OSCILLATING PRESSURE STORAGE AND GAS EXCHANGE IN APPLE FRUIT[1]

ADONAI GIMENES CALBO[2] and NOEL F. SOMMER[3]

ABSTRACT - An oscillating pressure storage system that is adapted to fruits and vegetables having low mass air flow resistance, is proposed. Periodic variations in air pressure induces high rates of gas exchange and reduces the internal level of ethylene. Apple (*Malus domestica* Borkh) fruit was used as the model commodity because it has a large intercellular volume and low mass air flow resistance. Frequency of 1 cycle/min and maximum pressure (P_i) to minimum pressure (P_f) reduction ratios $[(P_i - P_f)/P_i)]$ of 0.22 and 0.34, were tested in two storage trials. Oscillating pressure storage extended the preclimacteric life and decreased the rate of ethylene evolution from 'Gravenstein' and 'Granny Smith' apple. The pressure reduction ratio of 0.34 was more effective than 0.22. The effects of elevated CO_2 and oscillating pressure were additive. The potentiality of oscillating pressure as a substitute for the hypobaric storage is discussed.

Index terms: *Malus domestica*, controlled atmosphere, hypobaric storage.

ARMAZENAMENTO EM PRESSÃO OSCILANTE E TROCAS GASOSAS NA MAÇÃ

RESUMO - Propõe-se um sistema de pressão oscilante para frutos e vegetais com baixa resistência ao influxo ou efluxo de ar induzido pela aplicação de gradientes de pressão foi proposto. Maçã (*Malus domestica* Borkh) foi utilizada como produto modelo porque possui elevada percentagem de volume intercelular e baixa resistência aos fluxos de ar induzidos por gradientes de pressão. A freqüência de 1 ciclo/min e as relações de redução de pressão $[(P_i - P_f)/P_i)]$ de 0,22 e 0,34 foram utilizadas com e sem a adição de CO_2. Na relação de redução de pressão P_i e a pressão máxima e P_f é a pressão mínima em cada ciclo. Pressão oscilante estendeu a vida préclimática e reduziu a evolução de etileno da maçã nas cultivares 'Gravenstein' e 'Granny Smith'. A relação de redução de pressão de 0,34 foi mais efetiva que 0,22. Os efeitos de pressão oscilante e nível alto de CO_2 foram aditivos. Discute-se o potencial de uso de pressão oscilante como um substituto para o armazenamento hipobárico.

Termos para indexação: *Malus domestica*, atmosfera controlada, armazenamento hipobárico.

INTRODUCTION

Greater rates of mass transfer occur because of pressure gradients, than by diffusion, consequently the long distance transport in the xylem and floem are driven by pressure gradients (Nobel 1970). In the gas phase of plants mass flow can also occur when the tissues are submitted to artificial pressure gradients (Calbo 1985, Calbo & Sommer 1987, Devaux 1891) or even small natural pressure gradients caused by wind, diurnal changes in temperature and vapor pressure. As a working hypothesis it can be suggested that artificial pressure gradients could be used to increase the rate of gas exchange to reduce the intercellular concentration of ethylene and to delay repening in climacteric fruits.

The physiological effect of CO_2, O_2 and ethylene is a function of the internal concentration of those gases (Burg & Burg 1969, Thimann et al. 1954, Willians & Patterson 1962). The internal concentration of a component is equal to its external concentration, plus a gradient between the internal and the external atmospheres (Burton 1974, Claypool 1938). In a steady state condition this gradient is a function of the internal resistances to diffusion and the rate of production or consumption of the component (Burton 1974, 1982). Controlled atmospheres, with low O_2 or high CO_2, or both, along with low temperatures have been used to delay ripening and senescence (Burton 1982, Hulme 1971). Low CO_2 inhibits ethylene synthesis and action (Burg & Burg 1969, Willians & Patterson 1962), while CO_2 is a

---

[1] Accepted for publication on October 16, 1986.
Parte da tese do primeiro autor, desenvolvida no Departamento de Pomologia da Universidade da Califórnia em Davis, EUA.

[2] Eng. - Agr., Ph.D., EMBRAPA/Centro Nacional de Pesquisa Agropecuária (CNPH), Caixa Postal 07.0218, CEP 70359 Brasília, DF.

[3] Eng. - Agr., Ph.D., Prof., Department of Pomology, University of California, Davis CA 95616, USA.

competitive inhibitor of ethylene action (Chadwick & Burg 1967, Yang 1985). Hypobaric storages is based on the inverse relation between the velocity of diffusion (dN/dt) and the air pressure (P) for the same gradient of concentration (dC/dx). The Ficks first law states that dN/dt = D.dC/dx, where D, the diffusity coefficient (Moore 1972) is the ratio between the gas viscosity and pressure (D = NP). Large diffusity values at low pressures cause a reduction in the internal concentration of ethylene, making the use of low levels of O_2 very effective (Burg & Burg 1966). Hypobaric storage, however, requires a very strong and costly storage containers (Lougheed et al. 1978).

The objective was to test oscillating pressure storage as a technique to reduce the internal concentration of ethylene and delay ripening in 'Gravenstein' and 'Granny Smith' apple. Oscillating pressure was devised to increase the rates of gas exchange by pumping air in and out of the intercellular spaces of fruits and vegetables, with the use of periodic alternation of the gas pressure between two chosen levels during the entire storage period.

MATERIALS AND METHODS

Apple (*Malus domestica* Borkh) was chosen for studies of oscillating pressure storage because the large intercellular volume of this fruit permits the use of low oscillating pressure frequencies to reduce the internal level of ethylene (Calbo 1985). Preclimacteric 'Gravenstein' (Soluble solids equal to 10.14 ± 0.09 and firmness with a 8 mm tip equal to 41.10 ± 0.60) and 'Granny Smith' apples (Soluble solids equal to 9.63 ± 0.19 and firmness equal to 9.08 ± 0.19) were harvested during the 1984 season from commercial orchards near Sebastipol and Bakersfield and transported in the same day to the Pomology Postharvest Research Laboratory at the Univ. of California at Davis, where they were cooled to 10°C overnight. The fruits were then sorted for uniformity and obvious defects, randomized and grouped into the experimental units. The storage temperature of 10°C was chosen to reduce the experimental period.

Oscillating pressure experiments

Three gas exchange treatments were applied to 'Gravenstein' apples in an experiment with three replicates started on July 22, 1984. The experimental unit was a chamber having 10 randomly selected fruits. Gas flux was about 12 liter . kg^{-1} . h^{-1}. Fruits kept in air at ambient pressure were the controls. A frequency of 1 cycle . min^{-1} was used for both oscillating pressure treatments. The first oscillating pressure treatment used a pressure reduction ratio $[(P_i - P_f)/P_i)]$ of 0.22 ($P_i = 1.08.10^5 N/m^2$ and $P_f = 0.84.10^5 N/m^2$), where P_i is the maximum pressure and P_f is the minimum pressure in each oscillating pressure cycle. The second oscillating pressure treatment used a pressure reduction ratio of 0.34 ($P_i = 1.08.10^5 N/m^2$ and $P_f = 0.72.10^5 N/m^2$). Those pressure reduction ratios were used to test the interaction between 8% CO^2 and the increased rates of gas exchange in 'Granny Smith' apples in an experiment started on October 2, 1984.

Oscillating pressure apparatus

Fig. 1 illustrates the experimental apparatus used to study oscillating pressure storage. The frequency of change between high and low pressures is established by a repeating cycle clock. The pressure limits are set in the barostats or in an equivalent arrangement of pressure-relief valves. Pressure variations were transmitted to the fruits by plastic expansion bags which permitted each commodity chamber to be treated with a different controlled atmosphere mixture. A constant flow source was used to introduce air into the commodity chamber (Fig. 2). The constant flow source was made of a differential flow controlling valve fed by a constant

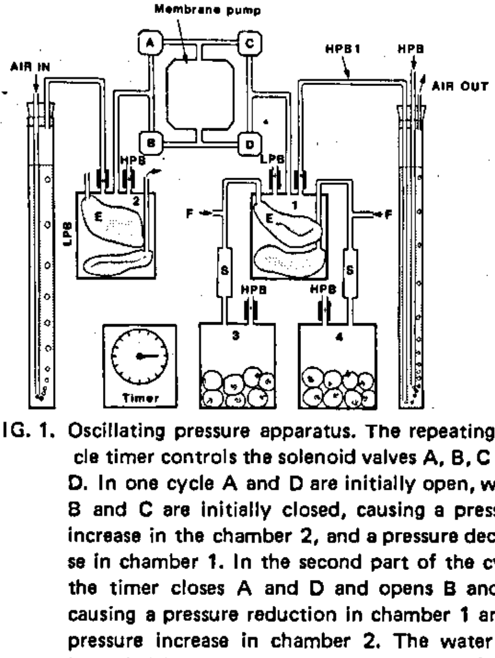

FIG. 1. Oscillating pressure apparatus. The repeating cycle timer controls the solenoid valves A, B, C and D. In one cycle A and D are initially open, while B and C are initially closed, causing a pressure increase in the chamber 2, and a pressure decrease in chamber 1. In the second part of the cycle the timer closes A and D and opens B and C, causing a pressure reduction in chamber 1 and a pressure increase in chamber 2. The water column height in the low pressure barostat (LPB) and high (HPB) pressure barostat was used to set the minimal and maximal pressure limits, for chambers 3 and 4. HPB1 is a tube set at least 10 cm deeper than HPB, in the high pressure barostat, to assure that the bags became completly empty in the high pressure part of the cycle. F is a constant flow source, E is the expansion bag and S is a purafil scrubber, while ( ) indicate unidiretional valve.

pressure source. That constant pressure was provided by a pressure relief valve fed by a high pressure source. Fig. 2 also shows the unidirectional valve.

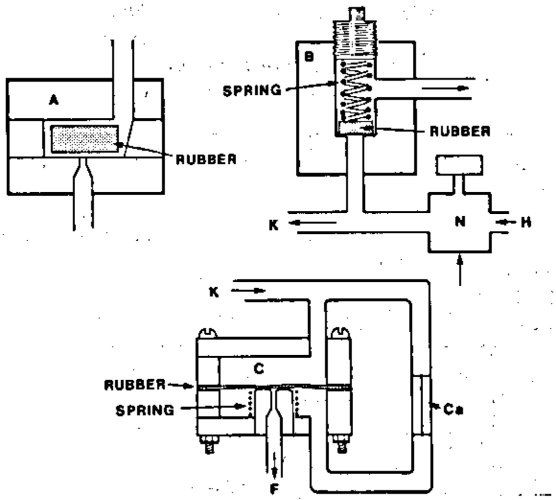

FIG. 2. Valves made of acrilic glued parts. A - unidirectional valve, B - pressure release valve, C - differential flow controlling valve, F - constant flow outlet, H - high pressure inlet, K - constant pressure source, N - needle valve, and Ca - capillary.

The following aspects were considered in the construction of the oscillating pressure apparatus: First, the volume of the expansion bag (V_b) should be proportional to the volume of the commodity chamber (V_c) and the difference between the maximum pressure (P_i) and the minimum pressure (P_f), was according to the expression $V_b > V_c \cdot (P_i - P_f)/P_i$. The expansion bag should not become completely full, nor press the controlling chamber wall, or another expansion bag because the fruits would not receive the desired low pressure. Second, the membrane pump should be capable of delivering a flow (F), much larger than the minimum necessary. That permits future increases in the frequency, or in the pressure reduction ratio. At a frequency (f), the minimal amount of flow necessary to drive the oscillating pressure to a number of chambers (n) is given by the expression $F = 2.n. (V_c + V_b/2) . f. (P_i - P_f)/P_i$, where V_c is the volume of a controlling chamber.

The following procedure was used for a preliminary test of the oscillating pressure system (Fig. 1). Close all the chambers; being sure that the high pressure barostat 1 (HPB1) is at least 10 cm deeper than the high pressure barostat (HPB). Turn on the clock operated valves. Turn on the membrane pump. The expansion bag should become completely empty in the high pressure part of the cycle. Check if air is bubbling in the low pressure barostat (LPB) and in HPB1, twice in each cycle. Connect a manometer to each commodity chamber to verify that the desired pressure oscillation limits are being obtained. Leakage in the commodity chambers or underestimation of the expansion bag volume are potential sources of deviation. Finally, introduce a gas mixture of known concentration using the constant flow apparatus (Fig. 2). The air should begin to bubble through HPB. Measure the gas concentration in the commodity chambers outlet. If the air is bubbling through HPB, and the outlet concentration is equal to the inlet concentration, then the system can be considered free of leaks, and ready for use.

Measurements

Gas was collected in 12 ml syringes for measurements of ethylene and CO_2. The rate of ethylene production was periodically measured using a Carle Analytical Gas Chromatograph Model 211 with a flame ionization detector. The internal concentration of CO_2, at the end of the experiment, was measured using another similar gas chromatograph equipped with a thermal conductivity detector.

The resistance to gas exchange, as well as the flesh firmness and the external color were measured at the end of the experiment. The resistance to gas exchange, was estimated as the ratio between the internal concentration of ethylene and its rate of production (Burg & Burg 1962). The internal atmosphere was vacuum extracted from fruits immersed in water, underneath a funnel closed by a sealing serum rubber cap (Bussel & Maxie 1965). After vacuum extraction (10,600 N/m^2) of 1 min, the air accumulated at the top of the funnel was removed with a syringe for measurement of ethylene or CO_2. Fruit firmness was measured with an Effegi penetrometer with a 8 mm tip. External color was measured using the Rd, a and b modes of the Gardner Color Difference Meter (CDM) Model XL-23 calibrated with a white reference plate (X = 18.7, Y = 84.1 and Z = 97.9).

RESULTS

Oscillating pressure storage caused a small delay in the onset of the climacteric rise of 'Gravenstein' apple (Fig. 3). This effect was more evident at the pressure reduction ratio of 0.34. Besides delaying the climacteric rise, the increased gas exchange also caused a large reduction in the rate of ethylene evolution. This effect was more evident at the pressure reduction ratio of 0.34, than at the pressure reduction ratio of 0.22. To evaluate the efficiency the gas exchange improvement, induced by oscillating pressure, measurements of internal concentration of ethylene and CO_2 were made. Oscillating pressure caused a reduction in the internal concentration of ethylene and CO_2 and lowered the resistance to gas exchange (Table 1). Oscillating pressure, however, did not improve the retention of firmness or color of 'Gravenstein' apples (Table 2).

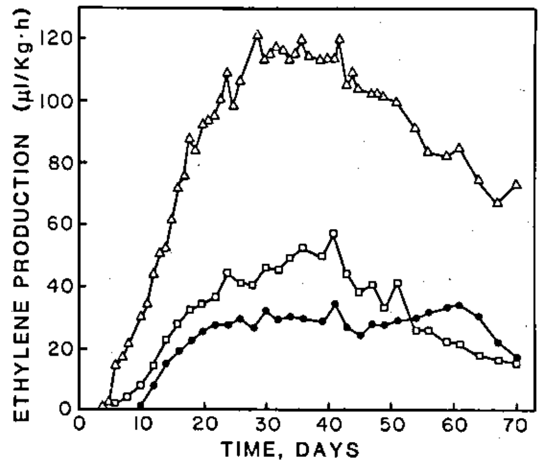

FIG. 3. Ethylene production by 'Gravenstein' apples stored at 10^{o}C in air at ambient pressure, and in oscillating pressure storage using a frequency of 1 cycle.min^{-1}, and pressure reduction ratios of 0 (Δ), 0.22 (□) and 0.34 (●). Analysis of variance yielded F values of 55.42 for pressure reduction ratio (df = 2), 1476.37 for time for time (df = 28), and 9.12 for the interaction (df = 56). These F values are significant at $P < 0.01$.

TABLE 1. Internal concentration of CO_2 (ml. liter^{-1}), ethylene µl . liter^{-1} and resistance to gas exchange [(µl . liter^{-1})/(µl . kg^{-1} . h^{-1})] of 'Gravenstein' apples. Storage was at 10^{o}C for 70 days in ambient pressure or in oscillating pressure storage using a frequency of 1 cyle . min^{-1}, and pressure reduction ratios of 0.22 and 0.34.

Pressure reduction ratio	Internal concentration		Resistance to gas exchange	
	CO_2	C_2H_4	CO_2	C_2H_4
0 (Control)	42.6 a	376.1 a	5.37 a	5.18 a
0.22	15.3 b	40.5 b	3.48 b	2.54 b
0.34	12.0 b	27.8 b	1.7 c	1.58 b

Mean separation in column by LSD at 5% level.

TABLE 2. Penetration force in newtons using a penetrometer with an 8 mm tip and reflected color (CDM "a" and "b" values) of 'Gravenstein' apple. Storage was at 10^{o}C for 70 days under ambient pressure or under oscillating pressure, using a frequency of 1 cycle/min and pressure-reduction ratios of 0.22 and 0.34.

Pressure reduction ratio	Color		Penetration force (N)
	a	b	
0 (Control)	- 5.77 a	51.9 a	25.4 a
0.22	- 4.29 a	52.1 a	22.8 b
0.34	- 5.57 a	52.2 a	23.1 ab

Mean separation in column by LSD test at 5% level.

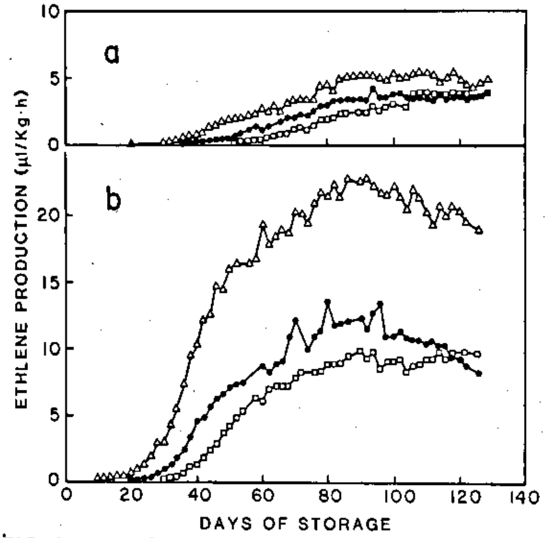

FIG. 4. Rate of ethylene production by 'Granny Smith apple stored at 10^{o}C in air (a) or in 8% CO_2 (b), at the ambient pressure (Δ) and in oscillating pressure storage, using a frequency of 1 cycle.min^{-1} and pressure reduction ratios of 0.22 (●) and 0.34 (□).

If CO_2 is a competitive inhibitor of ethylene action, its parallel reduction would offset the benefits of lowering the ethylene concentration. In an experiment with 'Granny Smith' apples, CO_2 was added to study this interaction. Fig. 4 shows that in air 'Granny Smith' apples behaved similarly to 'Gravenstein' apples. The time to reach an ethylene production rate of 0.2µl.kg^{-1}.hr^{-1} was used as an arbitrary indication of the end of the onset of the climacteric rise. The presence of high CO_2 delayed the climacteric rise. The effects of oscillating pressure and high CO_2 were additive in extending the preclimacteric period in 'Granny Smith' apple, since the statistical interaction between the effects of pressure reduction ratio and CO_2 was not significant. Table 3 shows the reduction in the internal concentration of ethylene and in the resistance to gas exchange caused by

TABLE 3. Internal concentration of ethylene and resistance to ethylene exchange $[(\mu l.liter^{-1})/(\mu l.kg^{-1}.h^{-1})]$ of 'Granny Smith' apples. Storage was at 10°C for 154 days, in ambient pressure or in oscillating pressure storage using a frequency of 1 cycle . min^{-1}, and pressure reduction ratios of 0.22 and 0.34.

Treatment		Internal C_2H_4 l/liter	Resistance to C_2H_4 exchange
Pressure reduction ratio	+ CO_2 level		
0 (Control)	+ 0.0	349.5	15.2
0.22	+ 0.0	141.3	13.4
0.34	+ 0.0	142.0	10.0
0	+ 8.0	56.3	9.2
0.22	+ 8.0	46.3	8.3
0.34	+ 8.0	42.8	4.9

TABLE 4. Penetration force in newtons using a 8 mm tip and reflected color (CDM "a" and "b" values) of 'Granny Smith' apples. Storage was at 10°C for 154 days at ambient pressure or in oscillating pressure using a frequency of 1 cycle . min^{-1}, and pressure reduction ratios of 0.22 and 0.34.

Treatment		Color		Penetration force (N)
Pressure reduction ratio	+ CO_2	a	b	
0 (Control)	+ 0.0	- 7.7	34.7	30.2
0.22	+ 0.0	- 8.2	35.0	22.5
0.34	+ 0.0	- 8.9	33.5	39.0
0	+ 8.0	- 12.1	29.4	27.7
0.22	+ 8.0	- 12.6	29.7	38.3
0.34	+ 8.0	- 14.7	29.4	41.9

oscillating pressure and high CO_2. The reduction in the resistance to ethylene exchange in presence of high CO_2 is possibly due to a large delay in ripening.

Oscillating pressure and CO_2 delayed chlorophyll degradation (Table 4). When CO_2 and oscillating pressures were used together, their effects were additive, with a non significant interaction (Table 5). For firmness the pressure reduction ratio of 0.22 caused a decrease in the fruit penetration force, while a pressure reduction ratio of 0.34 caused an increase in the penetration force. High CO_2 at the ambient pressure caused no improvement in the retention of fruit firmness but some of the fruits showed symptoms of CO_2 toxicity, localized browned areas. Those symptoms were not caused by low O_2 injury since the O_2 levels were about 19%. The fruit in oscillating pressure were firmer in the presence of high CO_2.

DISCUSSION

The cumulative physiological effect (E) of ethylene can be represented by Eq. [1] (Burg & Burg 1962, Peacock 1972):

$$E = k \,.\, t \,.\, \log [C_2H_4], \qquad [Eq. 1]$$

where k is a constant and t is the time of exposure to ethylene. This expression indicates that the

TABLE 5. Analysis of variance for rate of C_2H_4 evolution, internal concentration of ethylene (C), resistance to ethylene exchange (R), penetration force, refleted color a and b during the storage of 'Gravenstein' apple ins oscillating pressure.

Source of variation	df	F value Ethylene evolution	df	F value C	R	firmness	a	b
Pressure reduction ratio (A)	2	55.42**	2	55.36**	32.63**	6.12*	6.18*	3.75
Time (B)	28	1476.37**	-	-	-	-	-	-
A x B	56	9.12**	-	-	-	-	-	-
Error	174	-	6	-	-	-	-	-

*, ** Significant at $P < 0.05$ and $P < 0.01$, respectively.

internal concentration of ethylene needs to be substantially increased to result in a detectable physiological effect. Eq. [1] does not consider the inhibitory effect of the CO_2 on ethylene action (Chadwick & Burg 1967), that occurs in fruits.

The internal concentration of ethylene and CO_2 in the apple fruit is mainly a function of the rates of production and the resistance of the skin to diffusion (Burton 1982). The half life ($t\tfrac{1}{2}$) of the residence of a molecule inside the fruit, as a function of the resistance of the skin to diffusion (R) and the intercellular air volume (V_i) is presented in Eq. [2] (Calbo 1985).

$$R = t\tfrac{1}{2} / V_i \,.\, \mathrm{Ln}\ 2 \qquad [\text{Eq. } 2]$$

A mass air flow (F) that gives an ethylene or CO_2 molecule a residence $t_{1,2}$ equivalent to the diffusion $t\tfrac{1}{2}$ for the same commodity, can be calculated using Eq. [3].

$$F = V_i / 2 \,.\, t\tfrac{1}{2} \qquad [\text{Eq. } 3]$$

The maximum mass air flow that can be induced by a oscillating pressure system working between the pressures P_i and P_f at the frequency f is:

$$F = V_i \,.\, f \,.\, (P_i - P_f)/P_i \qquad [\text{Eq. } 4]$$

Eq. [2], [3] and [4] can be combined, to calculate the minimum expected oscillating pressure $t\tfrac{1}{2}$ [Eq. 5], or the minimum expected oscillating pressure resistance [Eq. 6].

$$t\tfrac{1}{2} = P_i / 2 \,.\, f \,.\, (P_i - P_f) \qquad [\text{Eq. } 5]$$

$$R = P_i / f \,.\, (P_i - P_f) \,.\, V_i \,.\, \mathrm{Ln}\ 4 \qquad [\text{Eq. } 6]$$

The use of oscillating pressure has some biological and physical limitations that make the system less efficient than predicted by Eq. [6]. First, commodity barriers to mass air flow (Calbo 1985, Calbo & Sommer 1987) places an upper limit on the frequency. Second, the system efficiency is a function of how readily the newly-pumped air mixes with the internal atmosphere during each cycle.

The minimal expected mass air flow resistance from an apple fruit (V_i = 0.2 liter kg^{-1}) in an oscillating pressure storage (f = 60 cycles . min^{-1}, $P_i = 1.08.10^5\ N/m^2$ and $P_f = 0.84 . 10^5\ N/m^2$), according to Eq. [5], is 0.273 [($\mu l . liter^{-1}$)/($\mu l . kg^{-1} . hr^{-1}$)]. The observed R values were more than 10 times larger than this calculated minimal resistance, indicating that mixing was poor in the internal atmosphere. This poor mixing indicates that a laminar flow, without any turbulence, should be occurring in the intercellular spaces. The observed resistance values of apples stored in oscillating pressures, may be a reflection of resistance to diffusion in the flesh because ethylene-free air beneath the cuticle was constantly renewed by pressure oscillations.

The concentration of ethylene inside 'Gravenstein' and 'Granny Smith' apples was greatly reduced by oscillating pressure, but still the internal ethylene concentration was large enough to cause physiological response. Ethylene removal was paralleled by a delay in the onset of the climacteric rise in ethylene production in those fruits. The high rates of gas exchange alone, however, had only a minor effect on the retention of color and firmness of 'Granny Smith' apples, and had a non significant effect in 'Gravenstein' apples. Such a small physiological effect could be interpreted in terms of Eq. 1, and the parallel reduction of the internal CO_2 concentration. This reduction partially offset the benefits of ethylene removal because CO_2 is a competitive inhibitor of ethylene action (Chadwick & Burg 1967). The onset of the climacteric rise in ethylene production was greatly delayed and a large improvement in the retention of color and firmness occurred, when 'Granny Smith' apples were stored in oscillating pressure with a high level of CO_2. Fruits in 8% CO_2 at atmospheric pressure, however, eventually presented internal browned areas as a symptom of CO_2 injury. The absence of CO_2 injury symptoms in fruits from oscillating pressure storage is an indication that the internal CO_2 was reduced.

For fruits which have a large intercellular air volume and low resistance to mass air flow oscillating pressure could be an alternative to hypobaric storage since it can also be used to

TABLE 6. Analysis of variance for internal concentration of C_2H_4, storage preclimacteric period, resistance to C_2H_4 exchange, penetration force, reflected color and rate of C_2H_4 production during storage of 'Granny Smith' apple.

Source of variation	df	F value				F value		df	C_2H_4 production rate
		Internal concentration C_2H_4	Storage preclimacteric period	Resistance to C_2H_4 exchange	Penetration force	Refleted color			
						a	b		
Pressure reduction ratio (A)	2	58.18**	10.17**	17.56**	45.70**	4.97*	1.56	2	1476.3**
CO_2 (B)	1	286.81**	28.67**	62.94**	25.28**	89.37**	149.67**	1	7733.4**
Time (C)	-	-	-	-	-	-		60	138.4**
A x B	2	46.41**	0.49	.17	25.78**	.85	.94	2	823.5**
A x C	-	-	-	-	-	-		120	9.6**
B x C	-	-	-	-	-	-		60	60.8**
A x B x C	-	-	-	-	-	-		120	5.2**
Error	12	-	-	-	-	-		732	-

*, ** Significante at $P < 0.05$ and $P < 0.01$, respectively.

reduce the internal concentration of ethylene. Oscillating pressure has some potential advantages over the hypobaric system. First, the containers need not to be so strong, because the gradient between the internal and the external pressures are smaller. Second, it could be a means to permit the use of higher levels of CO_2 than those currently applied in controlled atmosphere storage. Higher CO_2 will further delay ripening and may control some CO_2 sensitive pathogenic fungi (El - Goorani & Sommer 1981). For future commercial applications oscillating pressure could possibly be generated by simple and very energy efficient resonant systems.

CONCLUSIONS

1. Oscillating pressure reduced the internal ethylene concentration and extended the pre--climateric life of apples.

2. Oscillating pressure can substitute the hypobaric storage, with experimental advantages, to induce high rates of gas exchange and yet permits the use of high levels of O_2 and CO_2.

ACKNOWLEDGMENT

We would like to express our gratitude to: Dr. Adel A. Kader and Dr. Mikal E. Saltveit, for the suggestions and critique; Mr. Bob Fortlage, Mr. Richard F. Stalldman and Gene Mayer for his technical assistance.

REFERENCES

BURG, S.P. & BURG, E.A. Fruit storage at subatmospheric pressures. Science, 153:314-5, 1966.

BURG, S.P. & BURG, E.A. Gas exchange in fruits. Physiol. Plant., 18:870-4, 1965.

BURG, S.P. & BURG, E.A. Interaction between ethylene, oxygen and carbon dioxide in the control of fruit ripening. Qual. Plant. Mater. Veg., 19:185-200, 1969.

BURG, S.P. & BURG, E.A. Role of ethylene in fruit ripening. Plant Physiol., 37:179-89, 1962.

BURTON, W.G. Post-harvest physiology of food crops. New York, Longman, 1982. 339p.

BURTON, W.G. Some biophysical principles underlying the controlled atmosphere storage of plant material. Ann. Appl. Biol., 78:149-68, 1974.

BUSSEL, J. & MAXIE, E.C. Gas exchange in 'Bartlett' pears in relation to gamma irradiation. Proc. Am. Soc. Hortic. Sci., 88:151-9, 1965.

CALBO, A.G. Gas exchange in fruits and vegetables and the use of oscillating pressures for storage. Davis, University of California, 1985. 94p. Tese Ph.D.

CALBO, A.G. & SOMMER, N.F. Intercellular volume and resistance to mass air flow of fruits and vegetables. J. Amer. Soc. Hort. Sci., 112(1):131-4, 1987.

CAMERON, A.C. & YANG, S.F. A simple method for the determination of gas diffusion in plant organs. Plant Physiol., 70:21-3, 1982.

CHADWICK, A.V. & BURG, S.P. An explanation of the inhibition of the root growth caused by auxin. Plant Physiol., 42:415-20, 1967.

CLAYPOOL, L.L. Internal gas in fruits as influenced by external treatments. Proc. Am. Soc. Hortic. Sci., 36:371-8, 1938.

DEVAUX, H. Etude experimentale de l'aération des tissus massifs. Introductioñ a l'étude des mecanismes des échanges gazeux chez les plantes aériennes. Ann. Sci. Nat. Bot. Biol. Veg., 14:279-395, 1981.

EL-GOORANI, M.A. & SOMMER, N.F. Effects of modified atmospheres on postharvest pathogens of fruits and vegetables. **Hortic. Rev.**, 3:412-61, 1981.

HULME, A.C. **The biochemistry of fruits and their products.** London, Academic, 1971. v.2.

LOUGHEED, E.C.; MURR, D.P.; BERARD, L. Low pressure storage for horticultural crops. **Hort Science**, 13(1):21-7, 1978.

MOORE, W.J. **Physical chemistry.** London, Prentice-Hall, 1972.

NOBEL, P.S. **Introduction to biophysical plant physiology.** San Francisco, Freeman, 1970.

PEACKOCK, B.C. Role of ethylene in the initiation of fruit ripening. **Queensl. J. Agric. Anim. Sci.**, 29: 137-45, 1972.

THIMANN, K.V.; YOCUM, C.S.; HACKETT, D.P. Terminal oxidases and growth in plant tissues. III. Terminal oxidation in potato tuber tissue. **Arch. Biochem. Biophys.**, 53:239-57, 1954.

WILLIAMS, M.W. & PATTERSON, M.E. Internal atmosphere in 'Bartlett' pears stored in controlled atmosphere. **Proc. Am. Soc. Hortic. Sci.**, 81:129-36, 1962.

YANG, S.F. Biosynthesis and action of ethylene. **Hort-Science**, 20(1):41-5, 1985.