

The Climacteric Rise in Respiration Rate of the Fuerte Avocado Fruit

By J. B. BIALE,
University of California, Los Angeles, Calif.

The relationship between carbon dioxide evolution and fruit ripening has been investigated widely for some of the deciduous fruits. With the apple and pear, in particular, it has been shown (4, 5) that changes in certain manifestations of maturity are accompanied by a greatly accelerated rate of respiration. Similar observations were made for the banana (2). This rapid increase in carbon dioxide production is referred to by workers in this field as the "climacteric" rise in respiration. Not all fruits appear to exhibit this respiratory trend, however. In the lemon and orange, which have relatively low respiring power, no climacteric has thus far been observed (1).

Very meager information exists concerning the course of respiration of the avocado fruit after harvesting (6, 7). In one case it was obtained by placing fruits of the Fuerte variety into an air tight container, and subjecting them therefore to an environment the gaseous composition of which was continuously changing. The accumulation of carbon dioxide evolved by the fruit in a sealed container, associated with decreasing oxygen content was doubtless one of the causes for the declining respiration rate observed (6). The striking sensitivity of the avocado fruit to oxygen deficiency will be shown in some of the experiments here reported. The principal emphasis in these preliminary studies, however, was placed on the respiratory behavior of the avocado in relation to the ripening and softening processes.

THE CLIMACTERIC UNDER AIR

The Course of Respiration at 15 Degrees C (Experiment 1):—The procedure for this experiment, and also for those which follow, was essentially similar to that employed in studies on citrus fruits previously reported (1). The avocados were picked February 17, 1941, from 5-year-old trees in the orchard of the Division of Subtropical Horticulture at the University of California, Los Angeles. The next day each respiration jar, containing 30 fruits, was placed in an air conditioned room maintained at 15 degrees ± 0.5 degrees C. The fruit was horticulturally mature but firm. A continuous stream of air at 350 cubic centimeters/minute was used during the carbon dioxide determinations as well as between readings. While measuring respiration the air stream was freed of carbon dioxide by means of ascarite. The results are shown in Table I.

In this table the values for each jar were computed from three or more consecutive hourly or semi-hourly determinations. The largest increase in respiration rate above the initial reading varied from about 80 to 100 per cent for the three jars. However, when the maxima are considered by themselves without reference to the initial reading on February 20, it will be seen that they differ by approximately 1 to 4 per cent from the average. The rate of the climacteric rise appears to be somewhat more rapid for

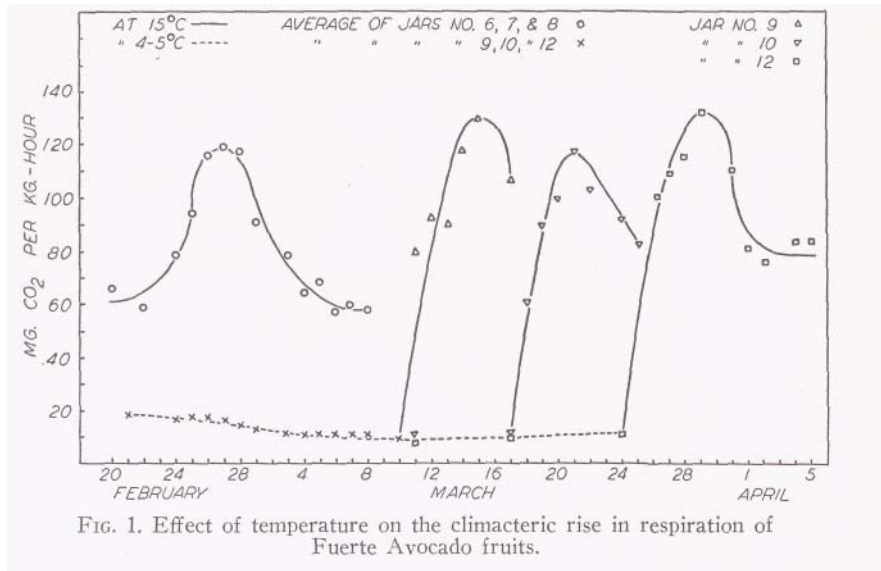
jar No. 6 than for the other two.

TABLE I—RESPIRATION OF FUERTE AVOCADOS SUBJECTED TO AIR AT 15 DEGREES C. (IN MILLIGRAMS CARBON DIOXIDE PER KG OF FRUIT PER HOUR)

Jar No.	February						
	20	22	24	25	26	27	28
6.....	67.2	67.4	109.0	112.9	126.6	113.5	103.3
7.....	63.2	—	65.6	80.6	109.3	122.5	127.2
8.....	67.6	51.0	58.7	89.5	111.0	120.4	119.2
Average.....	66.0	59.2	77.8	94.3	115.6	118.8	116.6
Jar No.	March						
	1	3	4	5	6	7	8
6.....	77.2	67.4	53.0	56.1	46.0	50.9	48.2
7.....	100.9	84.0	71.4	76.6	65.0	—	63.0
8.....	93.8	83.5	68.5	72.6	62.5	69.4	62.9
Average.....	90.6	78.3	64.3	68.4	57.8	60.2	58.0

It is of interest to compare the degree of softening of the fruit with its respiratory behavior. On February 25 all the avocados were firm. Three days later in jar No. 6 all were soft and in the edible stage while in No. 7 there were only two soft, and in No. 8 six soft fruits. On March 8 when the experiment was terminated two-thirds of the fruit in No. 6 had passed the edible stage, while in the two other containers less than one-third was classified as very soft. Darkening of the peel was observed at the same time in the three jars but was more pronounced in No. 6. Insufficient data are available to warrant conclusions at present as to the exact relationship between the climacteric and softening, but observations made in this and in other experiments suggest that the maximum in carbon dioxide output precedes softening by one to three days under the conditions employed here.

Effects of Low Temperature on Respiration (Experiment 2):—For the purpose of determining the effects of an initial exposure to low temperature on the subsequent respiration behavior, fruits from the same lot used in experiment 1 were placed at a temperature of 4 to 5 degrees C. In Fig. 1 the results are presented graphically and compared with the averages obtained from the previous experiment. Because of the close agreement between the three jars when exposed to the low temperature, averages only are reported for the period February 21 to March 10, both inclusive. At the end of this period all the fruit was found to be firm. At 4 p.m. on March 10, jar No. 9 was transferred to the ripening temperature of 15 degrees C. The next day the respiration rate rose immediately to a value higher than the initial rate for jars No. 6, 7, and 8, which had received no preliminary low temperature exposure. In 5 days the maximum carbon dioxide output was reached, and 3 days later the fruit started to soften and shortly thereafter reached the edible stage. Similarly, jar No. 10 was transferred to 15 degrees C on March 17 and jar No. 12 on March 26. The resultant responses were essentially similar to those of jar No. 9. The maximum rise in respiration for these three jars compares closely with that for jars No. 6, 7, and 8.



It is also of interest to evaluate the temperature coefficient, Q_{10} , for the avocado. In the range of 5 to 15 degrees C it changes from approximately 3.5 in the pre-climacteric phase through 7.0 at maximum respiration to about 3.3 in the final post-climacteric stage. The magnitude of respiration is very much higher for the avocado than for citrus fruits. At 15 degrees C green lemons immediately after picking when their respiration rate is at a maximum respire one-sixth to one-eighth as actively as do avocados in their pre-climacteric stage. As a matter of fact, avocados produce at least as much carbon dioxide at 4 to 5 degrees C as do lemons at 15 degrees C.

THE CLIMACTERIC AS AFFECTED BY DIFFERENT GASEOUS ATMOSPHERES

Aerobic Versus Anaerobic Respiration at 15 Degrees C (Experiment 3):—As a preliminary to gas storage trials, it seemed desirable to ascertain the effects on respiration of the limiting conditions of a completely anaerobic atmosphere. For this experiment the fruit was picked all from one tree in the orchard March 12, 1941, and subjected to 15 degrees C the same day. Twenty fruits were placed in each jar, with two jars under a continuous stream of nitrogen and two under air. A rate of 100 cubic centimeters/minute was employed except during respiration determinations when the rate was increased to 350 cubic centimeters/minute. The nitrogen was freed of traces of oxygen by passing it over hot copper filings. The variations between individual jars in each treatment were small with the exception of the air jars during the climacteric period. Under aerobic conditions maximum carbon dioxide output for jar No. 6 was 153 and for No. 7, 138 milligrams per kilogram-hour. This difference of approximately 10 per cent is greater than normally occurs, but excluding this instance the agreements between individual jars in each treatment were so close as to make it possible to present in Fig. 2 curves based on averages.

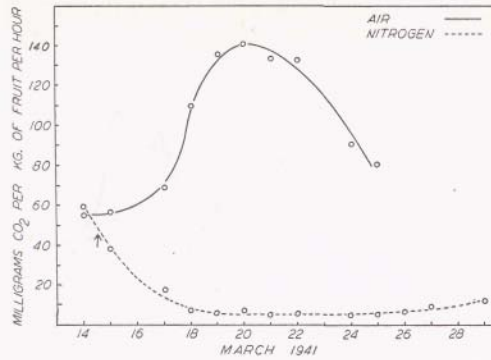


FIG. 2. Aerobic and anaerobic respiration of the Fuerte Avocado fruit (arrow indicates the start of exposure to nitrogen gas).

In this experiment the behavior of the fruit under air was similar to that in experiment 1 with the exception of a somewhat higher maximum. Here too softening followed the climacteric. On March 19 all fruit were firm, while on March 21 slight softening was noted though most of the fruits were still firm. The next day they were nearly all in the edible stage. This condition had developed 1 day after the maximum climacteric respiratory activity.

In striking contrast to the aerobic respiration, jars No. 1 and No. 5 under nitrogen showed a sharply declining carbon dioxide output until March 18 and a low level thereafter. At the height of the climacteric the ratio of aerobic to anaerobic carbon dioxide evolution was 8.2. This value is considerably higher than that obtained for other fruits in general. In citrus, for example, anaerobic carbon dioxide production has v been found not to differ appreciably from aerobic respiration. Apparently the enzymatic system of the avocado is highly sensitive to the lack of oxygen.

It is further to be noted that the fruit in the anaerobic atmosphere retained its firmness until the end of the experiment. A putrid odor was detectable in the air leaving the nitrogen jars. The experiment was discontinued when the fruit was covered with microorganisms, apparently fungi. The somewhat higher final respiration readings might have been due, therefore, to fungal invasion.

Aerobic Versus Anaerobic Respiration at Low Temperatures:— The effects of a nitrogen atmosphere were studied also at a storage temperature of 4 degrees C. The fruit for this study came from Escondido and was placed in storage February 15, 1941. In this experiment only six fruits per container were used. It was found that the uniformity of consecutive readings compared favorably with that obtained with larger samples. Initially all containers were placed under air for several days. On February 24, the differential treatment was started and respiration measurements were limited to two per day since the low carbon-dioxide losses made it necessary to carry the determinations over a 2-hour period. Table II presents the results of this experiment.

TABLE II—EFFECT OF AIR AND NITROGEN ON RESPIRATION OF AVOCADOS AT FOUR DEGREES C (IN MILLIGRAMS CARBON DIOXIDE PER KG OF FRUIT PER HOUR)

Jar	February								
	20	21	22	24	Differential Treatment	25	26	27	28
B	15.9	13.0	12.4	11.1	Air	16.8	12.6	11.9	15.9
C	17.2	11.3	11.1	8.7	Air	11.3	9.9	10.7	11.4
D	17.4	15.2	14.9	13.3	Nitrogen	18.0	11.8	8.8	9.9
E	20.3	17.1	16.6	14.4	Nitrogen	19.0	12.1	10.3	9.7
Jar	March								
	1	3	4	5	6	7	8		
B	17.2	12.3	12.8	10.6	12.8	12.1	12.6		
C	17.5	11.4	12.0	11.0	11.9	12.3	12.1		
D	7.8	6.8	8.6	6.4	6.2	5.8	5.8		
E	8.6	7.9	8.7	7.3	6.9	6.6	5.8		

In all containers a slight initial decrease is to be noted. Under air a steady state was soon attained while under nitrogen the fall was continuous. Some of the daily variations may be ascribed to temperature fluctuation in the chamber which could not be maintained as constant as the 15 degrees C room. Nevertheless, the data clearly show a depressing effect of nitrogen even at the lower temperature. This effect appears, however, to be reversible because upon change to air at the same temperature on March 10, an immediate recovery of the respiration rate took place. When jars D and E were subsequently transferred to air at 15 degrees C the characteristic climacteric rise in carbon dioxide output resulted. The maximum value in respiration was lower by 10 and 15 per cent, respectively, in these jars than in B and C which were continuously under air, but no material difference in the rate of softening was observed.

DISCUSSION OF RESULTS

The most obvious conclusion from these experiments seems to be that softening of the avocado fruit is associated with a climacteric rise in the rate of respiration. It is of interest therefore to compare the magnitude of this rise with that for other fruits which behave similarly. At a temperature of 20 degrees C Kidd and West (4) reported for the apple a maximum respiration of 25 milligrams CO₂ per kilogram hour. Magness and Ballard (5) working with pears at 15.5 degrees C found the respiration rate to attain a value of 50 to 60 milligrams CO₂ per kilogram hour, while Gane (2) has observed bananas at 15 degrees C to produce 60 to 70 milligrams CO₂ per kilogram-hour at the peak of the climacteric. The maximum carbon dioxide output by the Fuerte avocado of 120 to 150 milligrams per kilogram-hour is therefore much higher. When the percentage increase of the maximum over the initial respiration rates is considered, however, the avocado will be observed not to differ markedly from some of the other fruits referred to. The above mentioned workers have found this increase to be 100 to 200 per cent for the apple, 200 to 300 for the banana, and 300 to 400 per cent for the pear. In the avocado the rise in respiration at the peak of the climacteric over the initial rate is of the order of 100 to 200 per cent.

The reasons for this climacteric trend have not been established. Enzymatic activation may provide an explanation for the rapid acceleration in respiration rate during- the climacteric. The fall in carbon dioxide evolution in the post-climacteric

stage may be the result of substrate shortage. If it is assumed that sugars are the immediate respiratory foodstuffs, computations based on the data in Fig. 1 indicate utilization of 1.1 per cent of substrate in 7 days. The avocado has been reported (3) to contain a maximum of about 2 per cent of total sugars on fresh weight basis. Sugars may, however, be supplied by the hydrolysis of other compounds present in the flesh. Only a complete chemical analysis in conjunction with physiological studies seems likely to throw light on these questions.

CONCLUSIONS

The respiratory activity of fruits of the Fuerte avocado variety at 15 degrees C is characterized by a rapid acceleration in carbon dioxide evolution followed by a pronounced decrease. At the peak of the activity 120 to 150 milligrams of carbon dioxide are produced by 1 kilogram of fruit per hour. This quantity is equivalent to an increase of 100 to 200 per cent over the initial rate. The climacteric rise has not been found to occur at 4 to 5 degrees C for a period of 5 weeks. The maximum in respiration precedes the onset of softening by 1 to 3 days.

The anaerobic respiration rate has been shown to be much lower than the aerobic rate with no climacteric rise and no softening of the fruit observed.

LITERATURE CITED

1. BIALE, J. B., AND SHEPHERD, A. D. Respiration of citrus fruits in relation to metabolism of fungi. I. Effects of emanations of *Penicillium digitatum*, Sacc., on lemons. *Amer. Jour. Bot.* 28: 263-270. 1941.
2. GANE, R. The respiration of bananas in presence of ethylene. *New Phyt.* 36: 170-178. 1937.
3. HAAS, A. R. C. Chemical composition of avocado fruits. *Jour. Agr. Res.* 54:669-687. 1937.
4. KIDD, F., AND WEST, C. The effect of ethylene on the respiratory activity and the climacteric of apples. *Gt. Brit. Dept. Sci. Ind. Res., Fd. Inv. Bd. Kept, for* 1937:108-114. 1938.
5. MAGNESS, J. R., AND BALLARD, W. S. The respiration of Bartlett pears. *Jour. Agr. Res.* 32 : 801-832. 1926.
6. OVERHOLSER, E. L. Cold storage, ripening, and respiration studies of the Fuerte avocado. *Proc. Amer. Soc. Hort. Sci.* 25: 371-375. 1929.
7. WARDLOW, C. W. Notes on the physiology and biochemistry of tropical fruits. I. Avocados. *Trop. Agr. (Trinidad)* 14:34-41. 1937.