Available online at www.sciencedirect.com
SCIENCE DIRECT®
Journal of Food Engineering 78 (2007) 500–511
JOURNAL OF FOOD ENGINEERING
www.elsevier.com/locate/jfoodeng

A mathematical model for predicting grape berry drop during storage

Yun Deng [a,c], Ying Wu [b], Yunfei Li [b,*], Peng Zhang [a], Mingduo Yang [c], Changbo Shi [c], Changjiang Zheng [c], Shanming Yu [c]

[a] School of Mechanical and Power Engineering, Shanghai Jiao Tong University, Shanghai 200030, PR China
[b] Department of Food Science and Technology, School of Agriculture and Biology, Shanghai Jiao Tong University, Shanghai Qi Xin Road 2678, Shanghai 201101, PR China
[c] School of Tourism and Cuisine, Harbin University of Commerce, Harbin 150076, PR China

Received 20 May 2005; accepted 27 October 2005
Available online 20 December 2005

Abstract

Berry drop of grapes is a ubiquitous phenomenon during storage. A mathematical model based on biochemical changes in abscission zones was developed with aims of finding the relationship between the detachment force and abscission zone tissue change, and predicting the grape berry drop. The changes of hexose, middle lamella and cellulose as well as trans-membrane transfer of water were taken into account in the model. The parameters in the model were estimated by non-linear parameter fitting of experimental data. The proposed model was then validated under normal air and 4% O_2 + 9% CO_2 at 0 °C and 95% relative humidity for 60 days of storage. The mean relative percentage errors of the resulting model were 4.291% for air storage and 2.241% for controlled atmosphere (much less than 10%), the determination coefficients were 0.9592 and 0.9649, which indicated there was a good agreement between the simulating and experimental results, and the model was practical.
© 2005 Elsevier Ltd. All rights reserved.

Keywords: Grape; Abscission zone; Fruit detachment force; Berry drop; Storage

1. Introduction

China is the fourth largest grape producer and is the first largest fresh market consumption in the world. More than 65% of the grapes produced are consumed as fresh grapes. The 'Kyoho' grapes, which are famous for their large sized berries, crisp texture and good sugar to acid ratio, are one of the commercially important grape cultivars in China. However, the 'Kyoho'grapes are very susceptible to berry drop, which is the main problem for successful storage and marketing (Lv, Xiu, & Ma, 1994; Wu, Ren, Hua, & Liu, 1992). For this reason it is required to predict and control the harvested abscission of grape berries, which is not only of inherent scientific interest but it also has considerable commercial significance (González-Carranza, Lozoya-Gloria, & Roberts, 1998).

There are three categories of grape berry drop: (1) berry shatter, which consists of a detachment of berries from the cap stem due to the fragile tissue structure of the stalk, (2) wet drop, that is, berries are sloughed from the stems and attached to the pedicel because of the short and thin berry brush (Wu et al., 1992), (3) dry drop, or abscission, which is caused by the formation of an abscission zone (AZ) in the grape, localized at the junction between the pedicel and berry, at the stalk-pedicel junction, or at the most fragile portion of pedicel (Chen, Yu, Zhang, & Tan, 2000). Berry drop in the 'Kyoho' grapes usually occurs as dry-drop where ethylene, together with falling auxin levels, induces the formation of an abscission zone at the pedicel-berry junction, thus stimulating fruit drop (Taylor & Whitelaw, 2001; Wu et al., 1992).

Fruit detachment force (FDF), an index of berry adherence strength, consists of the linking force (between berry brush and berry flesh) and tensile strength of abscission zone. Because the brush of 'Kyoho' grape is very short

* Corresponding author. Tel./fax: +86 21 64783085.
E-mail address: yfli@sjtu.edu.cn (Y. Li).

0260-8774/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jfoodeng.2005.10.027

Nomenclature

Symbol	Description
A_a	total abscission zone surface area (m^2)
A'_a	specific abscission zone surface area (m^2/kg)
A_s	total membrane area in abscission zones (m^2)
A'_s	specific membrane area in abscission zones (m^2/kg)
a	regression coefficient in Eq. (24)
a_w	water activity coefficient
b	regression coefficient in Eq. (24)
C	cellulose
[C]	mole fraction of cellulose (mol/mol)
C	moles of cellulose per kg abscission zone weight (mol/ kg)
C_{mnl}	concentration of mannitol solution
c	regression coefficient in Eq. (36)
D	mass diffusion coefficient of water (mol/m^2 Pa s)
d	regression coefficient in Eq. (36)
F	fruit detachment force (N)
F_{cw}	tensile strength of the cell walls (N)
F_l	tensile strength of the middle lamella (N)
F_{fix}	linking force between berry and brush (N)
F_t	tensile strength of abscission zone (N)
f	transport rate of water (mol/s)
G	glucose
[G]	mole fraction of glucose (mol/mol)
G	moles of glucose per kg abscission zone weight (mol/ kg)
H	hexose unit
[H]	mole fraction of hexose (mol/mol)
H	moles of hexose per kg abscission zone weight (mol/ kg)
I	dissolution indexes
k	rate constant (1/s)
L	middle lamella
[L]	mole fraction of middle lamella (mol/mol)
L	moles of middle lamella per kg abscission zone weight (mol/kg)
M	molecular mass (g/mol)
m	mass of fruit (kg)
n	mole number (mol)
P	pectin substance
[P]	mole fraction of pectin (mol/mol)
P	moles of pectin per kg abscission zone weight (mol/ kg)
R	universal drying constant (8.314 J/mol K)
RH	relative humidity (%)
T	air temperature (°C)
t	time (s)
$\overline{V}_w$	partial molar volume of water (18×10^{-6} m^3/mol)
v	reaction rate (1/s)
[W]	mole fraction of water (mol/mol)
W	moles of water per kg abscission zone weight (mol/ kg)

Greek symbols

Symbol	Description
γ	activity coefficient
ψ	water potential (Pa)
ψ_m	matric potential (Pa)
ψ_p	turgor pressure (Pa)
Π	osmotic pressure (Pa)

Subscripts

Symbol	Description
0	initial condition
AZ	abscission zone
a	apoplast
ae	from the apoplast to environment
c	cellulose
g	glucose
h	hexose
l	middle lamella
mnl	mannitol
p	pectin
s	symplast
sa	from the symplast to the apoplast
w	water

and small, the change of linking force is very limited during the storage (Lv et al., 1994). Therefore, the detachment force depends mainly on the tensile strength of abscission zone that lies in cellular 'mechanical units' whose components are cell wall (responsible for turgor pressure support), cell membrane or plasmalemma (for turgor pressure development) and middle lamella (Rojas, Gerschenson, & Marangoni, 2001). The decline in strength of AZ is associated with up-regulated enzymes that dissolve pectic substances in the middle lamella and cellulose in cell wall in AZ (Chen, Wu, Feng, & Zhang, 2003; González-Carranza et al., 1998; Roberts, Whitelaw, Gonzalez-Carranza, & Mcmanus, 2000; Taylor & Whitelaw, 2001). The fruit abscission is also associated with storage conditions, such as temperature, relative humidity, air composition, and other factors (Artés-Hernández, Aguayo, & Artés, 2004; Lv et al., 1994). The optimal storage conditions of 'Kyoho' grapes are at 0 ± 1 °C and about 95% relative humidity. Controlled atmosphere (CA) of 3–5% O_2 + 8–10% CO_2 is also recommended for 'Kyoho' grapes storage.

The present work exhibited there was a high negative correlation between fruit detachment force and harvested berry abscission. Therefore, the progress of abscission could be determined by the changes in fruit detachment force. Model predictive control is a natural tool to implement this optimal trajectory in practice. As yet, no model

for the fruit detachment force as function of the storage conditions is available for quantitative prediction of berry drop and optimization of storage conditions of grapes. The aims of current work are: (a) to develop physiologically mechanistic models for describing the changes of sugars, middle lamella, cell wall, the water transfer through the tissue and their interactions at the cellular level in AZ; (b) to correlate the kinetic models with the fruit detachment force of grape for predicting grape berry drop.

2. Model development

2.1. Structural model

Anatomical observations performed on table grapes indicated that abscission zones between pedicel and berry were composed of a band of small, densely packed cells that elongated longitudinally more than did those of the adjacent tissue (Chen et al., 2000; Zhang et al., 2000). Every cell in AZ behaves similarity, thus the behavior of the whole AZ tissue is the same as the behavior of a single cell. Thereby, a simplified model is developed to represent AZ tissue and is shown in Fig. 1. The model consists of the symplast and the apoplast that are separated by a 'semi-permeable' membrane, the plasmalemma (De Smedt et al., 2002; Wu, 2003). The symplast includes the entire network cytoplasm interconnected by plasmodesmata, the apoplast contains the cell wall and the intercellular space. Differing from other cells, plant cells develop a turgor pressure inside the cells, therefore, water in the symplast may flow into the apoplast through the plasmalemma. The apoplast can also exchange water with the environment via a wax layer of AZ.

2.2. Kinetic model

The process of abscission is a concerted action of differently physiological processes. For model simplification, the assumptions were as follows: (1) the starch hydrolysis in AZ is not introduced into the model due to a minute amount of starch (less than 0.03 mg/g) (John, Downton, & Hawker, 1981); (2) the symplastic transport of small molecular solute is ignored through the plasmodesmata; (3) the amount changes of molecules or ions or pH in solution are not considered in the symplast; (4) time is only independent variable in the model. Therefore, the biochemical changes in AZ related with this model included mainly

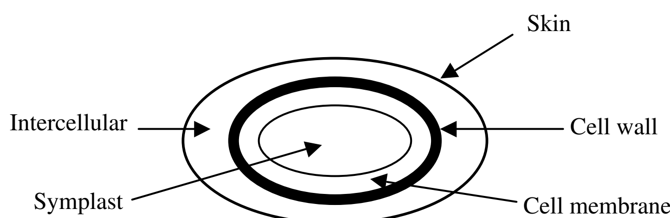

Fig. 1. Schematic diagram of a simplified abscission zone model.

hexose oxidation, dissolutions of the middle lamella and cellulose, and trans-membrane transport of water.

2.2.1. Respiration

Like other living plant organs, harvested grapes continue to respire and transpire, so that during storage the grapes are subjected to both physiological changes and to water losses. Physiological changes which alter the biochemical nature of the cell wall will in turn affects its mechanical properties. Appropriate conditions could be avoid anaerobic respiration. Respiration in vegetables and fruits is represented by the hexose oxidation reaction. Namely, hexose units (H) in AZ, combining with O_2, are transformed into carbon dioxide and water. Carbon dioxide diffuses to environment via AZ, and water fluxes from the symplast towards the apoplast and becomes reactive substrate.

$$\mathrm{H} + 6\mathrm{O}_2 \xrightarrow{k_\mathrm{h}} 6\mathrm{CO}_2 + 6\mathrm{H}_2\mathrm{O} \tag{1}$$

The amount of hexose in the symplast decreased gradually with respiration. The hexose changes over time are proportional to the oxidation rate of sugar, v_h, and the amount of molecules, $(n_\mathrm{h} + n_\mathrm{s})$, in the symplast.

$$\frac{\mathrm{d}n_\mathrm{h}}{\mathrm{d}t} = v_\mathrm{h}(n_\mathrm{h} + n_\mathrm{s}) \quad \text{for } t = 0, \quad n_\mathrm{h} = n_{\mathrm{h}_0} \tag{2}$$

where, v_h, the oxidation rate of hexose, is defined as a conversion of the amount of hexose per mole reaction medium and per second. This rate is associated with the physiological state and temperature. The mole number, n, is a ratio of mass (m) to molecular mass (M):

$$n = \frac{m}{M} \tag{3}$$

The concentration of oxygen is maintained to be constant before or after reaction in CA and air conditions. Further, autoxidation reaction (1) is assumed to be a simple reaction. Thus, the following expression is obtained according to law of mass action:

$$v_\mathrm{h} = k_\mathrm{h}[\mathrm{H}] \tag{4}$$

where k_h is the reaction rate constant for the oxidation of sugar; [H] is defined as the concentration of sugar expresses as a mole fraction

$$[\mathrm{H}] = \frac{n_\mathrm{h}}{n_\mathrm{h} + n_\mathrm{s}} \tag{5}$$

The specific concentration is also defined as follows for the simplification of calculation:

$$H = \frac{n_\mathrm{h}}{m_{\mathrm{AZ},0}} \tag{6}$$

where $m_{\mathrm{AZ},0}$ is the weight of grape AZ.

Introduction of Eqs. (3)–(6) into Eq. (2), the following equation is yielded:

$$\frac{\mathrm{d}H}{\mathrm{d}t} = -k_\mathrm{h}H \quad (\text{for } t = 0,\ H = H_0) \tag{7}$$

2.2.2. Degradation of cellulose

Cellulose, the characteristic substance of the plant cell, is a linear (unbranched) polysaccharide consisting of 1,4-linked β-D-glucopyranose units (Nobel, 1991). Cellulases represent a large gene family and have been associated traditionally with a variety of cell wall hydrolytic responses including organ abscission (González-Carranza et al., 1998; Roberts et al., 2000). Cellulases are directly involved in hydrolysis of β-1,4 linkage. To simplify the model, a simple hydrolysis reaction is assumed in which cellulose(C) is hydrolyzed to glucose unit (G).

$$\mathrm{C} + \mathrm{H_2O} \xrightarrow{k_c} \mathrm{G} \tag{8}$$

where k_c is the reaction rate constant for the hydrolysis of cellulose. The degradation of cellulose causes a decrease in its level and an increase in content of glucose in the apoplast. The cellulose changes over time are proportional to the degradation rate of cellulose, v_c, and the amount of molecules, $(n_c + n_{w_a} + n_g + n_l + n_p)$, in the apoplast.

$$\frac{\mathrm{d}n_c}{\mathrm{d}t} = -v_c(n_c + n_{w_a} + n_g + n_l + n_p) \quad (\text{for } t = 0,\ n_c = n_{c_0}) \tag{9}$$

$$\frac{\mathrm{d}n_g}{\mathrm{d}t} = v_c(n_c + n_{w_a} + n_g + n_l + n_p) \quad (\text{for } t = 0,\ n_g = n_{g_0}) \tag{10}$$

where v_c, the hydrolysis rate of cellulose, is defined as a conversion of the amount of cellulose per mole reaction medium and per second.

For simplicity, the reaction (8) is assumed to be a simple reaction. This is, the activity of a chemical component is approximately equal to its concentration. The rate is assumed to be proportional to both the concentration of cellulose and water in apoplast. According to law of mass action, v_c is expressed as follows:

$$v_c = k_c[\mathrm{C}][\mathrm{W_a}] \tag{11}$$

where [C] and $[\mathrm{W_a}]$ are defined as the concentrations of cellulose and water in the apoplast, respectively.

Similar to Eqs. (5) and (6):

$$[\mathrm{C}] = \frac{n_c}{n_c + n_{w_a} + n_g + n_l + n_p}, \quad [\mathrm{W_a}] = \frac{n_{w_a}}{n_c + n_{w_a} + n_g + n_l + n_p} \tag{12}$$

$$C = \frac{n_c}{m_{\mathrm{AZ},0}}, \quad G = \frac{n_g}{m_{\mathrm{AZ},0}}, \quad W_a = \frac{n_{w_a}}{m_{\mathrm{AZ},0}} \tag{13}$$

Rearranging Eqs. (9)–(13), the changes in cellulose and glucose in the apoplast are obtained:

$$\frac{\mathrm{d}C}{\mathrm{d}t} = -k_c C \frac{W_a}{C_0 + G_0 + L_0 + P_0 + W_a} \quad (\text{for } t = 0,\ C = C_0) \tag{14}$$

$$\frac{\mathrm{d}G}{\mathrm{d}t} = k_c C \frac{W_a}{C_0 + G_0 + L_0 + P_0 + W_a} \quad (\text{for } t = 0,\ G = G_0) \tag{15}$$

2.2.3. Dissolution of the middle lamella

The middle lamella is an amorphous region between contiguous cells and causes adjacent cells to adhere to each other. The middle lamella is composed mainly of the calcium salts of pectic acid. The basic structure of pectic substances consists of chains of D-galacturonic acid residues linked by a $(1 \to 4)$ glycosidic bonds. A large number of side chains are attached to the main chain. Pectin decay by enzymatic actions of pectinesterase (PE), polygalacturonase (PG) and peroxidase (POD), which degrade pectic substances in the middle lamella and promote cell separation and dissolution of cell wall (Mcmanus, 1994; Roberts et al., 2000). To simplify the model, a simple hydrolysis reaction is assumed in which galacturonic acid units are subsequently detached from the pectin main chain. Namely, the middle lamella (L) is transformed into pectin monomer (P) (De Smedt et al., 2002).

$$\mathrm{L} + \mathrm{H_2O} \xrightarrow{k_l} P \tag{16}$$

Similar to the hydrolysis of cellulose, the middle lamella changes in the apoplast over time can be expressed as the following sets of differential equations (17) and (18):

$$\frac{\mathrm{d}L}{\mathrm{d}t} = -k_l L \frac{W_a}{L_0 + P_0 + C_0 + G_0 + W_a} \quad (\text{for } t = 0,\ L = L_0) \tag{17}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = k_l L \frac{W_a}{L_0 + P_0 + C_0 + G_0 + W_a} \quad (\text{for } t = 0,\ P = P_0) \tag{18}$$

where k_l is the reaction rate constant for the hydrolysis of the middle lamella.

2.2.4. Water transport

Changes in water content which leads to differences in turgor pressure exert a profound effect on the stiffness and strength of the tissue, and have a strong bearing on the storage temperature, time, relative humidity, air composition, variety, and ripening stage (Murase, Merva, & Segerlind, 1980). So, during storage, the water transport of AZ consists primarily of two parts: one is trans-plasmalemma transport of water between the symplast and the apoplast, the second is exchange of water between the apoplast and ambient due to the differences in relative humidities. Differences in concentrations at the inner and outer surface of the plasmalemma cause water to flow into the apoplast by the process of osmosis. Water potential in plant tissue is the sum of the osmotic, turgor and matric potentials. The basic equation for water potential is expressed as (Nobel, 1991)

$$\psi = \Pi + \psi_p + \psi_m \tag{19}$$

where ψ is the water potential, Π the solute (osmotic) potential, ψ_p the turgor potential and ψ_m the matric potential. In the water potential measurements, ψ_m is neglected as it is more or less constant and of no physiological importance.

According to Fick's first law, the driving force, leading to the water molecular movement, is the concentration gradient, and the flux of water is proportional to the water potential. We can now write the following relation showing the dependence of the water flux from the symplast to the apoplast on the difference of water potential

$$f_{sa} = D_{sa}A_s(\psi_s - \psi_a) \tag{20}$$

where f_{sa}, D_{sa}, A_s, ψ_s and ψ_a are the transport rate of water from the symplast to the apoplast, the mass diffusion coefficient of water from the symplast to the apoplast, the total membrane area in the symplast, the water potential in the symplast, the water potential in the apoplast, respectively.

An increase in the concentration of solutes decreases the water activity and raises the osmotic pressure. In fact the osmotic pressure and water activity are related in the symplast (Nobel, 1991)

$$\Pi_s = \frac{R(273.15+T)}{\overline{V}_w}\ln a_{w_s} \tag{21}$$

where Π_s, R, T, $\overline{V}_w$, a_{w_s} are the osmotic pressure in the symplast (Pa), the gas constant (8.314 J/mol K), the temperature (°C), the partial molar volume of water (18×10^{-6} m^3/mol), and the water activity in the cell, respectively. The water activity (a_{w_s}) is related to its concentration ([W$_s$]) by means of an activity coefficient (γ)

$$a_{w_s} = \gamma[\mathrm{W_s}] \tag{22}$$

For an ideal solution or dilute solution, γ equals approximately to 1. For simplification, the activity coefficient of the symplast in AZ is assumed to be 1. By substituting the water activity in Eq. (22) to Eq. (21), the following equation is given:

$$\Pi_s = \frac{R(273.15+T)}{\overline{V}_w}\ln[\mathrm{W_s}] \tag{23}$$

In Eq. (20), ψ_s correlates linearly with the water content of fruit tissue (De Smedt et al., 2002).

$$\psi_s = a(W_s + W_a)M_w - b \tag{24}$$

where, M_w is water molecular mass, a and b are constants.

According to the definition, the hydrostatic pressure of the apoplast is equal to zero. From Eq. (19), the water potential in the apoplast is equal to its osmotic potential

$$\psi_a = \Pi_a = \frac{R(273.15+T)}{\overline{V}_w}\ln[\mathrm{W_a}] \tag{25}$$

In the symplast, the turgor pressure is non-negative. The turgor pressure is obtained from Eq. (19)

$$\psi_{p_s} = \psi_s - \Pi_s \tag{26}$$

When the relative humidity of the environment is lower, the flux of water from the apoplast to ambient is more. Similar to f_{sa}, the transfer rate of water from the apoplast to ambient, f_{ae} is given by:

$$f_{ae} = D_{ae}A_a(\psi_a - \psi_e) \tag{27}$$

where D_{ae}, A_a and ψ_e are mass transfer coefficient from the apoplast to the environment, the total AZ surface area, and the water potential of environment surrounding the grapes, respectively. ψ_e is also expressed as

$$\psi_e = \frac{R(273.15+T)}{\overline{V}_w}\ln(\mathrm{RH}) \tag{28}$$

where RH is the relative humidity of storage of grapes.

Collectively, the water balance in the symplast includes water produce by hexose oxidation and water loss through selective membrane, the water balance in the apoplast contains inflow water from the symplast, consumption water in the hydrolysis of pectin and cellulose, and water loss to environment.

$$\frac{dn_{w_s}}{dt} = 6v_h(n_h + n_s) - D_{sa}A_a(\psi_s - \psi_a) \quad (\text{for } t=0,\ n_{w_s} = n_{w_{s_0}}) \tag{29}$$

$$\frac{dn_{w_a}}{dt} = D_{sa}A_s(\psi_{w_s} - \psi_{w_a}) - v_c(n_c + n_a + n_p + n_l + n_g) - v_l(n_l + n_p + n_c + n_g + n_a) - D_{ae}A_a(\psi_a - \psi_e) \quad (\text{for } t=0,\ n_{w_a} = n_{w_{a_0}}) \tag{30}$$

By analogy, Eqs. (29) and (30) can be rearranged

$$\frac{dW_s}{dt} = 6k_hH - D_{sa}A'_s(\psi_s - \psi_a) \quad (\text{for } t=0,\ W_s = W_{s_0}) \tag{31}$$

$$\frac{dW_a}{dt} = D_{sa}A'_s(\psi_s - \psi_a) - k_cC\frac{W_a}{C_0+G_0+L_0+P_0+W_a} - k_lL\frac{W_a}{C_0+G_0+L_0+P_0+W_a} - D_{ae}A'_a(\psi_a - \psi_e) \quad (\text{for } t=0,\ W_a = W_{a_0}) \tag{32}$$

where A'_s and A'_a are the total membrane specific surface area in the symplast and the total AZ specific surface area, respectively.

2.3. Detachment force model

In simplification models for the cellular structure of plant tissue, cells were generally assumed to have uniform shapes, and each cell supported a portion of the external load (Wu & Pitts, 1999). Thus, the properties of individual cells can reflect he apparent properties of apparent tissue stress and strain, and the mechanical property of abscission zone lies on cell wall, cell membrane or plasmalemma, and middle lamellae in AZ (Rojas et al., 2001). The cell wall comprises cellulose microfibrils randomly oriented and embedded in a flexible pectin matrix, and its mechanical behavior determines the mechanical properties of the cellular conglomerate (Pitt, 1982). The plasmalemma has little mechanical resistance, it is the pressure exerted on the cell wall which accounts for the turgor pressure-induced elasticity of cells and tissue (Rojas et al., 2001). The middle lamella, a pectin layer between adjacent cells, bonds cells together and provides the cohesion necessary to maintain

a conglomerate structure (Pitt, 1982), which is the primary site of wall breakdown in AZ (Peterson et al., 1996).

The detachment force of grape (F) is considered to be built up by a variable part (F_t) that changes with the activities of enzymes in AZ and a fixed part (F_{fix}) that is invariable for the circumstances under study.

$$F = F_t + F_{fix} \tag{33}$$

During tension testing, cell rupture and cell separation could be observed in the same fracture face in both freshly harvested and stored fruits. Whether cell rupture or cell-to-cell de-bonding is determined by the strength of the cell wall relative to the adhesion between neighboring cells (Harker, Redgwell, Hallett, Murray, & Carter, 1997). If the strength of cell-to-cell adhesion falls below the tensile strength of the cell wall, the cells each other will debond without necessarily rupturing, whereas the cell will rupture. The strength of AZ can be measured in tension and be indicated using the maximum force. Therefore, the tensile strength of AZ may be expressed as the following formula:

$$F_t = (I_c + I_l)F_{cw} + (1 - I_l)F_l \tag{34}$$

In Eq. (34), I_c and I_l are the dissolution indexes of cellulose and middle lamella, defined as the ratios of the amount of undissolved cellulose to the total amount of cellulose and undissolved middle lamella to the total amount of middle lamella, respectively.

$$I_c = \frac{C}{C_0 + G_0} \quad I_l = \frac{L}{L_0 + P_0} \tag{35}$$

where F_{cw}, the tensile strength of the cell walls, is considered to be linearly dependent on cell turgor pressure (De Smedt et al., 2002; Murase et al., 1980).

$$F_{cw} = c + d\psi_{p_s} \tag{36}$$

The tensile strength of middle lamella in AZ may increases with increasing turgor pressure due to small and densely AZ cells that leading to the increase of the area of cell-to-cell contact (Harker et al., 1997). Whereas, the part of middle lamella that determines the strength of cell adhesion is only located at the edge of the cell faces (Waldron, Smith, Ng, Parr, & Parker, 1997). Therefore, F_l, the tensile strength of middle lamella, is assumed to be a constant.

3. Materials and methods

3.1. Fruits and storage conditions

'Kyoho' grapes (*Vitis vinifera X V. labrusca*), grown in a greenhouse, were harvested at commercial maturity stages from the vineyard of the Shanghai Grape Research Institute in Shanghai, China. All table grapes were transported under refrigerated conditions (10 °C) to the lab within 2 h. The clusters were selected on the basis of uniform color, size, firmness, and absence of blemishes or disease, and pre-cooled (4 °C, 14 h) immediately upon arrival.

All grapes were stored at 0 ± 1 °C in about 95% relative humidity. Two storage atmospheres were used: normal atmosphere (control), standard CA (8–10% CO_2 + 3–5% O_2). CA chamber ($105\ cm \times 55\ cm \times 100\ cm$) was connected to an atmosphere analyzer (GAC 1100, Italy). There were eight cartons of table grapes (about 5 ± 1 kg/carton) in each condition. The samples were assayed during the 60 days of storage.

3.2. Determinations of pectin and total cellulose

Plugs of abscission zone tissue measured 4 mm in width, and included 2 mm of tissue from the pedicel and 2 mm of tissue from berry side of the AZ (Chen et al., 2003; Zhang et al., 2000). Briefly, a sample of 5 g abscission zone tissue were ground rapidly in ice cold, heat-inactivated in 200 ml of 80% (v/v) boiling ethanol for 20 min, and centrifuged at 2000*g* for 10 min. The residue, rinsed twice with ethanol and centrifuged, was incubated overnight at 4 °C with 50 ml of dimethysulphoxide DMSO:water (9:1) to remove starch and was then washed with water and transferred to 200 ml of chloroform:ethanol (2:1). After 10 min the wall material was filtrated, then washed twice with 200 ml of acetone until total whitening. The cell wall was fractionated using the method of Deng, Wu, and Li (2005). The uronic acid content in the fraction was determined by the *m*-hydroxydiphenyl method (Blumenkrantz & Asboe-Hansen, 1973). Galacturonic acid (Fluka) was used as standard. The total cellulose content was quantified using the anthrone method. Glucose was used as standard for these assays. The glucose amount was measured by phenol-sulfuric acid method. The absorbance was measured at about 487 nm by an adsorption meter.

3.3. Fruit detachment force

The FDF between stem and berry was measured using a TA-XT2i texture analyzer (Stable Micro Systems Ltd., UK) with slight modifications. An individual grape stem was through a hole of a homemade plastic base and firmly clamped with a spring clamp. The spring clamp was fastened to the load cell fixture. The texture analyzer was programmed so that upward movement was perpendicular to the longitudinal axis of the stem-berry system until they were pulled apart. The maximum force encountered was recorded during the tension test. A speed of 2 mm/s was set for test and 5 mm/s for both pre-test and post-test. Trigger force was 5 g. Forty berries with stems from each treatment were measured.

3.4. Water potential of abscission zone

Water potential in AZ was determined by the modified method of Sajnin, Gerschenson, and Rojas (1999). Briefly, mannitol solutions ranged from 0.2 to 0.8 M and were buffered with 0.02 M KH_2PO_4 and 0.02 M K_2HPO_4. A sample of 10 g abscission zones were placed in each mannitol

solution and equilibrated at 1 °C. These samples were weighed at regular time intervals until a stable weight was obtained. These tissues that neither gained or lost water are in a solution with the same water potential. The ratio of AZ tissue to solution was 1:10 (w/w) to prevent changes in the a_w of the solution during the experiment.

At equilibrium, the water potential of AZ can be obtain from the following relationship (Nobel, 1991):

$$\psi = \frac{R(273.15 + T)}{\overline{V}_w} \ln a_{w_{mnl}} \cong -R(T + 273.17)C_{mnl} \qquad (37)$$

where $a_{w_{mnl}}$ and C_{mnl} are the water activity of mannitol solution and the corresponding mannitol concentration, respectively. The moisture content of AZ was determined using a vacuum oven. Samples were heated at 105 °C under the vacuum until a constant mass was reached. The diagram of equilibrium moisture content (kg/kg dry base) against the water potential of AZ was carried out to estimate a and b in Eq. (24).

3.5. Data analysis

The data were analyzed using ANOVA ($P < 0.05$). Mean differences were established by the Duncan's multiple range tests (SAS 8.0). The kinetic parameters (k_h, k_c, k_l, D_{sa}, D_{ae}), the invariable parameters (F_{fix}, F_l) and other values (c, d) were fitted by non-linear least squares. The system of ordinary differential equations was solved using the Runge–Kutta–Fehlberg method. The optimum of parameter values was done with the mixed genetic algorithm based on the idea of coupling genetic algorithm with Levevberg–Marquardt algorithm.

The determination coefficient (R^2) is one of the primary criteria to select the best model to account for variation in changes in FDF. In addition to R^2, the mean relative percentage error (E) is used to determine the quality of the fit. The higher the value R^2, lower E, which are chosen as the criteria for goodness of fit. The mean relative percentage error (E) is calculated according to (Boquet, Chirife, & Iglesias, 1978; Kaymak-Ertekin & Gedik, 2005)

$$E(\%) = \frac{100}{n} \sum_{1}^{n} \frac{|V_{exp} - V_{pre}|}{V_{exp}}$$

where V_{exp} and V_{pre} stand for experimental and predicted values, respectively. n is the number of experimental data points. A model is considered acceptable if E values is below 10% (Boquet et al., 1978; Kaymak-Ertekin & Gedik, 2005).

4. Results

4.1. Model parameters

The relevant values for the parameters used were taken from the literature data or linear regression (Table 1). The constants, a and b, in Eq. (24) were obtained from least squares fitting experimental data as shown in Fig. 2 ($R^2 = 0.9677$). A_a was estimated the surface of the plug of abscission zone which was composed approximately of a cylinder with a diameter of 4.53 mm and a height of 2 mm, and a spherical crown with a height of 2 mm and a spherical diameter of 26.1 mm. Compared with the arrangement and packing of cells within the apple tissue, though the cells in grape AZs were small, hetero-diameteric in shape, and closely packed with a high degree of contact between neighboring cells and a small volume of intercellular gas filled spaces, the cell wall area per kilogram AZ weight was assumed to be 6.45 m^2/kg (De Smedt et al., 2002).

Table 1
The relevant values for the model parameters taken from the literature or linear regression

Parameter	Value	Parameter	Value
M_h (kg/mol)	180×10^{-3}	T (°C)	0 ± 1
M_c (kg/mol)	162×10^{-3}	R (J/mol K)	8.314
M_g (kg/mol)	180×10^{-3}	RH	95%
M_l (kg/mol)	176×10^{-3}	a (Pa)	19.56947×10^6
M_p (kg/mol)	194×10^{-3}	b (Pa)	3.53229×10^6
M_w (kg/mol)	18×10^{-3}	A_a (m^2/kg)	0.6846
$\overline{V}_w$ (m^3/mol)	18×10^{-6}	A_s (m^2/kg)	6.45

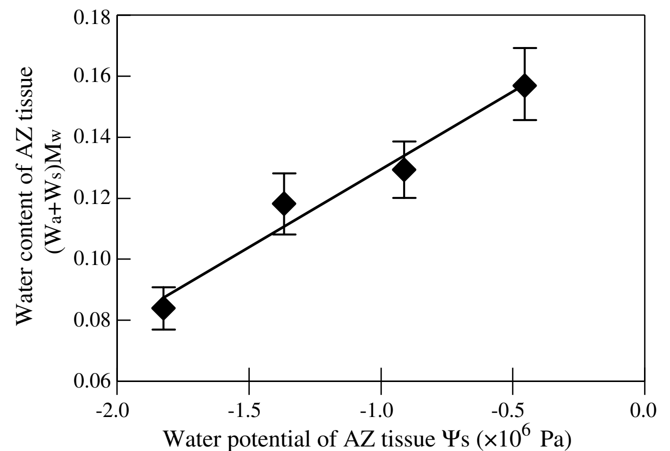

Fig. 2. Relationships between total water content with water potential of AZ tissue.

The estimate values and errors of parameters in the model are shown in Table 2. The rate constant values for hexoses oxidation were about 1.3998×10^{-8} (1/s) for air storage and 1.2958×10^{-8} (1/s) for CA storage in this study. The reaction rate constants for the sugars oxidation in potatoes varied from 8.39×10^{-5} and 1.53×10^{-2} (1 per day) in different seasons (Hertog, Tijskens, & Hak, 1997). Compared to the reaction rate constants for the middle lamella degradation obtained by De Smedt et al. (2002) on apples at 3 °C and 95% RH, which were 0.026×10^{-6} and 0.0702×10^{-6} (1/s) for, respectively, CA storage and air storage, the values presented here were one order of magnitude higher than those of the former due to

Table 2
Parameter estimated and their standard errors (S.D.) obtained from the data fitting (95% confidence level)

Parameters	Estimate ± S.D.	
	Air	CA
k_h (1/s)	$(1.3998 \pm 0.1635) \times 10^{-8}$	$(1.2958 \pm 0.3126) \times 10^{-8}$
k_c (1/s)	$(2.243 \pm 0.05247) \times 10^{-7}$	$(1.5723 \pm 0.066578) \times 10^{-7}$
k_l (1/s)	$(1.4861 \pm 0.028605) \times 10^{-7}$	$(1.1575 \pm 0.059265) \times 10^{-7}$
D_{sa} (mol/m^2 Pa s)	$(3.069 \pm 1549.1) \times 10^{-10}$	$(2.901 \pm 1416.4) \times 10^{-10}$
D_{ae} (mol/m^2 Pa s)	$(3.3690 \pm 793.79) \times 10^{-11}$	$(3.199 \pm 992.14) \times 10^{-11}$
F_l (N)	0.30072 ± 0.19974	
F_{fix} (N)	1.11 ± 0.2368	
c (mm^2 kg/mol)	8.4015 ± 0.19974	
d (N)	$4.1106 \times 10^{-1} \pm 0.19974$	

differences in enzymatic activities and tissues. The trans-membrane water diffusion coefficients (D) were also rather varied and may be from 10^{-12} to 10^{-8} (mol/m^2 Pa s), depending on the plant species, tissue, temperature, etc. (Rotstein & Cornish, 1978; Wu & Pitts, 1999). Noticeably, the parameters, D_{ae} and D_{sa}, had very large standard errors. This is because that the parameters were estimated from just a limited data points. The accuracy of this model might be enhanced by making a greater number of experimental data measurement, providing the measurement error is to too large. The tensile strength of the middle lamella, F_l, measured by De Smedt et al. (2002) was about (0.855 ± 3.1) N for apple tissues.

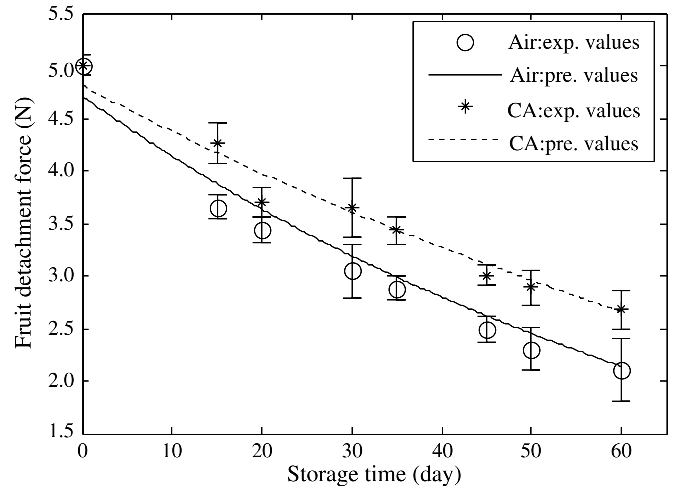

Fig. 3. Changes in fruit detachment force of grape during 60 days of storage at 0 °C.

The degradation rate constants of sugar, cellulose and middle lamella were greater in air-stored grapes than in CA-stored grapes. This is ascribed to the fact that low O_2 and high CO_2 could inhibit respiration and activities of

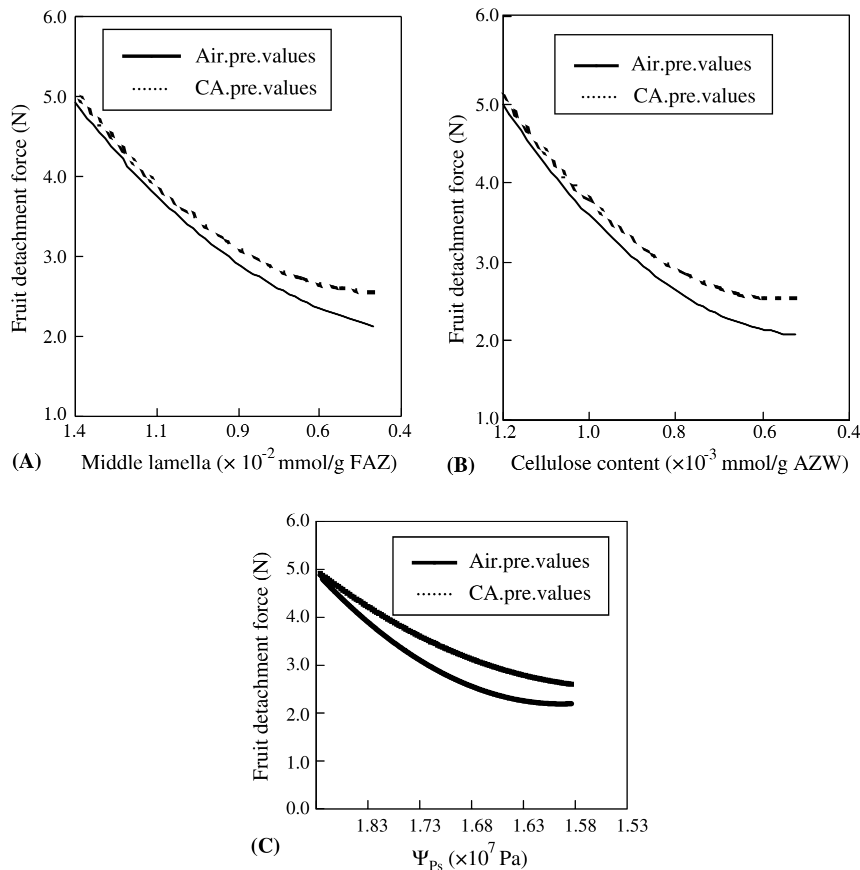

Fig. 4. Relationships between FDF and changes in middle lamella, cellulose and turgor in AZ during 60 days of storage at 0 °C.

degradation enzymes in grape AZs. The water diffusion coefficient from the symplast to the apoplast was slight higher for the grapes kept in CA compared with the grapes kept in normal air, which is due to a restraining effect of low O_2 and high CO_2 on loss in the integrity of cell membrane.

4.2. Simulations of changes in FDF

The FDF of grapes declined steadily, as a factor of length of storage, by about 62.8% in air and 53.1% in CA, respectively (Fig. 3). The mean relative percentage errors of the resulting model were 4.291% for air storage and 2.241% for controlled atmosphere (much less than 10%), the determination coefficients were 0.9592 and 0.9649, which indicated that there were good correlations between experimental data and predicted values. The present data also indicated that there was a high correlation between berry drop and FDF, and that berry drop increased gradually, concurrent with the reduction in FDF. Fruits kept in CA always exhibited a higher FDF and a lower susceptibility to berry drop than fruits stored in air, resulting in extension of post harvest life. By day 60, the FDF of grapes stored in CA was about 1.3-fold higher than that of grapes stored in air, correspondingly, the berry drop was about 0.8-fold.

During the storage period studied, the FDF under two treatments decreased continually with the reductions in levels of cellulose, middle lamella and turgor pressure (Fig. 4). However, there appeared to be different degrees of correlations under the same storage condition. That is, the correlations in all conditions were the highest between FDF and middle lamella (air: $R^2 = 0.9928$; CA: $R^2 = 0.9726$), intermediate between FDF and cellulose (air: $R^2 = 0.9811$; CA: $R^2 = 0.9625$) and the lowest between FDF and turgor (air: $R^2 = 0.9513$; CA: $R^2 = 0.9537$). Additionally, the decreases in middle lamella and cellulose of CA-stored fruits changed to a lesser extent than those of air-stored fruits (Fig. 4A and B), while there were more significant differences in turgor of air- or controlled atmosphere-treated grapes ($P < 0.05$) (Fig. 4C).

5. Discussion

It is well documented that natural fruit abscission is associated with declining detachment force (Trueman, Richards, McConchic, & Turnbull, 2000). The present results suggested the FDF of Kyoho grapes is a function of cell wall strength, cell-to-cell adhesion, cell packing and the internal pressure or turgor of cells in grape abscission zone tissue, and the progress of berry abscission may be determined by changes in FDF. A continual decreases in FDF in both air and controlled atmosphere storage were seen during the storage period studied (Fig. 3), consistent with the findings of Ou, Cao, Guo, Mao, and Yuan (1996). Rapid decreases in FDF in grapes are in agreement with cell wall dissolution and loss of cell-to-cell adhesion due to breakdown of the middle lamella (Fig. 4A and B), as reported in ultrastructural changes in abscission zones of many fruits (Henderson, Davies, Heyes, & Osborne, 2001; Tabuchi, Ito, & Arai, 2000). Previous studies also indicated that wall breakdown was associated with coordinated action of up-regulated enzymes during abscission, such as cellulase, polygalacturonse; pectinesterase, β-galactosidase and peroxidases (Chen et al., 2003; González-Carranza et al., 1998; Roberts et al., 2000).

The rigid cell wall of plants is made of fibrils of cellulose bonded into a matrix of several other kinds of polymers such as pectin and lignin. Cellulose degradation has been attributed primarily to the increase in cellulase activity (González-Carranza et al., 1998; Roberts et al., 2000). An increase in cellulase activity was detected in grape abscission zone (data not shown) and associated with the decrease in FDF, which was consistent with the results for *Wuheibai* grape (Chen et al., 2003) and tomato flower (del Campillo & Bennett, 1996). Compared with air storage, CA treatment retained higher FDF and cellulose content, which was due to the fact that high CO_2 levels may act as a competitive inhibitor of ethylene synthesis, leading to suppressing increased syntheses and activities of cellulase and PG in the AZ of fruit (Bonghi, Rascio, Ramina, & Casadoro, 1992; Gorny & Kader, 1996). Toole, Smith, and Waldron (2002) also observed that the sequential deconstruction and decrease of polysaccharide in the cell wall were directly responsible for the loss in tensile strength and reduction in modulus of elasticity, however, cellulose content alone did not determine mechanical properties of the cell wall.

The degradation of pectin in the middle lamella is characterized by uronide depolymerization and dissolution during fruit abscission due to the actions of PG and PE (González-Carranza et al., 1998; Roberts et al., 2000). PE removes the methyl groups of the galacturonic acid polymers, which contributes PG to depolymerise the de-esterified polygalacturomide chain (Abu-Goukh & Bashir, 2003). This is, PE provides substrate for PG to act upon. Together, they act mainly on the dissolution of the middle lamella, which results in cell separation in AZ. In addition, changes in the activity of peroxidase have been documented to accompany abscission (Mcmanus, 1994) and such activity in the middle lamella may be important in the control of cell adhesion. The present data suggested both pectin degradation and FDF reduction occurred simultaneously in both storages, consistent with previous reports on peach (Bonghi, Casadoro, Ramina, & Rascio, 1993). These results exhibited that pectin degradation in fruit detachment zone resulted in the reduced cell to cell adhesion, and supported a relationship between the ease of fruit detachment and pectin dissolution in AZs. It is well known that the insoluble pectin is the primary component of both the cell wall and the middle lamella. The results of this study indicated that the reduction in FDF was accompanied with a decrease in insoluble pectin and an increase in water-soluble pectin (data not shown). Similar results

were obtained by Pitt (1982), who highlighted that the decrease in insoluble pectin in apple tissue has been correlated with a softening of the tissue. The differential reduction of the fruit detachment force between air and CA storage (Fig. 3) was associated with a differential degree of pectin metabolism as indicated by solubility studies (Fig. 4A). Because high CO_2 and low O_2 could inhibit PG at the transcription level (Zhou et al., 2000), pectic substances involved in cell adhesion under normal atmosphere become soluble, and the cell separate easily, thereby weakening the strength of tissue. Similarly, previous studies on cell wall analyses suggested that CO_2 treatment declined the proportion of pectin that is water-soluble, and increased the proportion that is ionically embedded in the cell wall matrix (Goto, Goto, Chachin, & Iwata, 1995; Siriphanich, 1998), as a result, CO_2 treatment enhanced the strength of cell-to-cell bonds in fruit (Harker, Elgar, Watkins, Jackson, & Hallett, 2000).

Another factor that can influence the strength of fruit tissue is the turgor or pressure of the cell. Turgor has the effect of failure stressing of the cell wall and the consequence of this stressing depends on whether compressive or tensile loads are applied. When the tissues are subjected to tensile testing, turgor tends to harden the cell wall and a higher force is required to achieve cell wall rupture. In the current study, the FDF also decreased with reducing turgor in AZs (Fig. 4C), which was consistent with the findings of De Baerdemaeker, Segerlind, Murase, and Merva (1978), who found that the tensile strength of the cell wall, unlike compressive strength, increases with increasing water potential, and hence with increasing turgor potential. The declined turgor in tissue may be attributed to degradation of biological membranes upon ripening and senescence (Marangoni, Palma, & Stanley, 1996). An increase in membrane permeability allows water to move out of the cell, thereby resulting in a decrease in cellular, and therefore tissue, turgor. Therefore, tissue strength and bruise susceptibility are predicted to depended on the cell wall strength and cell turgidity. During storage, the loss water of AZs in grape fruits caused turgidity and turgor to decrease, and this reduced load-bearing capacity of tissue. In contrast to CA storage, the AZs of air-stored grapes appeared larger weight loss (data not shown), which was due to the fact that a large amount of symplastic water was lost through the apoplast to ambient. The effects of atmospheric constituents on cell turgor are statistically significant ($P < 0.05$). The present results demonstrated that the model value of symplastic water in AZs was lower in air than in CA (data not shown). De Smedt et al. (2002) also observed that the symplastic water concentrations of apples stored in air exhibited more significant loss than those of fruits kept in CA. Low O_2 and high CO_2 concentrations could inhibit respiration and decreased ethylene production, thus delaying ripening and senescence. Further research has shown that, in broccoli, CA storage retarded changes in phospholipid levels and free sterol:phospholipid ratios (Makhlouf, Willemot, Couture, Arul, & Castaigne, 1990) and also hindered any loss of membrane fluidity (Deschene, Paliyath, Lougheed, Dumbroff, & Thompson, 1991). High CO_2 may cause changes in pH (Harker et al., 2000) that can influence the membrane itself as well as the normal functioning of membrane-bound enzymes. These results could explain the differences in cell turgor between air storage and CA storage.

In addition, the structural arrangement in the tissue, such as, number of cells per unit volume, spatial distribution of cells, cell size and shape, as well as tissue dimensions will also significantly influence the tensile strength and the elastic modulus of tissue.

6. Conclusion

In this paper a simplified model was presented, which was capable of predicting the berry drop of *Kyoho* grapes during storage. The changes in cellulose, middle lamella pectin and turgor in grape AZs were high correlated with FDF and berry drop of grapes. The resulting models gave an of R^2 of 0.9592 and E of 4.291% for air storage and R^2 of 0.9649 and E of 2.41% for CA storage, which indicated that the simulation results shows a good fit to the experimental FDF data under all storage conditions. CA storage of grape fruits maintained a higher FDF and a lower berry drop than fruits stored in normal air due to an inhibitory effect of CA on loss in the integrity of plasmalemma, respiration, and degradations of cellulose and pectin.

However, a few experimental data were available to verify the feasibility and fitting quality of the model. More observation data would be needed to validate all assumptions of the development of the model. The reaction rate constant and water diffusion coefficient are generally considered to be dependent on temperature. In this model, the storage time is only independent variable, while the temperature and air compositions are assumed a constant and optimal for the storage of grapes. Further research is required to better understand and characterize the contribution of storage conditions to tensile strength of AZs. This makes the model suitable for use in cold-chains with any possibly occurring temperature trajectory and atmospheric constituents, etc.

Acknowledgement

This work was financed by Ministry of Science and Technology of China (Project no. 2004BA527B).

References

Abu-Goukh, A. A., & Bashir, H. A. (2003). Changes in pectic enzymes and cellulase activity during guava fruit ripening. *Food Chemistry, 83*, 213–218.

Artés-Hernández, F., Aguayo, E., & Artés, F. (2004). Alternative atmosphere treatments for keeping quality of 'Autumn seedless' table grapes during long-term cold storage. *Postharvest Biology and Technology, 31*, 59–67.

Blumenkrantz, N., & Asboe-Hansen, G. (1973). New method for quantitative determination of uronic acids. *Analytical Biochemistry, 54*(2), 484–489.

Bonghi, C., Casadoro, G., Ramina, A., & Rascio, N. (1993). Abscission in leaf and fruit explants of *Prunus persica* (L) Batsch. *New Phytologist, 123*, 555–565.

Bonghi, C., Rascio, N., Ramina, A., & Casadoro, G. (1992). Cellulase and polygalacturonase involvement in the abscission of leaf and fruit explants of peach. *Plant Molecular Biology, 20*, 839–848.

Boquet, R., Chirife, J., & Iglesias, H. A. (1978). Equations for fitting water sorption isotherms of foods. II. Evaluation of various two-parameter models. *Journal of Food Technology, 13*, 319–327.

Chen, F. H., Wu, G. B., Feng, Z. S., & Zhang, W. Y. (2003). The relation of grape berry abscission to changes of enzyme activity in abscission zone and plant growth regulators during storage. *Journal of Plant Physiology and Molecular Biology, 29*(2), 133–140.

Chen, F. H., Yu, X., Zhang, W. Y., & Tan, D. Y. (2000). Study on relationship between pedicel structure and berry abscission of '*xinjiang wuhebai*' grape cultivars. *Journal of Xinjiang Agricultural University, 23*(1), 44–48.

De Baerdemaeker, J., Segerlind, L. J., Murase, H., & Merva, G. E. (1978). Water potential effect on tensile and compressive failure stresses of apple and potato tissue. *ASAE* paper No. 78-3057.

del Campillo, E., & Bennett, A. B. (1996). Pedicel breakstrength and cellulase gene expression during tomato flower. *Plant Physiology, 111*, 813–820.

Deng, Y., Wu, Y., & Li, F. L. (2005). Changes in firmness, cell wall composition and cell wall hydrolases of grapes stored in high oxygen atmospheres. *Food Research International, 38*, 769–776.

Deschene, A., Paliyath, G., Lougheed, E. C., Dumbroff, E. B., & Thompson, J. E. (1991). Membrane deterioration during postharvest storage of broccoli florets; modulation by temperature and controlled atmosphere storage. *Postharvest Biology and Technology, 1*, 19–31.

De Smedt, V., Barreiro, P., Verlinden, B. E., Veraverbeke, E. A., De Baerdemaeker, J., & Nicolaï, B. M. (2002). A mathematical model for the development of mealiness in apples. *Postharvest Biology and Technology, 25*, 273–291.

González-Carranza, Z. H., Lozoya-Gloria, E., & Roberts, J. A. (1998). Recent developments in abscission: shedding light on the shedding process. *Trends in Plant Science, 3*(1), 10–14.

Gorny, J. R., & Kader, A. A. (1996). Controlled-atmosphere suppression of ACC synthase and ACC oxidase in 'Golden Delicious' apple during long-term cold storage. *Journal of the American Society for Horticultural Science, 121*, 751–755.

Goto, T., Goto, M., Chachin, K., & Iwata, T. (1995). Effects of high carbon dioxide with short term treatment on quality of strawberry fruits. *Journal of the Japanese Society for Food Science, 42*, 176–182.

Harker, F. R., Elgar, H. J., Watkins, C. B., Jackson, P. J., & Hallett, I. C. (2000). Physical and mechanical changes in strawberry fruit after high carbon dioxide treatments. *Postharvest Biology and Technology, 19*, 139–146.

Harker, F. R., Redgwell, R. J., Hallett, I. C., Murray, S. H., & Carter, G. (1997). Texture of fresh fruit. *Horticultural Reviews, 20*, 121–224.

Henderson, J., Davies, H. A., Heyes, S. J., & Osborne, D. J. (2001). The study of a monocotyledon abscission zone using microscopic, chemical, enzymatic and solid state 13^{C} CP/MAS NMR analyses. *Phytochemistry, 56*, 131–139.

Hertog, M. L. A. T. M., Tijskens, L. M. M., & Hak, P. S. (1997). The effects of temperature and senescence on the accumulation of reducing sugars during storage of potato tubers: a mathematical model. *Postharvest Biology and Technology, 10*, 67–79.

John, W., Downton, S., & Hawker, J. S. (1981). Enzymes of starch metabolism in leaves and berries of *Vitis vinifera*. *Photochemistry, 12*(7), 1557–1563.

Kaymak-Ertekin, F., & Gedik, A. (2005). Kinetic modelling of quality deterioration in onions during drying and storage. *Journal of Food Engineering, 68*, 443–453.

Lv, C. W., Xiu, D. R., & Ma, Y. S. (1994). Countermeasure and analysis of obstacle to storage of 'Kyoho' grapes. *Tianjian Agricultural Science, 3*, 8–11.

Makhlouf, J., Willemot, C., Couture, R., Arul, J., & Castaigne, F. (1990). Effect of low temperature and controlled atmosphere storage on the membrane lipid composition of broccoli flower buds. *Scientia Horticulturae, 42*, 9–19.

Marangoni, A. G., Palma, T., & Stanley, D. W. (1996). Membrane effects in postharvest physiology. *Poshtharvest Biology and Technology, 7*, 193–217.

Mcmanus, M. T. (1994). Peroxidases in the separation zone during ethylene-induced bean leaf abscission. *Phytochemistry, 35*, 567–572.

Murase, H., Merva, G. E., & Segerlind, L. J. (1980). Variation of Young's modulus of potato as a function of water potential. *Transactions of the ASAE, 23*(3), 794–796, 800.

Nobel, P. S. (1991). *Physicochemical and environmental plant physiology*. New York: Academic Press.

Ou, Y., Cao, Z. C., Guo, A. M., Mao, Q. C., & Yuan, T. L. (1996). Effects of spraying calcium IAA before harvest on the physiological characters and storage ability of table grape. *Southwest China Journal of Agricultural Science, 9*(3), 110–115.

Peterson, M., Sander, L., Child, R., Van Onckelen, H., Ulvskov, P., & Borkhardt, B. (1996). Isolation and characterization of a pod dehiscence zone-specific polygalacturonase from *Brassica napus*. *Plant Molecular Biology, 31*, 517–527.

Pitt, R. E. (1982). Models for the rheology and statistical strength of uniformly stressed vegetative tissue. *Transactions of the ASAE, 25*(6), 1776–1784.

Roberts, J. A., Whitelaw, C. A., Gonzalez-Carranza, Z. H., & Mcmanus, M. L. (2000). Cell separation processes in plants-models, mechanisms and manipulation. *Annals of Botany, 86*, 223–235.

Rojas, A. M., Gerschenson, L. N., & Marangoni, A. G. (2001). Contributions of cellular components to the rheological behaviour of kiwifruit. *Food Research International, 34*, 189–195.

Rotstein, E., & Cornish, A. R. H. (1978). Influence of cellular membrane permeability on drying behavior. *Journal of Food Science, 43*, 926–934, 939.

Sajnin, C., Gerschenson, L. N., & Rojas, A. M. (1999). Turgor pressure in vegetable tissues: comparison of the performance of incipient plasmolysis technique using mannitol and polyethylenglycol. *Food Research International, 32*, 531–537.

Siriphanich, J. (1998). High CO_2 atmosphere enhances fruit firmness during storage. *Journal of the Japanese Society for Horticultural Science, 67*, 1167–1170.

Tabuchi, T., Ito, S., & Arai, N. (2000). Structural changes in the abscission zones of pedicels at different ripening. *Journal of the Japanese Society for Horticultural Science, 69*(6), 705–707.

Taylor, J. E., & Whitelaw, C. A. (2001). Signals in abscission. *New Phytologist, 151*, 323–339.

Toole, G. A., Smith, A. C., & Waldron, K. W. (2002). The effect physical and chemical treatment on the mechanical properties of the cell wall of the alga *Chara corallina*. *Planta, 214*, 468–475.

Trueman, S. J., Richards, S., McConchic, C. A., & Turnbull, C. G. N. (2000). Relationships between kernel oil content, fruit removal force and abscission in macadamia. *Australian Journal of Experimental Agriculture, 40*, 859–866.

Waldron, K. W., Smith, A. C., Ng, A., Parr, A. J., & Parker, M. L. (1997). New approaches to understanding and controlling the effects of cell separation on fruit and vegetable texture. *Trends in Food Science and Technology, 8*, 213–221.

Wu, W. H. (2003). *Plant physiology*. Beijing: Science Press.

Wu, N. Q., & Pitts, M. J. (1999). Development and validation of a finite element model of an apple fruit cell. *Postharvest Biology and Technology, 16*, 1–8.

Wu, Y. M., Ren, J. C., Hua, X. Z., & Liu, Y. (1992). Postharvest berry abscission and storage of grape fruit. *Acta Phytophysiologica Sinica, 18*(3), 267–272.

Zhang, Y. L., Li, H., Chen, J. P., Liu, Q. H., Xiao, Y. P., & Zhang, B. S. (2000). Studies on the relationship among the change of ABA content, the development of abscission layer and the rate of dropping berry after harvest in grape. *Acta Horticulturae Sinica, 27*(6), 396–400.

Zhou, H. W., Lurie, S., Amnon, L., Andrei, K., Lillian, S., & Ben-Arie, R. (2000). Delayed storage and controlled atmosphere storage of nectarines: two strategies to prevent wolliness. *Postharvest Biology and Technology, 18*, 133–141.