

Respiration & Internal Atmosphere of Avocado Fruit¹

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The relationship between respiration, ripening, and the composition of the internal atmosphere has been studied in several fruits. In the case of the banana (*Musa sapientum*) and the papaya (*Carica papaya*), Wardlaw and Leonard (24, 25) observed the coincidence of the onset of the climacteric rise with the peak in oxygen concentration inside these fruits. With the respiratory rise the oxygen level dropped, reaching very low values of 1% at late stages of senescence. Impressed with the marked changes in the gaseous composition, they suggested that the internal oxygen concentration is the controlling mechanism of the climacteric pattern. Trout et al. (22) reported that in mature apples oxygen deficiency depressed respiration and retarded ripening. Observations on the epidermal layers as the tissue that offers major resistance to gaseous diffusion were made by Trout et al. (22) for the apple and by Clendenning (7) for the tomato. Biale (4) included in his review a brief account of the studies dealing with the internal atmospheres of fruits.

The avocado fruit is distinguished from other fruits by its low fermentative capacity, shown by depression of CO₂ evolution and ripening under anaerobic conditions (3). This study was undertaken, therefore, with the purpose of finding an explanation for the physiological behavior of the avocado in terms of changes in the composition of the internal atmosphere.

Materials & Methods

Fruit of the Hass and Fuerte varieties of avocado (*Persea americana*, Miller) were obtained from the orchard of the Horticultural Science Department for this work.

In describing the stages in the respiratory pattern of the fruit the following terminology is used: pre-peak period, from picking to the respiratory peak; lag period, from picking until the onset of the respiratory rise; climacteric rise, from onset of the respiratory rise until its peak; and postclimacteric, from

the climacteric peak until final breakdown of the fruit.

Fruit respiration was measured by CO₂ absorption in alkali as described by Biale and Shepherd (5) and modified by Biale (3), by the Beckman oxygen analyzer described by Young and Biale (26), and by simultaneous analysis of CO₂ evolution and O₂ uptake in a closed system using the method of Haller and Rose (11), as modified by Platenius (16).

Fruit samples were peeled in each phase of the climacteric history. Precautions against contamination were sufficient when the experiments were carried out under sanitary conditions.

The internal atmosphere of the fruit was studied by a method described by Wardlaw and Leonard (24) and modified by Trout et al. (22). A small area near the stem end of the fruit was sterilized by alcohol. A sterilized cork borer 0.5 cm in diameter was inserted through the mesocarp up to the seed. This cylinder of tissue was replaced by a tube 0.5 cm in diameter and 3 cm long inserted to a distance of 0.5 cm from the seed. The cavity and glass tube displaced a volume of 0.5 to 1.0 ml³. The tapered glass tube was sealed by valve tubing 0.2 cm in diameter. Sampling of the internal atmosphere from the cavity was done by the Bonnier and Magnin apparatus described by Thoday (21). The error of determination was no more than $\pm 0.5\%$ of the volume of the gas. The resistance of fruits to gaseous diffusion was calculated with the formulae described by Trout et al. (22): $R_c = C_c/R$, in which R_c = resistance of fruit to diffusion of CO₂, C_c = volumetric concentration of CO₂ in the internal atmosphere of the fruit, and R = respiration rate; $R_o = (\delta O + 0.2 \delta N)/R$, in which R_o = resistance of fruit to diffusion of O₂, δO = O₂ percentage in air minus O₂ percentage in internal atmosphere, and δN = N₂ percentage in air less N₂ percentage in internal atmosphere. The formulae assume that the respiratory activity in fruit is independent of C_c or C_o (volumetric concentration of CO₂ & O₂, respectively) and is always inversely proportional to the resistance to gaseous exchange. In the case of inhibitory CO₂ concentration in the intercellular atmosphere, the resistance values would be lower than calculated. However, on the basis of the results obtained by Biale (3) and Young et al. (27) the formulae give rough approximations of fruit resistance.

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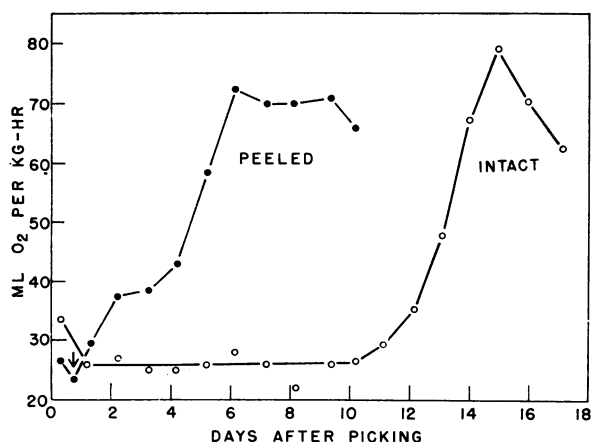


Fig. 1. Effect of peeling on respiration of Hass avocado fruit at 15 C (arrow indicates time of peeling).

Results

Effects of Peeling. The response to peeling varied with the phase of the climacteric during which the fruit was peeled. In the preclimacteric stage the onset of the respiratory rise was induced by peeling immediately (fig 1). The main effect of peeling seemed to be a time shift of the respiratory pattern resulting in a climacteric rise 3 to 11 days earlier than in intact fruit. The shift was more marked at 15 C than at 20 C because of a longer lag period (11 days at 15 C & 4 days at 20 C). The respiratory rise of the peeled fruit was more gradual at 15 C than at 20 C. The time required for fruit softening and the prepeak period were both shortened greatly by the elimination of the lag period. In both intact and peeled fruit softening occurred just at the climacteric peak or 1 to 3 days after the peak. The effect of peeling was quite reproducible as demonstrated in table I. The significance of the effect was checked by statistical methods. Peeled fruit kept in a saturated atmosphere ripened normally and developed satisfactory flavor. It was essential that the air be thoroughly saturated with moisture, but even under these conditions new tough skin formed around the

Table I

Acceleration of Lag & Prepeak Periods by Peeling

Variety	Date	Temp. C	Gas measured	Magnitude of acceleration in days	
				Lag	Prepeak
Hass	July	20	CO ₂	3	4
"	"	"	"	4	6
"	"	"	"	3	4
Fuerte	Oct	"	O ₂	4	4
"	Mar	"	"	4	4
"	"	"	"	3	3
Hass	April	"	"	2	2
"	May	"	"	3	2
"	June	15	"	10	8
"	"	"	"	11	9

fruit. Microscopic observations suggested that the new skin was formed from dried cutinized cells. When avocados were cut into halves and peeled they softened in 85 % relative humidity while whole peeled fruit did not. Under these conditions the peeled halves lost more water than the peeled whole. These results suggested that loss of water was not the only factor preventing the ripening of peeled fruit in unsaturated atmosphere. The main difference between the peeled whole fruit and the peeled half is the presence of the seed inside the whole fruit, which is very likely to impair the gaseous diffusion. Wardlaw and Leonard (25) reported that in low humidity, gaseous exchange was impaired by partial desiccation of tissues. Consequently one is tempted to suggest that the gaseous exchange is the other factor involved in the prevention of ripening in peeled fruit kept in unsaturated atmosphere.

Table II

Effect of Postclimacteric Peeling on Respiration Rate

Variety	Tempera- ture	Gas measured	ml O ₂ or CO ₂ /kg-hr	
			Before peeling	After peeling
Fuerte	25	O ₂	107	23
"	"	"	50	16
"	"	"	100	31
"	20	"	72	20
"	"	CO ₂	100	40
Hass	"	"	96	18

The effects of peeling during the postclimacteric phase (table II) differed strikingly from the effects of preclimacteric peeling. Respiration dropped to a low value and bacterial contamination took place rapidly. The peeled tissues hardly dried out, and the fruit appeared as mushy pulp lacking any skin. Removal during the postclimacteric phase of skin formed by fruit peeled during the lag period gave results similar to postclimacteric peeling.

Since peeling might remove a major obstacle to gas exchange, the first step in seeking a possible explanation was to study the internal atmosphere of the peeled and of the intact fruit.

Internal Atmosphere of Avocado Fruit. The internal atmosphere measurements of Hass and Fuerte fruit gave similar results. Furthermore, the changes in the internal atmosphere of the avocado fruit associated with the ripening process followed a pattern similar to the changes in other fruits such as banana and papaya described by Wardlaw and Leonard (24, 25). The internal atmosphere measurements were made at 20 C and at 15 C.

At 20 C the internal atmosphere of freshly picked fruit consisted of 15 to 19 % O₂ and 1 to 3 % CO₂ (table III, fig 3, Intact). At the onset of the climacteric rise the O₂ content dropped and CO₂ level rose, as one might expect from the trends in respiration. At the climacteric peak the O₂ dropped to

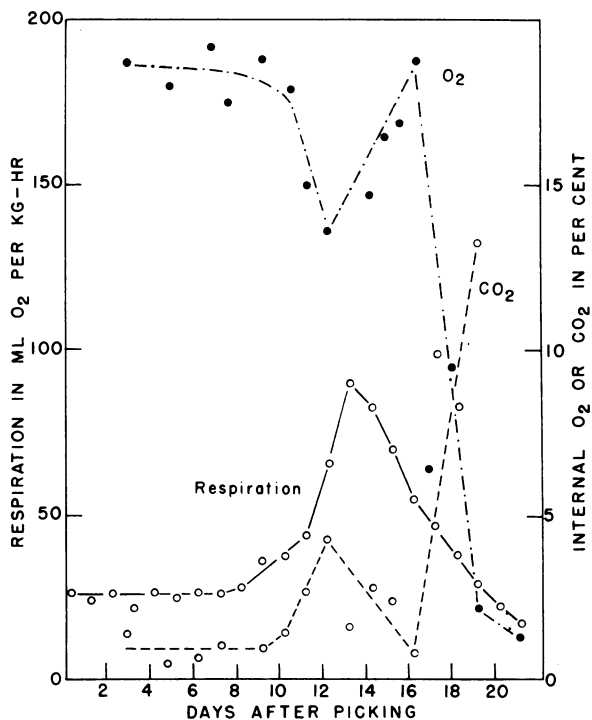


FIG. 2. Internal gaseous composition of Hass avocado fruit in relation to respiration at 15 C.

5 to 10% and the CO_2 rose to 5 to 10%. After the climacteric peak, the relation between respiration rate and internal atmosphere changed, and with the decline in respiration rate the O_2 percentage dropped while the CO_2 content remained high. In late stages of senescence the O_2 concentration was as low as 0.5 to 2%, and CO_2 rose to 15%.

The changes in the internal atmosphere at 15 C prior to the peak followed the same trends as at 20 C (fig 2). The O_2 level during the lag period was approximately constant at 17 to 20%. It started dropping simultaneously with the rise in respiration rate, reaching the value of about 13% at the climac-

teric peak, but unlike the pattern at 20 C it rose again to 15 to 19%, with the decline in respiration rate following the peak. The change in direct correlation between respiration rate and internal atmosphere occurred later at 15 than at 20; only at late senescence, 4 days after the climacteric peak, did the O_2 content drop despite a decline in respiration rate. The internal CO_2 concentration remained constant at around 1% during the lag period. In correspondence with the respiratory rise the CO_2 rose to approximately 4% at the climacteric peak, but dropped back to approximately 1% with the respiratory decline in the postclimacteric phase. Only in late senescence did the CO_2 rise sharply. Since internal atmosphere is a function of both respiration rate and permeability to gaseous diffusion, the change in the relationship between respiratory rate and internal atmosphere suggests that there were some changes in the resistance of the fruit to gaseous diffusion.

Fruit Resistance to Gaseous Diffusion. The general trends for resistance to gaseous flow appeared to be the same for O_2 and CO_2 (table III). The changes in R_0 and R_c were of little significance prior to the climacteric peak. For intact fruit the R_0 values during the lag period were 0.6 to 1.0 units, reached 0.8 to 1.3 units at the climacteric peak, and then rose steeply to the levels of 3.0 to 10.0 units with fruit softening. The resistance to CO_2 diffusion, R_c , started at 0.4 to 0.8 units and increased gradually to 0.5 to 1.0 at the climacteric peak. The resistance to both O_2 and CO_2 rose sharply during the post-climacteric stage.

Peeling Effect on Internal Atmosphere of Pre-climacteric Fruit. The peeling effect on the composition of internal atmosphere seemed to be associated with the time shift in the climacteric rise induced by skin removal. The early respiratory rise brought parallel but earlier changes in the internal atmosphere (fig 3, table III). The trend in oxygen content of peeled fruit is similar to that in intact fruit, in comparable positions along the climacteric pattern. However, the CO_2 percentage seemed to

Table III

Effect of Peeling on Composition of Internal Atmosphere & on Resistance to Gas Diffusion of Hass Avocado at 20 C.

Days from picking	Stage of climacteric		R^*		C_0		C_c		$R_0 \times 10$		$R_c \times 10$	
	Intact	Peeled	Intact	Peeled	Intact	Peeled	Intact	Peeled	Intact	Peeled	Intact	Peeled
1	Lag period	Rise induced										
3	Rise	Peak	36	43	17.6	14.1	2.9	2.8	0.9	1.4	0.8	0.6
5	Peak	Postclim.	70	77	14.6	9.2	5.2	5.5	0.9	1.4	0.7	0.7
12	Postclimacteric		119	38	5.2	2.7	12.3	9.2	1.3	4.3	1.0	2.4
			52	...	1.7	...	12.8	...	3.5	...	2.5	...

R^* = Rate of respiration in ml O_2 per kg/hr

C_0 = Internal O_2 concentration

C_c = " CO_2 "

R_0 = Resistance to oxygen diffusion

R_c = " " CO_2 "

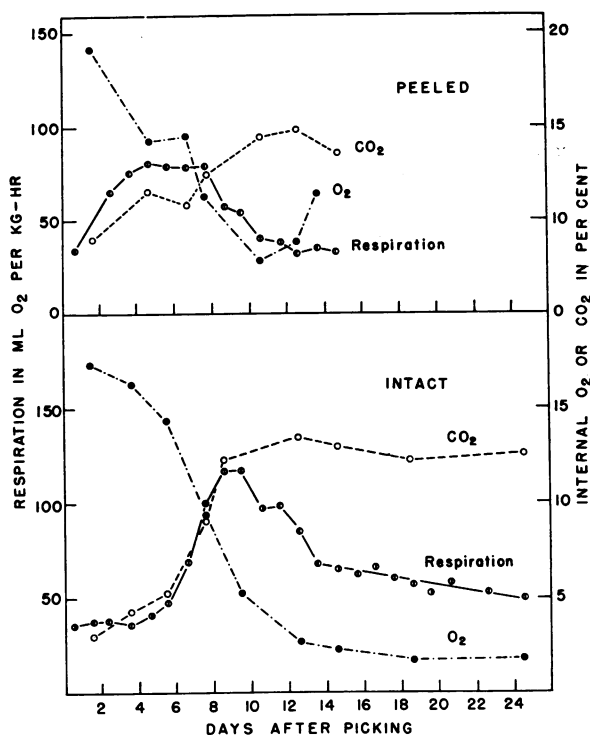


FIG. 3. Effect of peeling on the composition of the internal atmosphere of Hass avocado fruit at 20 C.

drop slightly with peeling, and it did not rise as fast as the CO_2 percentage in intact fruit. It should be noted that the techniques used do not allow sampling and analysis of the intercellular atmosphere before 12 to 24 hours after peeling. It is probable that peeling the skin gave more marked an improvement of gaseous exchange immediately after peeling and prior to the drying of the new periderm.

Resistance measurements of peeled fruit (table III) substantiated these observations. The R_0 values closely resembled those of intact fruit, possibly rising even faster. The R_c values of peeled fruit were slightly lower than those of intact fruit. Thus it seemed that the new periderm formed after peeling showed a higher resistance to O_2 diffusion and lower resistance to CO_2 diffusion than the original peel. However, since the respiration rates of peeled fruit appeared to be lower than those of intact fruit, the resistance values of peeled fruit would give slightly lower results for fruit resistance.

Site of resistance to gaseous diffusion. It appeared that the new periderm formed after preclimacteric peeling had similar resistance to gaseous diffusion as the skin. Biale (3) reported that avocado fruit ripened uniformly throughout the tissue when stored in 2.5% O_2 . Since ripening did not occur in anaerobic environment, one can deduce that fruit under 2.5% O_2 had some O_2 throughout its mass, which suggests in turn that the skin is not a serious barrier to oxygen diffusion. Yet, by gently rubbing

the wax away from the skin, the ripening process was hastened significantly. Sealing the stem-end scar delayed ripening, demonstrating that the stem scar is an important route of gaseous exchange. Both observations suggest that the avocado skin is intermediate in its resistance between semipermeable peels such as those of the Granny Smith apple (22) and tomato (7), and permeable skins as in the case of Delicious apple (10). The site of resistance to gaseous exchange probably changed along with the ripening process. In a trial to determine the site of resistance of gaseous exchange of peeled fruit at its postclimacteric phase, the new periderm formed after peeling was punctured in one fruit and a ring of peel one cm in diameter was removed from another fruit. The results in both fruit showed no effect on the intercellular atmosphere, suggesting that in the postclimacteric fruit the peel does not represent the major resistance to gaseous diffusion. The resistance to gaseous exchange should be ascribed to the tissue itself. It was probably related to the clogging of the air spaces by the cell exudate. Sacher (18) reported extensive liquid logging in senescent cells of bean endocarp and some fruits.

Changes in coefficient of oxygen diffusion and air space. A rough estimate of the diffusion coefficient for gaseous oxygen can be made from the data on internal atmosphere. The avocado can be assumed to be a spherical body respiring uniformly throughout its mass. Assuming further that the resistance to gaseous diffusion is uniform throughout the fruit, the concentration of O_2 in the intercellular spaces at any distance from the center is described by the formula (8): $C = C_0 - (a/6D)(R^2 - r^2)$, where C = partial pressure of O_2 in atmospheres in the intercellular space at a distance r (in cm) from the center, C_0 = partial pressure of O_2 in atmospheres at the surface of fruit, $a = \text{O}_2$ uptake in ml O_2 per minute per ml tissue, R = radius of fruit in cm, and D = diffusion coefficient of O_2 in ml per sq cm per minute with gradient of 1 atmosphere per cm.

This formula could be rearranged in terms of the diffusion coefficient $D = aR^2/6(C_0 - C)$.

D values of 1 to 2×10^{-2} ml per cm^2 per minute were obtained for freshly picked fruit and for fruit at the climacteric peak, whereas senescent fruit has a D of 3×10^{-3} ml per cm^2 per minute. These D values are probably lower estimates of the coefficient since the calculations did not take into account the skin resistance. Another possible error might be due to the assumption of uniform respiration rate throughout the fruit. If this assumption were proven wrong, one might expect a lower coefficient of diffusion, since the diffusion routes for the bulk of the gas would be shorter. Since the air space is continuous throughout the fruit, one could safely assume that the oxygen diffusion inside the fruit depends on its rate of diffusion in the air space rather than through the cells. Diffusion through cells may be assumed to equal diffusion through water, which is 370,000 times as slow as diffusion in air (6). Con-

sequently, one can calculate the cross-section area of the air-space used in O₂ diffusion. This calculation of cross-sectional area of air spaces involves the assumption that the gas-spaces consist of a series of parallel tubes, but the real path of the gas spaces is possibly tortuous. However, for comparative purposes this calculation of apparent cross-sectional area is still valid. The ratio of

$$\frac{\text{cross-section area of air spaces}}{\text{total cross-section area}} = \frac{D}{\text{oxygen diffusion in air}}$$

The cross-section area of air space of picked fruit is $1 \times 10^{-2}/12.5 = 8 \times 10^{-4}$ of the total cross-section area. In senescent fruit it is $\frac{3 \times 10^{-3}}{12.5} = 2 \times 10^{-4}$.

Assuming that the skin resistance does not change with ripening, one can get from these values a rough estimate of the extent of the clogging of the air spaces in the ripe fruit. The cross-section area of the air space of fresh fruit is four times as large as the cross-section area of senescent fruit. Similar ratios appeared both in intact fruit at 15 C and in peeled fruit at 20 C.

Ventilation and injury as factors in fruit ripening. The peeling effect might be explained on the basis of improvement in gaseous exchange or on the basis of injury. Several treatments were applied in order to separate effects evoked by injury from the effects of improvement in gaseous exchange. Experiments were carried out on a scale allowing statistical analysis of data. Respiration measurements were done in each experiment on 24 individual fruit with the Beckman oxygen analyzer. Each treatment (table IV) was applied to 3 or 5 fruit. In addition to respiration measurement the ripening behavior was observed on parallel runs by recording

the time duration between the application of treatment and fruit softening. Previous experiments have shown that the peak of the climacteric rise in respiration occurred 0 to 1.5 days before softening. Respiration measurements were run at 20 C, and later in 15 C in order to prolong the ripening period.

The results may be summarized as follows: I. All the treatments which improved ventilation shortened the lag, prepeak, and softening periods. II. Not all treatments that injured the fruit had significant effects. However, it was shown that treatments exerting injury without any improvement in gaseous exchange, such as inserting needle into a fruit immersed in a mercury bath and sealing the injured spot, accelerated the ripening process.

The effects of ventilation is strikingly demonstrated by: I. The response evoked by the ventilation of the internal atmosphere with air flow applied into the seed cavity after removing the seed compared with sealing the fruit after removing the seed. II. Comparing the softening period of fruit with sealed and unsealed knife incisions. III. The effect of removing the stem end (button) of fruit.

Any impediment of the gaseous exchange had a marked delaying effect on the ripening process. Ventilation elicited a response only when it was applied continuously. A brief improvement in gaseous exchange, as in sealed seedless and sealed incision treatments, frequently gave no response whereas continuous ventilation consistently accelerated ripening.

Injury effect was best demonstrated by shaking the fruit, which evoked two responses: I. Immediate effect of promotion of respiration which reached its climax in about one hour. Then the respiration rate gradually declined for 5 to 6 hours to a level intermediate between the peak and the initial levels. This was followed by a gradual climacteric rise. II. Striking acceleration of the onset of the respiratory

Table IV

Effect of Various Treatments on Respiratory Behavior of Avocado Fruit

Treatment	Nature of Treatment Injury Ventilation		Temp. C	Days			
				Lag Period		Prepeak Period	
				Mean	Δ	Mean	Δ
Intact			15	11.5	...	14.5	...
Sealed seedless	+	temporary	"	10.0	1.5	13.5	1.0
Ventilated		+	"	6.0	5.5	9.5	5.0
Shaken	+		"	3.0	8.5	5.0	9.5
Peeled	+	+	"	3.0	8.5	6.0	8.5
Stem end injury	+		"	7.0	4.5	11.0	3.5
Stylar end injury	+		"	8.0	3.5	10.0	4.5
Intact			20			8.0	...
Knife incision—sealed	+		"			7.0	1.0
Knife injury—not sealed	+	+	"			5.0	3.0
Button removed		+	"			6.0	2.0
Gravitational fall (1 m) once	+		"			6.0	2.0
Gravitational fall (1 m) 5 times	+		"			5.0	3.0

Δ represents time difference between treatment and intact.
L.S.D. at 95% probability for the experiment at 15 C was 3 days.

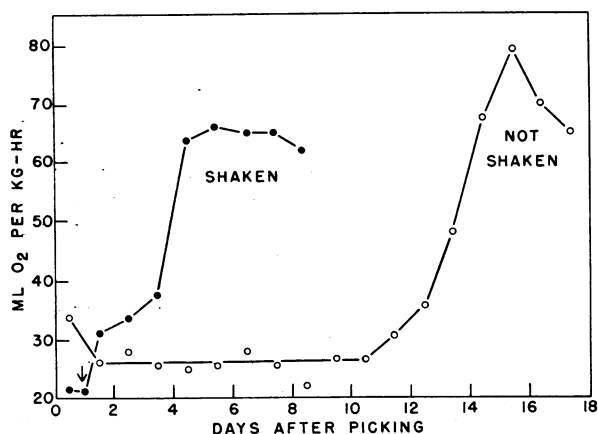


FIG. 4. The respiratory response of Hass avocado fruit to shaking at 15 C (shaking started on day indicated by arrow).

rise and concomitant softening (fig 4).

The effect of mechanical handling at the post-climacteric phase differed strikingly from the effects of preclimacteric handling. Respiration dropped from 80 to 100 ml O₂/kg-hr to low values of 15 to 30 ml O₂/kg-hr. The observation resembled the postclimacteric peeling effect.

Results indicated that either ventilation or injury might be the sole reason for acceleration of the ripening process to an extent equal to the response evoked by peeling. However, considering the consistent result elicited by peeling and ventilation, with the erratic responses to injury, it appears more plausible to suggest that the main reason for the peeling effect is the improvement in gaseous exchange.

Autogenous inhibitor. Laties (13) proposed that the metabolism of potato tubers is controlled both quantitatively and qualitatively by a volatile inhibitor in the internal atmosphere of the tuber. If such an inhibitor were present in fruit it could explain the effect of improvement in gaseous exchange. Therefore, an experiment was designed to compare the ripening and respiration of avocado fruit under continuous ventilation with the ripening and respiration of fruit in a closed environment. Volatiles of 10 fruit and fruit segments were collected for 24 hours and transferred to the closed system of the Haller-Rose type (11), which permitted the simultaneous measurements of CO₂ evolution and O₂ uptake. The respiration pattern and softening period of fruit in the closed system were similar to those of fruit under well ventilated conditions. However, negative data cannot be considered as conclusive evidence for the absence of the inhibitor, since such a volatile inhibitor might polymerize or be absorbed by the strong base present in apparatus of the closed system.

Discussion

The peeling and ventilation experiments indicated that improvement in gaseous exchange accelerated the ripening process. Such a response may result

from increased oxygen supply and removal of internal inhibitory CO₂ concentration or other volatile inhibitors.

The internal atmosphere studies showed that peeling did not elicit any improvement in oxygen supply, since the O₂ % in the internal atmosphere of peeled fruit was similar to that of intact fruit in comparable positions in the climacteric history. Furthermore, the data suggested that the peel and the new periderm formed after peeling have a similar resistance to O₂ diffusion. The possibility that the peeling effect was exerted by a short duration change of O₂ concentration in the internal atmosphere before the formation of the new periderm is eliminated by the observation that only continuous ventilation could elicit a consistent response. Consequently, the explanation that peeling evoked its effect by removing O₂ deficiency is discarded. Increasing the oxygen in the external atmosphere to 100 % (3) did not significantly affect the duration of ripening or the lag period. Thus, there appears to be no deficiency of oxygen in the avocado fruit. Trout et al. (22) reported a deficiency in apples. However, even in this case the level of oxygen may affect the climacteric pattern, but it does not trigger it. Hackney (9) reported that the respiration of the Granny Smith apple was limited by the internal oxygen concentration, and that its climacteric could be hastened by increasing the external oxygen concentration. Yet, despite a decline of the internal oxygen concentration in apple fruit in storage, the climacteric was induced.

The role of CO₂ in relation to respiration and the climacteric rise has been the subject of several studies. High CO₂ concentration in the external atmosphere was shown to retard the climacteric and the ripening of several fruits (12, 14, 27). At the enzymatic level it was reported that 10 % CO₂ inhibited markedly succinate oxidation (1, 17) and phosphoenolpyruvate carboxylase activity (23). Ranson et al. (17) related inhibition of the succinoxidase enzyme to previous observations on succinate accumulation when inhibitory levels of CO₂ were encountered in fruits. Scott (19) suggested that the high respiratory activity of tissue slice from bulky storage organ might be ascribed to the release of the cells from the suppression by excessive carbon dioxide.

The possibility of removal of native volatile inhibitor other than CO₂ is still open, yet the internal CO₂ inhibition would conform better with data. It appears that the decrease in CO₂ exerts only an acceleration rather than a primary induction of the climacteric, as the internal CO₂ content was higher at the onset of the respiratory rise than immediately after picking. The internal CO₂ concentration of apples (22) was constant throughout the storage, and presumably did not affect ripening. In summary, it seems that improvement in gaseous exchange accelerated rather than induced the ripening process.

The results of this study on avocado do not agree with Wardlaw and Leonard's contention (24) that

in papaya the postclimacteric respiratory decline is related to the failure of oxygen to gain access to the fruit tissues. At 15 C the respiration rate declined despite an increase in oxygen and a decrease in carbon dioxide; that is, the internal atmosphere was not the cause of the respiratory decline but its product. The decline of oxygen and increase in carbon dioxide concentration at late senescence was preceded by a cellular exudation process, which suggests that the biological machinery of the cell collapses before the internal atmosphere changes.

The internal atmosphere studies indicated a marked increase in the resistance of fruit to gas diffusion associated with fruit softening. Estimations of the cross-section area of peeled and unpeeled fruit indicated a decrease in the air-space volume in ripe avocado. Consequently, it is suggested that the increase in resistance in avocado is due to a clogging up of air spaces by liquid logging. Sacher (18) reported extensive water logging in senescent cells of bean endocarp and of some fruits. Water logging in avocado could be inferred from demonstration of the leakage process in ripe fruit (2). Rate of leakage increased progressively with the ripening process. The increase in resistance to gas diffusion should be borne in mind when response of fruit to changes in external atmosphere is investigated. It is obvious that the internal oxygen concentration in an atmosphere of 5% oxygen should be different in ripe fruit than in firm fruit.

Mechanical stimulation and injury were shown to elicit, in addition to the well known temporary respiratory rise, acceleration of the climacteric and the ripening process. Smock et al. (20) reported similar observations on apple fruit. Marks et al. (15) reported that bruising injury prevented, rather than accelerated, normal ripening of the tomato. They related this effect to the inhibition of oxidative phosphorylation. The difference in structure between tomato and avocado might explain the discrepancy of observations. The dual effect of shaking in both temporary stimulation of respiration and acceleration of the ripening process suggests that a long-time influence on the cellular machinery is involved.

Summary

The relation of the ripening process of avocado fruit to gaseous exchange, internal atmosphere, and injury effects was investigated. Peeling the fruit eliminated all or most of the lag period and hastened the onset of the respiratory rise. The acceleration was related to improvement in gaseous exchange and mechanical stimulation; the ripening process was accelerated by shortening the lag period. Removal of the skin of postclimacteric fruit resulted in a marked inhibition of the respiration rate. Mechanical handling produced similar effects. A correlation was established between internal atmosphere and respiration rate for the lag period and the respiratory

rise; upon softening this correlation changed. Despite the decline in respiratory activity the oxygen percentage dropped to as low as 1 to 2% and carbon dioxide percentage rose to 15. The resistance to gaseous diffusion was calculated to be approximately constant up to softening; subsequently it rose markedly for both carbon dioxide and oxygen diffusion. This rise was related to the clogging of air spaces by cell exudates. The cross-sectional area of air-space of firm fruit was calculated to be at least four times larger than the cross-section of air-space of ripe fruit. Peeling the fruit resulted in a shift of the changes of internal atmosphere in accordance with expectations from the shift in the respiratory activity. It also appeared that the concentration of carbon dioxide was reduced, whereas the oxygen concentration was not affected significantly. It was established that the internal atmosphere exerts an inhibitory effect upon the onset of the climacteric rise. However, the delay was not ascribed to oxygen deficiency.

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