
Preclimacteric tomatoes and bananas; lemons, potatoes, sweet potatoes, and cabbage	20% O_2 plus 60% CO_2 (CA)	24 h	Kubo, Inaba, and Nakamura (1989)
Guavas, onion bulbs and oranges	20% O_2 plus 0–30% CO_2 (CA)	24 h	Pal and Buescher (1993)
Mushrooms	0.81–20.6% O_2 plus 0.18–9.7% CO_2 (CA)	1–3 days	Peppelenbos et al. (1993)
'Heritage' red raspberry	1–12% O_2 plus 1–14% CO_2 (MA)	3–12 days	Joles et al. (1994)
'Golden Delicious' and 'Elstar' apples	0–21% O_2 plus 0.5–5% CO_2 (CA)	4 days	Peppelenbos and Leven (1996)
Cut iceberg lettuce	0–6 kPa O_2 plus ND % CO_2 (MA)	6 days	Smyth et al. (1998)

[a] ND – not described.

Table 3
Products with reduced respiration rates due to high CO_2[a]

Product	CA/MA conditions	Exposure period	References
Apples	16–17% O_2 plus 5–14% CO_2 (MA in closed system)	ND	Jurin and Karel (1963)
Broccoli	2–21% O_2 plus 0–20% CO_2 (CA)	2–11 days	Lebermann et al. (1968)
Tomatoes	4–21% O_2 plus 0–21% CO_2 (MA in closed system)	ND	Henig and Gilbert (1975)
Tomatoes	5–20% O_2 plus 0–20% CO_2 (CA and MA)	Up to 40 days	Yang and Chinnan (1988)
Pears	1.5–21% O_2 plus 0–20% CO_2 (CA)	4 days	Kader (1989)
Apples, lemons, ripening tomatoes, bananas and broccoli	20% O_2 plus 60% CO_2 (CA)	24 h	Kubo et al. (1989)
Strawberries	1–20% O_2 plus 0–20% CO_2 (CA)	24 h	Talasila et al. (1992)
Ripening bananas, tomatoes and pickling cucumbers	20% O_2 plus 0–30% CO_2 (CA)	24 h	Pal and Buescher (1993)
Cut broccoli	0.9–17.8% CO_2 plus 1.7–21% O_2 (CA)	1–48 h	Lee et al. (1991)
Blueberries	2–16 kPa O_2 plus 5–60 kPa CO_2	4 days	Beaudry (1993)
Asparagus	0–20% O_2 plus 0–20% CO_2 (CA)	4 days	Peppelenbos and Leven (1996)
Broccoli	1–21% O_2 plus 0–10% CO_2 (CA)	4 days	Peppelenbos and Leven (1996)
Mungbean sprouts	0–21% O_2 plus 0–5% CO_2 (CA)	4 days	Peppelenbos and Leven (1996)

[a] ND – not described.

Table 4
Products in which respiration rate was increased due to high CO_2

Product	CA conditions	Exposure period	References
Lemons	10% or 21% O_2 plus 0%, 5% or 10% CO_2 (CA)	15–21 days	Young et al. (1962)
Lettuce, eggplants and cucumbers	60% CO_2 plus 20% O_2 (CA)	24 h	Kubo et al. (1989)
Potatoes	20% O_2 plus 0%, 10%, 20% or 30% CO_2 (CA)	24 h	Pal and Buescher (1993)

Varoquaux, Mazollier, & Albagnac, 1996). The respiration rates of most root and bulb-type vegetables are also stimulated by high CO_2 levels (Herner, 1987). Another possible explanation for CO_2-induced respiratory increases is the increase of sugars in the cells exposed to high CO_2 concentrations (Meyer et al., 1973).

It is possible to evaluate the factors affecting the RQ in works in which determinations of O_2 consumption and CO_2 production rates were made. Jurin and Karel (1963) did not observe an influence of CO_2 concentration on RQ for apples but Beaudry (1993) observed an RQ increase in high CO_2 concentrations for blueberries. The RQ depended on both O_2 concentration and temperature (Beaudry et al., 1992; Joles et al., 1994; Lakakul et al., 1999; Maneerat et al., 1997; Talasila et al., 1994). The RQ of blueberry fruit increased as O_2 concentration approached zero and the RQ breakpoint (the lowest O_2 concentration that does not induce anaerobic respiration) increased with temperature. Beaudry et al. (1992) explained this latter observation as being due to the fruit skin's permeability not rising as rapidly as O_2 consumption for a given temperature change. Thus, the risk of anaerobiosis increases with temperature. The RQ for aerobic O_2 concentrations was constant for blueberry (Beaudry et al., 1992) and for cut broccoli (Talasila et al., 1994) but increased gradually for raspberry (Joles et al., 1994) as O_2 levels declined.

5. Mathematical modelling

There are a number of limitations to the development of predictive models. Potentially large experimental errors and time consuming experiments for the determination of respiration rates for MAP design, as well as the complex nature of the process are limitations to the development of predictive models. Thus, a constant respiration rate is sometimes considered in MAP modelling reported in the literature (Emond, Castaigne, Toupin, & Desilets, 1991; Fonseca, Oliveira, Brecht, & Chau, 1999). However, this approach can only be accepted as a simplified model, as, in fact, MAP relies on the ability to control the respiration rate by changing the atmospheric composition. The development of more accurate analytical techniques and equipment as well as the sophistication of computing tools for data fitting and numerical integration, have led in the last few decades to various studies on determination of predictive respiratory models. But attention must be focused on the experimental set-up, the range of variables, and the number of points studied in that range, in order to develop accurate predictive models.

Recognising that modelling the respiratory process with all the factors involved in the enzymatic reactions included would be very difficult or even impossible, as already mentioned, the usual strategy has been to

Table 5
Summary of the studies on respiration rate as a function of gas concentration and temperature

References	R_{O_2} determination	R_{CO_2} determination	CO_2 influence	Temperature influence
Jurin and Karel (1963)	Yes	Yes	Yes	NA
Henig and Gilbert (1975)	Yes	Yes	Yes	NA
Yang and Chinnan (1988)	Yes	Yes	Yes	NA
Cameron et al. (1989)	Yes	No	NA	NA
Andrich et al. (1991)	Yes	No	NA	NA
Lee et al. (1991)	Yes	Yes	Yes	NA
Beaudry et al. (1992)	Yes	Yes	NA	Yes
Haggar et al. (1992)	Yes	Yes	Yes	Yes
Song et al. (1992)	Yes	Yes	Yes	Yes
Talasila et al. (1992)	Yes	No	Yes	Yes
Talasila (1992)	Yes	Yes	No*	Yes
Beaudry (1993)	Yes	Yes	Yes	NA
Emond et al. (1993)	Yes	Yes	NA	Yes
Peppelenbos et al. (1993)	Yes	Yes	No*	Yes
Gong and Corey (1994)	Yes	No	NA	NA
Joles et al. (1994)	Yes	Yes	No*	Yes
Talasila et al. (1994)	Yes	Yes	NA	NA
Dadzie et al. (1996)	Yes	No	NA	NA
Fishman et al. (1996)	Yes	No	NA	NA
Makino et al. (1996)	Yes	No	NA	NA
Peppelenbos and Leven (1996)	Yes	No	Yes	NA
Ratti et al. (1996)	No	Yes	NA	Yes
Maneerat et al. (1997)	Yes	Yes	Yes	Yes
Andrich et al. (1998)	Yes	Yes	NA	Yes
Smyth et al. (1998)	Yes	Yes	No*	Yes
Lakakul et al. (1999)	Yes	Yes	NA	Yes
McLaughlin and O'Beirne (1999)	Yes	No	Yes	Yes

* Analysed and concluded no CO_2 influence; NA – not analysed.

develop empirical models for each type of commodity as a function of the controllable variables, i.e., temperature and gas concentrations.

In general, studies on respiration rates have been oriented toward studying the influence of temperature or for analysing the effects of gas concentrations, but rarely were both factors considered simultaneously. Table 5 presents published work that analysed respiration rate as a function of O_2 levels. The table also indicates the determinations that were made and whether CO_2 and temperature influence were also analysed. Temperature may vary significantly along the distribution chain. A package that is designed for a specific storage temperature may not be properly designed for other temperatures due to the different effects of temperature on permeability and respiration rate. Thus, the importance of knowing the influence of temperature on the respiration rate is clear. Another limitation on respiration rate models is that many of the data available are either O_2 consumption or CO_2 production rates only (Table 5), thus assuming the RQ to be unity. If the RQ were actually greater than unity, the model would underestimate CO_2 production and if the RQ were smaller it would overestimate it.

Table 6 summarises the information on respiration rate models presented in the literature. Quality of fit based only on graphical visualisation is also included. No other parameter was used to analyse the fit adequacy because of lack of standardisation among papers. Even experimental data plots and fitted curves were missing in many works. Because of these limitations a rating scale with only three indices was chosen (not good, acceptable and good). The non-uniformity of units in respiration rate models led to increased difficulty in their comparison. Table 7 presents the factors for conversion of the different units used in the published works to the International System (SI) of units proposed by Banks, Cleland, Cameron, Beaudry, and Kader (1995).

Cameron et al. (1989) developed different models of O_2 consumption rate as a function of O_2 partial pressure, according to the developmental stage of tomatoes, but found no differences between breaker, pink and red tomatoes (Table 6). Song et al. (1992) reported differences in respiration rates of three different cultivars of blueberry and developed independent models for each of them (Table 6).

The influence of time on respiration rate was modelled by Yang and Chinnan (1988) for tomatoes with a polynomial equation, describing also the influence of initial O_2 and CO_2 levels (Table 6). But time and O_2 and CO_2 levels were not independent variables, because gas samples were taken periodically in a closed system. Smyth et al. (1998) reported a mathematical model describing CO_2 production rate as a function of time for

Table 6
Respiration rate models presented in the literature

Reference	Produce	Experimental method (equipment)	O_2 concentration	CO_2 concentration	T (°C)	Model	Model equations	Fit quality
Henig and Gilbert (1975)	Tomato	Closed system (gas chromatograph)	4–21%	0–21%	23	Linear	No CO_2: R_{O_2} = linear increase; slope = 2.00 ml kg^{-1} h^{-1} %$^{-1}$; $4\% < y_{O_2} < 11.53\%$ R_{O_2} = 23.135 ml kg^{-1} h^{-1}; $11.53\% < y_{O_2} < 21\%$ Presence of CO_2: R_{O_2} = linear increase; slope = 1.815 ml kg^{-1} h^{-1} %$^{-1}$; $4\% < y_{O_2} < 12.08\%$ R_{O_2} = 21.94 ml kg^{-1} h^{-1}; $12.08\% < y_{O_2} < 21\%$ R_{CO_2} = 18.52 ml kg^{-1} h^{-1}; $0\% < y_{CO_2} < 9\%$ R_{CO_2} = 12.19 ml kg^{-1} h^{-1}; $9\% < y_{CO_2} < 21\%$	NA (no data)
Yang and Chinnan (1988)	Tomato	Closed system (gas chromatograph)	5–20%	0–20%	21	Polynomial	R_{O_2} (ml kg^{-1} h^{-1}) $= 5.2 + 0.448y_{O_2}$ (%) $- 0.0908y_{CO_2}$ (%) $-0.172t$ (days) $+ 0.00492t^2 - 0.0157y_{O_2} \times t$ R_{CO_2} (ml kg^{-1} h^{-1}) $= 5.96 + 0.767y_{O_2}$ (%) $-0.165y_{CO_2}$ (%) $- 0.29t$ (days) $-78.9 \times 10^{-4}y_{O_2}^2 + 0.0068t^2 - 39.8 \times 10^{-4}y_{O_2} \times y_{CO_2}$ $-1.89 \times 10^{-2}y_{O_2} + 0.37 \times 10^{-2}y_{CO_2} \times t$	NA (no fit)
Cameron et al. (1989)	Tomato	Closed system (O_2 probe)	0–21%	0%	25	Exponential	Breaker: R_{O_2} (ml kg^{-1} h^{-1}) $= 15.7 \times [1 - \exp(-15.6 \times p_{O_2}\ (\text{atm}))]^{0.959}$ Pink: R_{O_2} (ml kg^{-1} h^{-1})$= 17.5 \times [1 - \exp(-10.9 \times p_{O_2}\ (\text{atm}))]^{\{0.963\}}$ Red: R_{O_2} (ml kg^{-1} h^{-1}) $= 14.4 \times [1 - \exp(-13.8 \times p_{O_2}\ (\text{atm}))]^{0.748}$	NA (no data)
Andrich et al. (1991)	Apple	Closed system (gas chromatograph)	1.9–28.4 kPa	0 kPa	20.5	MM	R_{O_2} (mol kg^{-1} h^{-1}) $= 0.75 \times 10^{-3}\ C_{O_2}^{cs}$ (mol kg^{-1})$/(2.1 \times 10^{-5} + C_{O_2}^{cs})$	Good
Lee et al. (1991)	Cut broccoli	Data of Lieberman and Hardenburg (1954)			23.9	MM	No equation presented	Good
	Apple	Data of Jurin and Karel (1963)			20			Good
	Bananas	Data of Karel and Go (1964)			19			Good
	Apple	Data of Fidler and North (1967)			3.3			Good
	Tomato	Data of Henig and Gilbert (1975)			23			Acceptable
	Tomato	Data of Cameron et al. (1989)			25			Good
	Asparagus	Data of Thornton (1933)			25	MMU	No equation presented	Good
	Apple	Data of Jurin and Karel (1963)			20			Acceptable
	Broccoli	Data of Lebermann et al. (1968)			7.2		R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 10.8$ ml kg^{-1} h^{-1}, $\phi = 3.55\%$, $\gamma_u = 27.98\%$	Acceptable
	Cut broccoli	Flow system (gas chromatograph)	1.7–19.4%	0%	24	MM	No equation presented	Good
			2.6–16.5%	0.9–12.1%	24	MMU	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 219.4$ ml kg^{-1} h^{-1}, $\phi = 1.4\%$, $\gamma_u = 114.7\%$ R_{CO_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 191.1$ ml kg^{-1} h^{-1}, $\phi = 1\%$, $\gamma_u = 42.3\%$	NA

Table 6 (*continued*)

Reference	Produce	Experimental method (equipment)	O_2 concentration	CO_2 concentration	T (°C)	Model	Model equations	Fit quality
Beaudry et al. (1992)	Blueberry	SS permeable system (electrochemical O_2 detection cell; infrared CO_2 analyser)	1–18 kPa	–	0	Exponencial	R_{O_2} (mmol kg^{-1} h^{-1}) $= 0.1024 \times [1 - \exp(-0.5427 \times p_{O_2}\ (\text{kPa}))]^{0.8506}$, $RQ = 1.3,\ p_{O_2} > 1.8$ kPa	Good
					5		R_{O_2} (mmol kg^{-1} h^{-1}) $= 0.1469 \times [1 - \exp(-0.8461 \times p_{O_2}\ (\text{kPa}))]^{1.401}$, $RQ = 1.3,\ p_{O_2} > 1.8$ kPa	Wide dispersion of data
					10		R_{O_2} (mmol kg^{-1} h^{-1}) $= 0.2765 \times [1 - \exp(-0.3829 \times p_{O_2}\ (\text{kPa}))]^{0.8795}$, $RQ = 1.3,\ p_{O_2} > 2.0$ kPa	Good
					15		R_{O_2} (mmol kg^{-1} h^{-1}) $= 0.514 \times [1 - \exp(-0.2067 \times p_{O_2}\ (\text{kPa}))]^{0.9205}$, $RQ = 1.3,\ p_{O_2} > 2.5$ kPa	Good
					20		R_{O_2} (mmol kg^{-1} h^{-1}) $= 1.871 \times [1 - \exp(-0.01235 \times p_{O_2}\ (\text{kPa}))]^{0.4968}$, $RQ = 1.3,\ p_{O_2} > 3.0$ kPa	Good
					25		R_{O_2} (mmol kg^{-1} h^{-1}) $= 4.561 \times [1 - \exp(-0.009111 \times p_{O_2}\ (\text{kPa}))]^{0.6428}$, $RQ = 1.3,\ p_{O_2} > 4.0$ kPa	Good
Haggar et al. (1992)	Cut broccoli	Closed system (gas chromatograph)	1–21%	0–15%	0	MMU	R_{O_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 59.22$ mg kg^{-1} h^{-1}, $\phi = 2.18\%$, $\gamma_u = 5.07\%$ R_{CO_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 46.32$ mg kg^{-1} h^{-1}, $\phi = 1.51\%$, $\gamma_u = 7.23\%$	NA
					7	MMU	R_{O_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 210.3$ mg kg^{-1} h^{-1}, $\phi = 0.57\%$, $\gamma_u = 2.26\%$ R_{CO_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 235.2$ mg kg^{-1} h^{-1}, $\phi = 1.69\%$, $\gamma_u = 1.93\%$	NA
					13	MMU	R_{O_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 380.54$ mg kg^{-1} h^{-1}, $\phi = 1.4\%$, $\gamma_u = 2.2\%$ R_{CO_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 474.79$ mg kg^{-1} h^{-1}, $\phi = 1.52\%$, $\gamma_u = 1.61\%$	NA
					24	MMU	R_{O_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 676.52$ mg kg^{-1} h^{-1}, $\phi = 3.19\%$, $\gamma_u = 3.96\%$ R_{CO_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 772.3$ mg kg^{-1} h^{-1}, $\phi = 0.1\%$, $\gamma_u = 2.92\%$	NA
Song et al. (1992)	Coville blueberry	Closed system (gas chromatograph)	15–21%	0–20%	5	MMU	R_{O_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 16.602$ mg kg^{-1} h^{-1}, $\phi = 1.488\%$, $\gamma_u = 7.417\%$ R_{CO_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 12.539$ mg kg^{-1} h^{-1}, $\phi = 0.429\%$, $\gamma_u = 15.486\%$	NA
					15	MMU	R_{O_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 68.006$ mg kg^{-1} h^{-1}, $\phi = 0.444\%$, $\gamma_u = 2.914\%$ R_{CO_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 51.046$ mg kg^{-1} h^{-1}, $\phi = 0.177\%$, $\gamma_u = 4.896\%$	NA
					25	MMU	R_{O_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%) $\alpha = 127.356$ mg kg^{-1} h^{-1}, $\phi = 5.200\%$, $\gamma_u = 6.684\%$ R_{CO_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 99.032$ mg kg^{-1} h^{-1}, $\phi = 0.520\%$, $\gamma_u = 13.502\%$	NA

	Blueray blueberry	Closed system (gas chromatograph)	1.5–21%	0–20%	5	MMU	R_{O_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 11.802$ mg kg^{-1} h^{-1}, $\phi = 1.593\%$, $\gamma_u = 11.725\%$ R_{CO_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 8.956$ mg kg^{-1} h^{-1}, $\phi = 0.705\%$, $\gamma_u = 19.648\%$	NA
					15	MMU	R_{O_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 34.670$ mg kg^{-1} h^{-1}, $\phi = 0.130\%$, $\gamma_u = 6.783\%$ R_{CO_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 30.203$ mg kg^{-1} h^{-1}, $\phi = -0.104\%$, $\gamma_u = 9.441\%$	NA
					25	MMU	R_{O_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 76.247$ mg kg^{-1} h^{-1}, $\phi = 0.100\%$, $\gamma_u = 11.044\%$ R_{CO_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 76.049$ mg kg^{-1} h^{-1}, $\phi = 0.125\%$, $\gamma_u = 19.057\%$	NA
	Jersey blueberry				5	MMU	R_{O_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 9.863$ mg kg^{-1} h^{-1}, $\phi = 2.106\%$, $\gamma_u = 7.606\%$ R_{CO_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 7.347$ mg kg^{-1} h^{-1}, $\phi = 0.797\%$, $\gamma_u = 12.693\%$	NA
					15	MMU	R_{O_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 35.868$ mg kg^{-1} h^{-1}, $\phi = 0.678\%$, $\gamma_u = 3.296\%$ R_{CO_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 29.942$ mg kg^{-1} h^{-1}, $\phi = 0.784\%$, $\gamma_u = 4.449\%$	NA
					25	MMU	R_{O_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%) $\alpha = 51.285$ mg kg^{-1} h^{-1}, $\phi = 0.411\%$, $\gamma_u = 9.361\%$ R_{CO_2} (mg kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 48.234$ mg kg^{-1} h^{-1}, $\phi = 0.101\%$, $\gamma_u = 16.701\%$	NA
Talasila et al. (1992)	Strawberry	Flow system (gas chromatograph)	1–20%	0–30%	5,10,20	Exponential and polynomial	R_{O_2} (ml kg^{-1} h^{-1}) $= \exp(0.081 \times T\ (^\circ\mathrm{C})) \times [2.4546 + 1.6994 y_{O_2}\ (\%) - 0.0305 y_{O_2}^2 + 0.0018 y_{CO_2}^2 - 0.013 y_{O_2} \times y_{CO_2}\ (\%)]$	Not good
Talasila (1992)	Strawberry	Closed system (gas chromatograph)	2–18%	3–22%	1, 4 8, 19	Exponential and polynomial	R_{O_2} (mol kg^{-1} s^{-1}) $= 3.384 \times 10^{-10} \times [1 - \exp(-0.6004 y_{O_2}\ (\%))] \times (0.132 + 2.716 \times 10^{-2} T + 9.4211 \times 10^{-4} T^2)$ R_{CO_2} (mol kg^{-1} s^{-1}) $= 3.018 \times 10^{-10} \times [1 - \exp(-0.695 y_{O_2}\ (\%))] \times (0.079 + 1.949 \times 10^{-2} T + 1.483 \times 10^{-3} T^2)$	Wide dispersion of data
Beaudry (1993)	Blueberry	SS permeable system (paramagnetic O_2 detection cell; infrared CO_2 analyser)	2–16 kPa	5–60 kPa	15	Multi-exponential	$RQ = 6.722 \times \exp(-0.568 p_{O_2}\ (\mathrm{kPa})) \times \exp[(-0.01453 + (0.007551 p_{O_2})) \times p_{CO_2}\ (\mathrm{kPa})] + 1.33$	Good
Emond et al. (1993)	Blueberry	Closed system (gas chromatograph)	6–21%	0–15%	4.5	Exponential	R_{O_2} (cm^3 kg^{-1} s^{-1}) $= 1.8648 \times \exp(0.024459 y_{O_2}\ (\%))$ R_{CO_2} (cm^3 kg^{-1} s^{-1}) $= 1.8728 \times \exp(0.025308 y_{O_2}\ (\%))$	Wide dispersion of data

Table 6 (*continued*)

Reference	Produce	Experimental method (equipment)	O_2 concentration	CO_2 concentration	T (°C)	Model	Model equations	Fit quality
			4–21%	0–17%	20	Experimental	R_{O_2} (cm^3 kg^{-1} s^{-1}) $= 10.0569 \times \exp(0.040356 y_{O_2}(\%))$ R_{CO_2} (cm^3 kg^{-1} s^{-1}) $= 8.095 \times \exp(0.040769 y_{O_2}(\%))$	Wide dispersion of data
Peppelenbos et al. (1993)	Mushrooms	Closed system (gas chromatograph)	0.81–20.6%	0.18–9.7%	8	MM	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%); $\alpha = 43.8$ ml kg^{-1} h^{-1}, $\phi = 3.37\%$	Good
							R_{CO_2} (ml kg^{-1} h^{-1}) $= R_{O_2} \times 0.82 + 43.8/(1.79 + y_{O_2})$ R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%); $\alpha = 121.7$ ml kg^{-1} h^{-1}, $\phi = 0.6\%$	
					18	MM	R_{CO_2} (ml kg^{-1} h^{-1}) $= R_{O_2} \times 0.86 + 121.7/(5.45 + y_{O_2})$	
Cameron, Beaudry, Banks, and Yelanich (1994)	Blueberry	Data of Beaudry et al. (1992)				MM and exponential	R_{O_2} (mmol kg^{-1} h^{-1}), T (°C), p_{O_2} (kPa); $\alpha = 0.101 \times \exp(0.117T)$, $\phi = 0.810 \times \exp(0.099T)$	Good
Gong and Corey (1994)	Tomato	Closed system (gas chromatograph)	1– 21%	–	20	Polynomial	R_{O_2} (ml kg^{-1} h^{-1}) $= 24.5 \times (0.75^2 - 28.28 \times 10^{-3} \times (20.64 - y_{O_2}(\%)))^{0.5}$	NA
Joles et al. (1994)	Raspberry	SS permeable system (electrochemical O_2 detection cell; infrared CO_2 analyser)	1–10 kPa	1–10 kPa	0	MM and exponential	R_{O_2} (mmol kg^{-1} h^{-1}) $= [0.872 \times 1.92^{(T\ (°C)/10)} \times p_{O_2}\ (\text{kPa})]/(5.59 + p_{O_2})$ $RQ = 1 + 1.43 \times \exp[0.053T(°C)]/p_{O_2}$ (kPa)	Acceptable
			1–12 kPa	1–13 kPa	10			
			1–12 kPa	1–14 kPa	20			
Talasila et al. (1994)	Cut broccoli	SS permeable system (electrochemical O_2 detection cell; infrared CO_2 analyser)	0–16 kPa	–	0	MM	R_{O_2} (nmol kg^{-1} s^{-1}), $p^{i}_{O_2}$ (kPa); $\alpha = 147 \pm 3$nmol kg^{-1} s^{-1}, $\phi = 0.26 \pm 0.025$ kPa	Good
Dadzie et al. (1996)	C.O.P. apple	Flow system (O_2 electrode; infrared CO_2 analyser)	0–20 kPa	–	20	MM	R_{O_2} (nmol kg^{-1} s^{-1}), p_{O_2} (kPa); $\alpha = 306 \pm 29.6$ nmol kg^{-1} s^{-1}, $\phi = 2.2 \pm 0.82$ kPa	Good
	G.S. apple						R_{O_2} (nmol kg^{-1} s^{-1}), p_{O_2} (kPa); $\alpha = 210 \pm 28.1$ nmol kg^{-1} s^{-1}, $\phi = 4.2 \pm 1.68$ kPa	Good
Fishman et al. (1996)	Mango fruit	Closed system (gas chromatograph)	2.5–20%	–	ambient	Linear	R_{O_2} (m^3 kg^{-1} h^{-1}) $= 0.918 \times 10^{-4} y_{O_2}$ (v/v)	NA
Lee et al. (1996)	Tomato	Data of Henig and Gilbert (1975); US permeable system				MMU	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 53.1$ ml kg^{-1} h^{-1}, $\phi = 27.9\%$, $\gamma_u = -14.7\%$ R_{CO_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 36.1$ ml kg^{-1} h^{-1}, $\phi = 1.5\%$, $\gamma_u = 16\%$	NA
	Cut broccoli	Data of Lee et al. (1991); US permeable system				MMU	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%) $\alpha = 276.1$ ml kg^{-1} h^{-1}, $\phi = 2.5\% = 26.8$ R_{CO_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 206.7$ ml kg^{-1} h^{-1}, $\phi = 1.6\% = 21.2$	NA
	Blueberry	Data of Beaudry et al. (1992); SS permeable system			0	MMU	R_{O_2} (mmol kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 0.121$ mmol kg^{-1} h^{-1}, $\phi = 0.39\%$, $\gamma_u = 17.042\%$ R_{CO_2} (mmol kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%) $\alpha = 0.131$ mmol kg^{-1} h^{-1}, $\phi = 0.029\%$, $\gamma_u = 96.682\%$	NA

					5	MMU	R_{O_2} (mmol kg^{-1} h^{-1}), y_{O_2}(%), y_{CO_2} (%) $\alpha = 0.171$ mmol kg^{-1} h^{-1}, $\phi = 1.197\%$, $\gamma_u = 117.84\%$ R_{CO_2} (mmol kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 0.173$ mmol kg^{-1} h^{-1}, $\phi = 1.064\%$, $\gamma_u = -21.913\%$	NA
					10	MMU	R_{O_2} (mmol kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 0.32$ mmol kg^{-1} h^{-1}, $\phi = 3.662\%$, $\gamma_u = -11.593\%$ R_{CO_2} (mmol kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 0.462$ mmol kg^{-1} h^{-1}, $\phi = 2.191\%$, $\gamma_u = -174.799\%$	NA
					15	MMU	R_{O_2} (mmol kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 0.95$ mmol kg^{-1} h^{-1}, $\phi = 2.875\%$, $\gamma_u = 3.457\%$ R_{CO_2} (mmol kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 1.425$ mmol kg^{-1} h^{-1}, $\phi = 2.848\%$, $\gamma_u = 3.244\%$	NA
					20	MMU	R_{O_2} (mmol kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 1.521$ mmol kg^{-1} h^{-1}, $\phi = 0.979\%$, $\gamma_u = 2.502\%$ R_{CO_2} (mmol kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 1.524$ mmol kg^{-1} h^{-1}, $\phi = -0.72\%$, $\gamma_u = 3.971\%$	NA
					25	MMU	R_{O_2} (mmol kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 2.364$ mmol kg^{-1} h^{-1}, $\phi = 3.664\%$, $\gamma_u = 3.198\%$ R_{CO_2} (mmol kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 1.817$ mmol kg^{-1} h^{-1}, $\phi = 1.676\%$, $\gamma_u = 14.25\%$	NA
Makino et al. (1996)	Shredded lettuce	Closed system (gas chromatograph)	2, 5, 10, 15, 21%	0%	15	LA	R_{O_2} (mmol kg^{-1} h^{-1}) $= 0.395 \times 1.17 \times p_{O_2}$ (kPa)$/(1 + 0.395 \times p_{O_2})$	Good
	Tomato				16	LA	R_{O_2} (mmol kg^{-1} h^{-1}) $= 0.35 \times 0.39 \times p_{O_2}$ (kPa)$/(1 + 0.35 \times p_{O_2})$	Good
	Broccoli				16	LA	R_{O_2} (mmol kg^{-1} h^{-1}) $= 0.548 \times 6.47 \times p_{O_2}$ (kPa)$/(1 + 0.548 \times p_{O_2})$	Good
	Apple	Data of Fidler and North (1967)			3.3	LA	R_{O_2} (mmol kg^{-1} h^{-1}) $= 0.232 \times 0.24 \times p_{O_2}$ (kPa)$/(1 + 0.232 \times p_{O_2})$	Good
	Broccoli	Data of Lee et al. (1991)			24	LA	R_{O_2} (mmol kg^{-1} h^{-1}) $= 0.254 \times 12.4 \times p_{O_2}$ (kPa)$/(1 + 0.254 \times p_{O_2})$	Good
	Banana	Data of Karel and Go (1964)			19	LA	R_{O_2} (mmol kg^{-1} h^{-1}) $= 0.278 \times 0.59 \times p_{O_2}$ (kPa)$/(1 + 0.278 \times p_{O_2})$	Good
	Blueberry	Data of Beaudry et al. (1992)			15	LA	R_{O_2} (mmol kg^{-1} h^{-1}) $= 0.222 \times 0.63 \times p_{O_2}$ (kPa)$/(1 + 0.222 \times p_{O_2})$	Good
Peppelenbos and Leven (1996)	Golden Delicious apple	Closed system (gas chromatograph)	0–21%	0.5–5%	19	MM	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 23$ ml kg^{-1} h^{-1}, $\phi = 6.4\%$	Good
	Elstar apple		0–21%	0.5–5%	19.6	MM	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 15.2$ ml kg^{-1} h^{-1}, $\phi = 4.57\%$	Good
	Asparagus		0–20%	0–20%	18.6	MMC	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 43$ ml kg^{-1} h^{-1}, $\phi = 1.22\%$, $\gamma_c = 5\%$	Good
						MMCU	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 44.9$ ml kg^{-1} h^{-1}, $\phi = 1.57\%$, $\gamma_c = 8.19\%$, $\gamma_u = 135\%$	Good

Table 6 (*continued*)

Reference	Produce	Experimental method (equipment)	O_2 concentration	CO_2 concentration	T (°C)	Model	Model equations	Fit quality
	Broccoli		1–21%	0–10%	18.7	MMC	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 132$ ml kg^{-1} h^{-1}, $\phi = 2.51\%$, $\gamma_c = 2.37\%$	Good
						MMCU	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 137$ ml kg^{-1} h^{-1}, $\phi = 2.82\%$, $\gamma_c = 3\%$, $\gamma_u = 59.9\%$	Good
	Mungbean sprouts	Closed system (gas chromatograph)	0–21%	0–5%	17.9	MMC	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 24.9$ ml kg^{-1} h^{-1}, $\phi = 0.19\%$, $\gamma_c = 0.71\%$	Good
						MMU	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 28.4$ ml kg^{-1} h^{-1}, $\phi = 0.81\%$, $\gamma_u = 13.1\%$	Good
						MMN	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 28.1$ ml kg^{-1} h^{-1}, $\phi = 0.67\%$, $\gamma_n = 14.2\%$	Good
						MMCU	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 26.1$ ml kg^{-1} h^{-1}, $\phi = 0.26\%$, $\gamma_c = 1.41\%$, $\gamma_u = 27.5\%$	Good
	Cut chicory		0–20%	0–20%	8.1	MMU	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 59$ ml kg^{-1} h^{-1}, $\phi = 0.81\%$, $\gamma_u = 8.05\%$	Good
						MMN	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 52.1$ ml kg^{-1} h^{-1}, $\phi = 3.68\%$, $\gamma_n = 13.5\%$	Good
	Apple	Data of Fidler and North (1967)			3.3	MMU	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 5.59$ ml kg^{-1} h^{-1}, $\phi = 4.16\%$, $\gamma_u = 3.05\%$	NA
						MMN	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 5.32$ ml kg^{-1} h^{-1}, $\phi = 3.45\%$, $\gamma_n = 4.49\%$	NA
	Tomato	Data of Yang and Chinnan (1988)			21	MMU	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 22.4$ ml kg^{-1} h^{-1}, $\phi = 24.1\%$, $\gamma_u = 15.5\%$	NA
						MMN	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 19.1$ ml kg^{-1} h^{-1}, $\phi = 18.4\%$, $\gamma_n = 41.4\%$	NA
	Cut broccoli	Data of Lee et al. (1991)			24	MM	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), y_{CO_2} (%); $\alpha = 229$ ml kg^{-1} h^{-1}, $\phi = 1.92\%$	NA
Ratti et al. (1996)	Cauliflower	Closed system (gas chromatograph)	0–300 mg l^{-1}	–	1, 6.5, 12, 23	MM and Arrhenius	R_{CO_2} (mg kg^{-1} h^{-1}), T (°C), y_{O_2} (mg l^{-1}), $\alpha = \exp(45.08) \times \exp(-1.189 \times 10^4/T)$, $\phi = \exp(25.78) \times \exp(-6.703 \times 10^3/T)$	Good
Maneerat et al. (1997)	Banana	Closed system (gas chromatograph)	–	–	10–30	MMU and Arrhenius	R_{O_2} (ml kg^{-1} h^{-1}), T (K), y_{O_2} (%), y_{CO_2} (%), $\alpha = 6.72 \times 10^9 \times \exp(-5697.54/T)$, $\phi = 3.59 \times 10^{10} \times \exp(-6555.24/T)$, $\gamma_u = 3.73 \times 10^{10} \times \exp(-6598.78/T)$ R_{CO_2} (ml kg^{-1} h^{-1}), T (K), y_{O_2} (%), y_{CO_2} (%), $\alpha = 5.77 \times 10^8 \times \exp(-4961.34/T)$, $\phi = 1.08 \times 10^9 \times \exp(-5488.17/T)$, $\gamma_u = 1.09 \times 10^{13} \times \exp(-8274.66/T)$	NA
Andrich et al. (1998)	G.D. apple	Closed system (gas chromatograph)	0–21 kPa	0 kPa	1–21	MM and Arrhenius	R_{O_2} (mol kg^{-1} h^{-1}), $C_{O_2}^{cs}$ (mol kg^{-1}); $\alpha = 4.19 \times 10^4 \times \exp(-5.19 \times 10^3/T)$, $\phi = 1.1 \times 10^{-26} \times \exp(1.31 \times 10^4/T)$	Good
Smyth et al. (1998)	Cut Iceberg lettuce	Flow system (electrochemical O_2 detection cell; infrared CO_2 analyser)	21 kPa	0	5	Exponential	R_{O_2} (pmol g^{-1} s^{-1}) $= 125.7 + [713.8 \times \exp(-0.345t\ (\text{h}))]$, $2 < t < 80$ h	Good

	SS permeable system (electrochemical O_2 detection cell; infrared CO_2 analyser)	0–6 kPa	–	5	MM	R_{O_2} (pmol g^{-1} s^{-1}), y_{O_2} (kPa), $\alpha = 143$ pmol g^{-1} s^{-1}, $\phi = 0.26$ kPa	Acceptable
				10	MM	R_{O_2} (pmol g^{-1} s^{-1}), y_{O_2} (kPa), $\alpha = 213$ pmol g^{-1} s^{-1}, $\phi = 0.19$ kPa	Acceptable
Lakakul et al. (1999)	Apple slices	SS permeable system (paramagnetic O_2 analyser and CO_2 analyser)	0–15 kPa	–	0, 5, 10, 15	MM, linear and exponential	R_{O_2} (mol g^{-1} s^{-1}), T (°C), p_{O_2} (kPa) $\alpha = 1.67 \times 10^{-10} \times \exp(0.069T) - 1.06 \times 10^{-10}$, $\phi = (50T + 660) \times 10^{-3}$	Not good
McLaughlin and O'Beirne (1999)	Coleslaw mix	Flow system (gas chromatograph)	2–10%	0%	5	MM	R_{O_2} (ml kg^{-1} h^{-1}), y_{O_2} (%), $\alpha = 22.72$ ml kg^{-1} h^{-1}, $\phi = 1.083\%$,	Good
			21%	0–25%	5	MMU	R_{O_2} (ml kg^{-1} h^{-1}), T (K), y_{O_2} (%), y_{CO_2} (%), $\gamma_u = 23.16\%$	Good

C^{cs} – concentration in the cellular solution; p^i internal partial pressure; MM Michaelis–Menten-type equation; MMU – Michaelis–Menten-type equation with uncompetitive inhibition of CO_2; MMN – Michaelis–Menten-type equation with non-competitive inhibition of CO_2; MMC – Michaelis–Menten-type equation with competitive inhibition of CO_2; MMCU – Michaelis–Menten-type equation with competitive and uncompetitive inhibition of CO_2; LA – Langmuir adsorption theory; NA – not analysed.

cut iceberg lettuce, maintaining gas concentrations and temperature constant (Table 6).

6. Influence of gas composition

The models in the literature (Table 6) are either best-fitted equations (Beaudry, 1993; Beaudry et al., 1992; Cameron et al., 1989; Emond et al., 1993; Fishman et al., 1996; Gong & Corey, 1994; Henig & Gilbert, 1975; Talasila, 1992; Talasila et al., 1992; Yang & Chinnan, 1988), based on enzyme kinetics (Andrich et al., 1991; Andrich et al., 1998; Cameron et al., 1994; Dadzie et al., 1996; Haggar et al., 1992; Joles et al., 1994; Lakakul et al., 1999; Lee et al., 1991; Lee et al., 1996; Maneerat et al., 1997; McLaughlin & O'Beirne, 1999; Peppelenbos & Leven, 1996; Peppelenbos et al., 1993; Ratti et al., 1996; Smyth et al., 1998; Song et al., 1992; Talasila et al., 1994) or based on adsorption theories (Makino et al., 1996) as the controlling mechanisms.

The simplest equation was presented by Henig and Gilbert (1975) for tomato, which is a linear increase of respiration rate with O_2 concentrations between 4% and 11.5%, and a constant rate for higher O_2 concentrations. Other best-fitted equations were polynomial functions that require many adjustable coefficients (Gong & Corey, 1994; Talasila et al., 1992; Yang & Chinnan, 1988) or exponential functions (Beaudry, 1993; Beaudry et al., 1992; Cameron et al., 1989; Emond et al., 1993; Talasila, 1992). The models describe a biphasic pattern of respiration rate versus O_2 concentration: an initial gradual decrease at relatively high O_2 levels followed by a rapid decline as the O_2 level approaches zero. Recently, dependence of the rate of respiration on O_2 concentration has been widely expressed by a Michaelis–Menten-type equation (Eq. (7)), which is the simplest enzymatic kinetic mechanism. This model is a simplification that tends to fit the experimental data very well, being based on one limiting enzymatic reaction in which the substrate is O_2. Another reason for its use is the similarity with microbial respiration, for which this equation is widely used. In Eq. (7), α is the maximum rate of O_2 consumption or CO_2 production and ϕ is the dissociation constant of the enzyme–substrate complex or the concentration corresponding to the half-maximal respiration rate. In MAP, the maximum O_2 concentration is 21% v/v, so a respiration rate equal to α would never be achieved. Indeed the constants in the model are not real Michaelis–Menten parameters, but apparent constants that incorporate the influence of all processes involving O_2 and CO_2, as already mentioned. Thus, both of them may depend on temperature. This model was previously suggested by Lee et al. (1991) and has been used since then for modelling the respiration rate of apples (Andrich et al., 1991; Andrich et al., 1998; Dadzie et al., 1996; Lee et al., 1991; Peppelenbos & Leven, 1996),

Table 7
Conversion factors to SI units

Units to be converted	Conversion factor	Units obtained
mg kg^{-1} h^{-1}	$2.778^{*}10^{-7}/m_M$	mol kg^{-1} s^{-1}
ml kg^{-1} h^{-1}	$3.341^{*}10^{-11*}p_T/(R_c\,T)$	mol kg^{-1} s^{-1}
mol kg^{-1} h^{-1}	$2.778^{*}10^{-10}$	mol kg^{-1} s^{-1}
%	$p_T^{*}10^{-2}$	Pa
mol kg^{-1}	$p_T^{*}m_M/1000$	Pa
atm	101325	Pa

apple slices (Lakakul et al., 1999), bananas (Lee et al., 1991; Maneerat et al., 1997), blueberries (Cameron et al., 1994; Lee et al., 1996; Song et al., 1992), raspberries (Joles et al., 1994), asparagus (Lee et al., 1991; Peppelenbos & Leven, 1996), broccoli (Lee et al., 1991; Peppelenbos & Leven, 1996), cut broccoli (Haggar et al., 1992; Lee et al., 1991; Lee et al., 1996; Peppelenbos & Leven, 1996; Talasila et al., 1994), cut chicory (Peppelenbos & Leven, 1996), cut lettuce (Smyth et al., 1998), cauliflower (Ratti et al., 1996), coleslaw mix (McLaughlin & O'Beirne, 1999), mungbean sprouts (Peppelenbos & Leven, 1996), mushrooms (Peppelenbos et al., 1993), and tomatoes (Lee et al., 1991; Lee et al., 1996; Peppelenbos & Leven, 1996). Makino et al. (1996) presented a model based on the Langmuir adsorption theory in which the equation is mathematically equivalent to the Michaelis–Menten equation. These authors considered the controlling mechanism to be the adsorption of one molecule of O_2 at an active site of the cytochrome oxidase complex.

Fishman et al. (1996) presented a linear dependence of mango respiration rate on O_2 concentration after testing the Michaelis–Menten-type equation and observing redundancy in the estimated parameters. The linear dependence indicates a low affinity of the enzyme for the substrate, as compared with the affinity of cytochrome oxidase for O_2. Banks et al. (1989) also concluded that a linear relation between respiration rate and internal O_2 concentrations better describes the experimental data for apples than the hyperbolic relationship of Michaelis–Menten kinetics. In contrast, Andrich et al. (1991) reported a ϕ constant relating respiration rate and cellular O_2 concentrations for apples close to that reported for cytochrome oxidase.

The role of CO_2 in respiration was suggested to be mediated via inhibition mechanisms of the Michaelis–Menten equation and to be:

(i) competitive (Eq. (8)),
(ii) uncompetitive (Eq. (9)),
(iii) non-competitive (Eq. (10)) and
(iv) a combination of competitive and uncompetitive types of inhibition (Eq. (11)) (Haggar et al., 1992; Lee et al., 1991; Lee et al., 1996; Maneerat et al., 1997; McLaughlin & O'Beirne, 1999; Peppelenbos & Leven, 1996; Renault, Souty, & Chambroy, 1994; Song et al., 1992) (Table 6).

Competitive inhibition occurs when both the inhibitor (CO_2) and the substrate compete for the same active site of the enzyme. Thus, the maximum respiration rate is lower in high CO_2 concentrations. Uncompetitive inhibition occurs when the inhibitor reacts with the substrate–enzyme complex. Thus, the maximum respiration rate is not much influenced at high CO_2 concentrations. Non-competitive inhibition occurs when the inhibitor reacts both with the enzyme and with the enzyme–substrate complex. The maximum rate lies between the two previous ones:

$$R = \frac{\alpha \times y_{O_2}}{\phi + y_{O_2}}, \tag{7}$$

$$R = \frac{\alpha \times y_{O_2}}{\phi \times \left(1 + \frac{y_{CO_2}}{\gamma_c}\right) + y_{O_2}}, \tag{8}$$

$$R = \frac{\alpha \times y_{O_2}}{\phi + y_{O_2} \times \left(1 + \frac{y_{CO_2}}{\gamma_u}\right)}, \tag{9}$$

$$R = \frac{\alpha \times y_{O_2}}{(\phi + y_{O_2}) \times \left(1 + \frac{y_{CO_2}}{\gamma_n}\right)}, \tag{10}$$

$$R = \frac{\alpha \times y_{O_2}}{\phi \times \left(1 + \frac{y_{CO_2}}{\gamma_c}\right) + y_{O_2} \times \left(1 + \frac{y_{CO_2}}{\gamma_u}\right)}. \tag{11}$$

Lee et al. (1991, 1996) modelled previously published and experimental data for different commodities using an uncompetitive inhibition equation. Peppelenbos and Leven (1996) studied the influence of the four mechanisms of CO_2 inhibition on different products using experimental and literature data. None of the inhibition models used showed the best results for all products and more than one model gave good representations of the experimental data. McLaughlin and O'Beirne (1999) rejected the non-competitive model, but both the competitive and uncompetitive inhibition models gave reasonably good fits, suggesting that both types of inhibition occurred. When no selection could be performed all models were presented in Table 6. The dif-

ferent model equations would not be statistically distinguishable from each other due to experimental error (Walter & Pronzato, 1997).

The parameters of the Michaelis–Menten equation may be estimated by linearisation of the equation and subsequent multiple linear regression analysis (Andrich et al., 1991; Andrich et al., 1998; Haggar et al., 1992; Lee et al., 1991; Lee et al., 1996; McLaughlin & O'Beirne, 1999; Song et al., 1992) or directly by non-linear regression analysis (Cameron et al., 1994; Dadzie et al., 1996; Joles et al., 1994; Peppelenbos & Leven, 1996; Peppelenbos et al., 1993; Ratti et al., 1996; Smyth et al., 1998; Talasila et al., 1994). Makino et al. (1996) estimated the parameters of the adsorption theory model by linearisation of the equation. However, linearising the equations is equivalent to changing the weight given to the data in the estimation procedure and thus should be avoided.

7. Influence of temperature

For distribution and retail temperatures (0–25 °C), the effect of low temperature in lowering biochemical reaction rates is positive. One exception is low temperature sensitive products such as avocado, banana, cherimoya, grapefruit, lemon, lime, mango, papaya, pineapple, and beans, cucumber, okra, pepper, and tomato (Kader, 1997; Saltveit, 1997).

The influence of temperature on respiration rate was first quantified with the Q_{10} value, which is the respiration rate increase for a 10 °C rise in temperature (Eq. (12)):

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{10/(T_2-T_1)}, \tag{12}$$

where R_2 is the respiration rate at temperature T_2 and R_1 is the respiration rate at temperature T_1. For various products, Q_{10} values may range from 1 to 4 depending on the temperature range (Kader, 1987). Talasila (1992) reported Q_{10} values for strawberries varying from 2 to 5.5 and Emond et al. (1993) reported Q_{10} values from 2.8 to 3.2 for blueberries. Exama, Arul, Lencki, Lee, and Toupin (1993) listed Q_{10} values ranging from 1.8 to 3.0 for different products in air and 3% O_2.

The Arrhenius equation (Eq. (13)) is also used to quantify the effect of temperature on respiration rate. The simultaneous use of this equation to describe the influence of temperature on film permeability simplifies the mathematical modelling of MAP systems (Exama et al., 1993; Mannapperuma, Zagory, Singh, & Kader, 1989). The activation energy parameter (E) in non-activated processes loses its physical meaning and only characterises the temperature dependence:

$$R = \delta \times \exp\left(-\frac{E}{R_c T}\right). \tag{13}$$

Eq. (13) may be rewritten with a reference temperature to improve the estimation procedure (Nelson, 1983; Van Boekel, 1996):

$$R = \delta_{\text{ref}} \times \exp\left[-\frac{E}{R_c}\left(\frac{1}{T} - \frac{1}{T_{\text{ref}}}\right)\right]. \tag{14}$$

Activation energy values range from 29.0 to 92.9 kJ mol^{-1} for common fruits and vegetables in air (Exama et al., 1993). Table 8 summarises activation energies reported in the literature or estimated from data reported in the literature.

Other empirical relations with temperature were also reported. Talasila (1992) and Talasila et al. (1992) modelled the influence of temperature with polynomial and exponential relations, respectively (Table 6).

8. Influence of gas composition and temperature

The dependence of the Michaelis–Menten equation parameters on temperature was expressed with the Q_{10} concept (Joles et al., 1994), an Arrhenius-type equation (Andrich et al., 1998; Maneerat et al., 1997; Ratti et al., 1996), a linear relation (Lakakul et al., 1999) or an exponential function (Cameron et al., 1994; Lakakul et al., 1999) (Table 6). Andrich et al. (1998) found that all Michaelis–Menten equation parameters, except ϕ, increased with temperature. Renault et al. (1994) proposed using a Michaelis–Menten-type equation with uncompetitive inhibition by CO_2 and an Arrhenius law to describe the influence of temperature on the maximum rate parameter, but experimentally at 10 °C strawberries showed no influence of O_2 concentrations from 2% to 21% on respiration rate (Renault et al., 1994). Song et al. (1992) concluded that the Michaelis–Menten parameter α did not follow an Arrhenius equation but did not propose another model.

Other works developed mathematical models relating respiration rate to gas concentrations for each temperature studied but did not analyse the relationships of the estimated parameters to temperature (Beaudry et al., 1992; Emond et al., 1993; Haggar et al., 1992; Lee et al., 1996; Peppelenbos et al., 1993; Smyth et al., 1998) (Table 6). One possible justification was the insufficient number of temperatures. But this is not the case for all of them (6, 4, 2, 2, 6 and 2 different values of temperature tested, respectively). Cameron et al. (1994) used the data of Beaudry et al. (1992) to include the influence of temperature in the Michaelis–Menten-type model (Table 6).

The RQ was modelled empirically as the inverse of O_2 concentration and exponentially with temperature by Joles et al. (1994) and as a multi-exponential function of

Table 8
Activation energy values for the respiration rate of some fresh produce

Reference	Product	Range of atmosphere composition	Range of temperatures (°C)	E_{O_2} (kJ mol^{-1})	E_{CO_2} (kJ mol^{-1})
Beaudry et al. (1992)	Blueberry	Air	0–25	59.4	–
Haggar et al. (1992)	Cut broccoli	Air	0–24	43.0	43.1
Song et al. (1992)	Coville blueberry	Air	5–25	45.3	50.3
	Blueray blueberry	Air	5–25	48.7	48.0
	Jersey blueberry	Air	5–25	42.7	47.3
Exama et al. (1993)	Apple	Air	–	–	65.7
	Asparagus	Air	–	–	51.3
	Avocado	Air	–	–	59.7
	Banana	Air	–	–	67.0
	Beans (broad)	Air	–	–	48.1
	Beets	Air	–	–	52.9
	Blueberry	Air	–	–	92.9
	Broccoli (sprouting)	Air	–	–	55.9
	Brussels sprout	Air	–	–	56.2
	Cabbage	Air	–	–	54.2
	Cantaloupe	Air	–	–	72.0
	Carrot	Air	–	–	29.0
	Cauliflower	Air	–	–	57.3
	Cellery (white)	Air	–	–	53.1
	Cherry	Air	–	–	75.3
	Cucumber	Air	–	–	31.8
	Grape	Air	–	–	69.6
	Grapefruit	Air	–	–	55.7
	Green pepper	Air	–	–	48.2
	Leek	Air	–	–	56.0
	Lemon	Air	–	–	63.6
	Lettuce	Air	–	–	51.1
	Lime	Air	–	–	77.9
	Melon	Air	–	–	50.5
	Mushroom	Air	–	–	65.5
	Onion	Air	–	–	30.4
	Orange	Air	–	–	72.8
	Peach	Air	–	–	87.6
	Peas (in pod)	Air	–	–	63.4
	Pear	Air	–	–	73.5
	Plum	Air	–	–	72.6
	Potato (new)	Air	–	–	41.6
	Radish	Air	–	–	71.4
	Raspberry	Air	–	–	67.8
	Spinach	Air	–	–	36.0
	Strawberry	Air	–	–	70.7
	Tomato	Air	–	–	54.9
	Turnip	Air	–	–	33.6
Mannapperuma and Singh (1994)	Broccoli (Green Valiant)	Air	0–20	105	105
		1.5% O_2 + 10% CO_2	0–20	50.95	50.95
	Cabbage (Decema)	Air	0–20	63.15	63.15
		3% O_2	0–20	59.8	59.8
	Green beans (Blue Lake)	Air	5–20	54.9	54.9
		3% O_2 + 5% CO_2	5–20	42.2	42.2
McLaughlin and O'Beirne (1999)	Coleslaw mix	–	3–10	74.8	84.2

O_2 and CO_2 concentrations by Beaudry (1993). Lakakul et al. (1999) used an exponential model to describe the relationship between temperature and O_2 partial pressure at the RQ break point.

9. Conclusions

The success of modified atmosphere packaging (MAP) greatly depends on the accuracy of the predictive

respiration rate models. Due to the complexity of the respiration process, only empirical models have been developed. The particular variables that influence the O_2 uptake and CO_2 production rate should be identified and quantified for each fruit or vegetable product. Considerably more research is needed in this area. Fresh-cut products bring more variables that may influence respiration rate, such as preparation method, cutting size and time after cutting.

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