EFFECT OF OXYGEN CONCENTRATION ON THE RESPIRATION OF SOME VEGETABLES[1]

HANS PLATENIUS

(WITH SEVEN FIGURES)

Introduction

Commercial methods of storing fruits and vegetables in modified atmosphere are based on the fact that respiration, ripening, and other physiological processes can be retarded by maintaining an atmosphere in which the oxygen content is lower and the carbon dioxide concentration higher than in normal air. Many investigators assume that it is the presence of carbon dioxide rather than the limited oxygen supply which has a depressing effect on the physiological activity of the plant tissue. In fact, modified atmosphere storage is frequently spoken of as "carbon dioxide storage."

There is reason to believe, however, that the importance of a limited oxygen supply itself has been underestimated. Indirect evidence for this view is found in the results of THORNTON (**8**) which make it clear that the presence of carbon dioxide in the storage atmosphere does not always depress the respiration of plant material. On the contrary, he found that the respiration rate of potatoes and onions was markedly increased when held in an atmosphere of normal oxygen content to which varying quantities of carbon dioxide had been added. On the other hand, the same treatment had a depressing effect on the respiratory activity of asparagus and strawberries.

In the literature few experiments are reported which deal exclusively with the effect of low concentrations of oxygen on the respiration of plant tissue. Some of these experiments were conducted for a few hours only, and there is no assurance that the results would have been the same had the storage period been extended to several days. Other studies were carried out in the complete absence of oxygen. Obviously, the course of respiration under anaerobic conditions is entirely different from that which is followed when a low, but constant supply of oxygen is maintained.

Most textbooks merely state that the oxygen concentration of the air can be changed over a wide range without materially affecting the rate of respiration. Evidence cited in a review of the literature by MACK (**5**) indicates that such a broad statement is subject to several exceptions. PARIJA (**6**) observed that the production of carbon dioxide of apples was lowest when the oxygen concentration of the air was about 5 per cent.; it rose to higher levels above and below this critical concentration. STEWARD, BERRY, and BROYER (**8**), working with thin disks of carrot and artichoke tissue suspended in weak salt solutions, observed that aeration of the solution with a gas mixture containing only 2.7 per cent. oxygen markedly depressed the carbon dioxide production of the tissues. On the other hand, raising the

[1] Paper no. 254. Department of Vegetable Crops, Cornell University, Ithaca, N. Y.

oxygen concentration of the aeration stream to 40 per cent. did not result in respiration rates higher than were observed in normal air. More recently CHOUDHURY (3) investigated the effect of different oxygen concentrations on the respiration of several vegetables. He found that the respiration rate of potatoes remained fairly constant at oxygen concentrations ranging from 6.2 to 98.6 per cent. Artichokes decreased in respiratory intensity at oxygen levels below normal, and the respiration rate of carrots increased or decreased with corresponding changes in the supply of oxygen.

What little experimental evidence is available points to the conclusion that the effect of low oxygen concentrations on respiration varies with different kinds of plant tissue. This is to be expected considering the wide variations in the normal rate of respiration and the differences in relative surface and permeability to gases of plant material. Moreover, the results are likely to be influenced by the length of exposure, the temperature, and other experimental conditions.

The following experiments were conducted for the purpose of obtaining data which would serve as a basis for developing practical methods of modified atmosphere storage. It is reasonable to expect that any combination of gases in the storage atmosphere which effectively reduces the normal respiration rate also retards the process of deterioration. Carbon dioxide gas in the respiration chamber was kept at a fraction of one per cent. in order to study respiration at low levels of oxygen without the complicating effect of another variable. Oxygen consumption as well as carbon dioxide production were measured because both gases play an equally important rôle in the process of respiration. In particular, it was desired to know how far the oxygen concentration could be reduced without affecting the normal course of respiration.

Methods

All experiments were carried out in constant temperature rooms where fluctuations in temperature did not exceed 2° C. Except for brief periods when readings were taken, the vegetables were kept in the dark. Oxygen consumption and carbon dioxide production were measured simultaneously by a method described in detail in an earlier paper (7). Carbon dioxide was absorbed by a normal solution of sodium hydroxide in the bottom of the chamber while oxygen entered the chamber under atmospheric pressure at the same rate as it was utilized by the respiring tissue. At the beginning of each experiment, the chamber was flushed with nitrogen long enough to reduce its oxygen content approximately to the level desired. The exact oxygen concentration was determined by gas analysis at the beginning and end of each experiment. In all instances, the original gas composition was maintained within 0.3 per cent. throughout the experiment.

Readings of oxygen consumption and carbon dioxide production were taken at intervals of 24 hours. All data were expressed on the basis of the original fresh weight. Because of the high humidity in the chambers, there were practically no losses from transpiration and total weight losses over a period of several days were less than 5 per cent.

Methods approved by the Association of Official Agricultural Chemists (**1**) were used for chemical analyses. Sugars were determined by weighing the cuprous oxide precipitate. The quantity of soluble nitrogen was found by evaporating the alcoholic extract under vacuum, treating the residue with sodium sulphite, and digesting it with a mixture of sulphuric acid, salicylic acid, and mercuric oxide. Protein nitrogen was determined in the residue from the alcohol extraction, using the Kjeldahl-Gunning-Arnold method.

Vegetables used for these experiments were garden-fresh, harvested less than two hours before each experiment was started. Great care was taken to have comparable samples for storage under different oxygen concentrations. Each lot was divided into smaller ones containing an identical number of individuals and these were as uniform in size and shape as could be obtained by careful selection. According to the size of individual specimens, samples ranging from 100 to 700 grams were used in the respiration studies. In no instance did a sample contain less than 15 specimens.

Results

Asparagus

In the first series of experiments, the gas exchange of asparagus held at a temperature of 20° C. was studied simultaneously at nine different levels of oxygen ranging from 1.0 to 20.5 per cent. In figure 1 the average rates

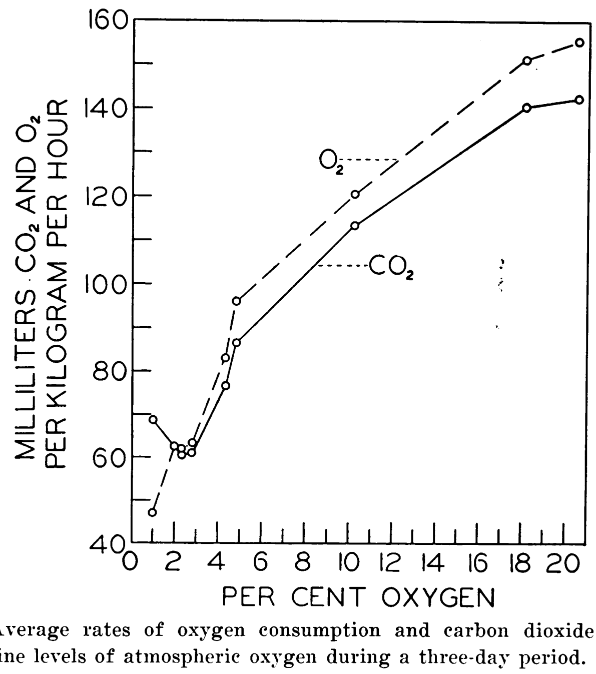

FIG. 1. Average rates of oxygen consumption and carbon dioxide production of asparagus at nine levels of atmospheric oxygen during a three-day period.

of carbon dioxide evolution and oxygen consumption during a three-day interval are plotted against the oxygen concentrations maintained in the different chambers. Attention is called to the fact that the abscissa represents oxygen concentrations, not time intervals. On the ordinate, respiration rates are plotted in terms of milliliters. Using this expression instead of milligrams, deviations from unity in the respiratory quotient can be recognized at a glance by inspecting the relative position of the two curves.

The data show that any change in the oxygen content of the storage atmosphere caused corresponding changes in the respiration rate of the tissue. This effect became increasingly pronounced as lower levels of oxygen were approached. Based on the values for carbon dioxide production,

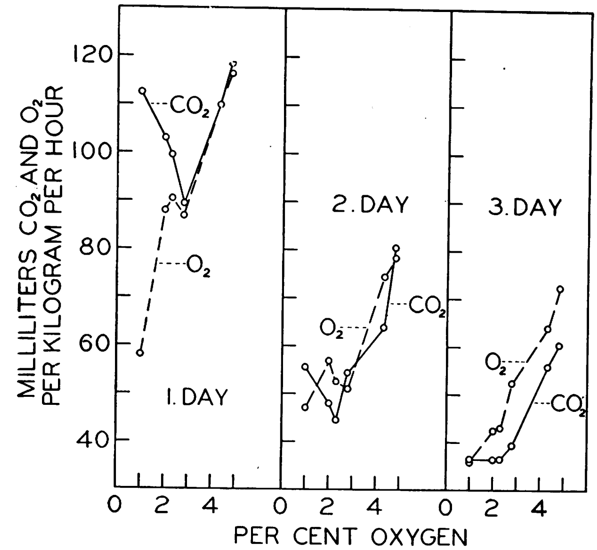

FIG. 2. Average daily rates of oxygen consumption and carbon dioxide production of asparagus at low levels of atmospheric oxygen.

a minimum in respiratory activity was reached at an oxygen concentration of 2.3 per cent. At this point the respiration rate was only 40 per cent. of that occurring in normal air. At still lower levels, carbon dioxide production began to rise again while oxygen consumption continued to fall off sharply. According to the terminology used by BLACKMAN (**2**), 2.3 per cent. of oxygen represents the "extinction point of N R"; it is the concentration at which the type of respiration occurring in pure nitrogen becomes extinct. Above the extinction point of N R sufficient oxygen is available to maintain aerobic respiration and to suppress fermentation completely. Below this point aerobic respiration still takes place but diminishes rapidly in intensity. Fermentation, on the other hand, increases; at a concentration of one per cent. oxygen, the combined output of carbon dioxide from aerobic and anaerobic respiration becomes considerably larger than it is at the extinction point.

In figure 2 the respiration rates for the range from 1.0 to 4.8 per cent. of oxygen are plotted separately for each of the three days. Following the usual drift that occurs with time, the respiratory activity declined at any one oxygen concentration during successive days. It is also evident that the position of the extinction point shifted with time. During the first day, it was located at 2.8 per cent.; during the second, at 2.3 per cent.; and during the third day it had dropped to 1.0 per cent. This shift of the extinction point is probably associated with the normal decline in respiratory intensity as time progresses. At any rate, it shows that the tissue becomes more tolerant to low oxygen concentrations as the storage period is lengthened.

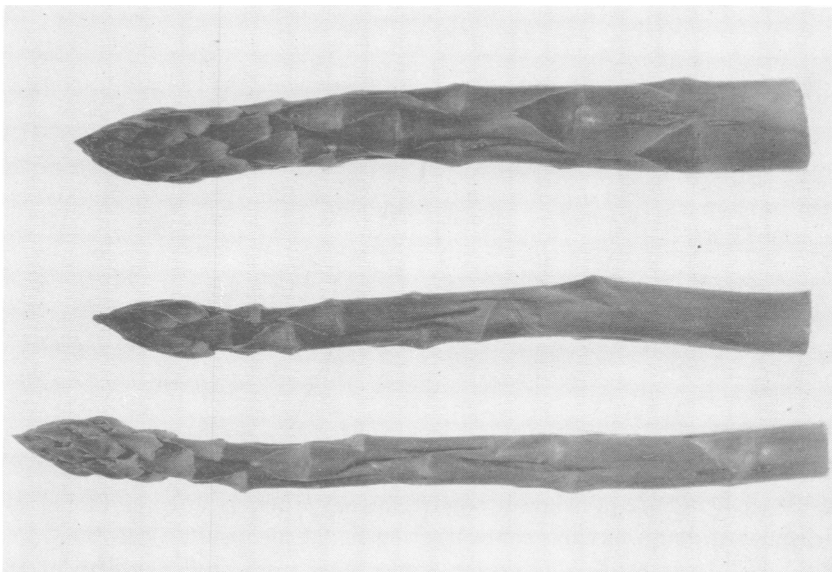

FIG. 3. Injury to asparagus stalks caused by anaerobic respiration at concentrations of atmospheric oxygen below 2.8 per cent.

There was evidence that anaerobic respiration at low levels of oxygen resulted in the accumulation of toxic end products of incomplete oxidation. This was indicated by definite signs of injury of the tissue which appeared after one day of storage in all the samples held at oxygen concentrations of less than 2.8 per cent. As shown in figure 3, sections of the external tissue had collapsed, forming deep longitudinal channels in the upper portion of the spears. These symptoms of injury were identical with those that are produced when asparagus is covered with a fairly thick coat of wax or when spears are exposed to temperatures just above the freezing point for several weeks. Aside from visible injury, the samples held at one and two per cent. oxygen had a pronounced musty and alcoholic odor at the time the experiment was discontinued. It is possible that the injury to the tissue caused changes in the permeability to gases. This would explain the secondary rise in oxygen consumption in the range between 2.0 and 2.8 per cent. oxygen concentration which was observed during the first and second day of storage. The sharp rise in carbon dioxide production with decreasing levels of oxygen likewise may be attributed to increased permeability of the tissue, although the principal reason for this rise is to be sought in conditions becoming more favorable for rapid anaerobic respiration.

The practical significance of reduced respiration at low levels of oxygen is that losses in carbohydrates, which in asparagus consist chiefly of sugars, are greatly reduced. This conclusion is substantiated by the results of chemical analyses taken at the beginning and end of the storage period. Table I shows that after three days of storage in normal air, asparagus had

TABLE I

EFFECT OF OXYGEN CONCENTRATION IN THE ATMOSPHERE ON TOTAL SUGARS, PROTEIN AND SOLUBLE NITROGEN OF ASPARAGUS HELD AT 20° C. DATA ARE EXPRESSED ON THE BASIS OF ORIGINAL FRESH WEIGHT

OXYGEN CONTENT OF THE STORAGE ATMOSPHERE	STORAGE PERIOD	TOTAL SUGARS	SUGARS RETAINED*	PROTEIN NITROGEN	SOLUBLE NITROGEN
%	*days*	%	%	%	%
....	0	2.32	100.0	0.315	0.093
20.5	3	1.39	59.9	0.244	0.129
10.2	3	1.56	67.2	0.249	0.146
4.8	3	2.09	90.1	0.260	0.149
2.8	3	2.13	91.8	0.283	0.125
2.0	3	2.01	86.6	0.253	0.154

* Percentage of original.

lost 40 per cent. of its original sugar content whereas only eight per cent. had been lost at an oxygen concentration of 2.8 per cent. In other words, sugar losses from asparagus under low oxygen were only one-fifth of those occurring in normal air.

Comparing the respiration data with the results of the chemical analyses, it became apparent that in any one treatment sugar losses account for only one-half to two-thirds of the total quantity of carbon dioxide evolved. The same observation was made by the writer in earlier experiments (**7**), and at that time the suggestion was offered that part of the substrate used in respiration of asparagus is furnished by the products of protein hydrolysis. The present data confirm this assumption. There was a definite decrease in protein nitrogen with a corresponding rise in soluble nitrogen during storage. Proteolysis was most active in the sample stored in normal air, it was somewhat slower at low concentrations of oxygen.

Essentially the same trends in respiration rates were observed when asparagus was stored at a temperature of 10° C. at three levels of oxygen. Because of technical difficulties, records were obtained only for carbon dioxide production. The results of this experiment (table II) show that

TABLE II

RESPIRATION RATES OF ASPARAGUS STORED AT 10° C. AND AT THREE LEVELS OF OXYGEN FOR SEVEN DAYS

OXYGEN CONTENT OF THE STORAGE ATMOSPHERE	MILLILITERS CARBON DIOXIDE PER KILOGRAM PER HOUR					
	1ST DAY	2ND DAY	3RD DAY	4TH AND 5TH DAY	6TH AND 7TH DAY	AVERAGE FOR SEVEN-DAY PERIOD
%	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*
20.5	86.3	68.9	61.9	52.8	53.6	61.4
2.1	57.5	40.8	51.9	41.7	28.5	41.5
1.2	44.2	28.3	28.6	20.3	25.2	27.4

the respiration rate could be reduced as much as 55 per cent. by lowering the oxygen content of the storage atmosphere to 1.2 per cent. Significant is the fact that 1.2 per cent. oxygen in the air was sufficient to maintain aerobic respiration at a temperature of 10° C. After seven days, the samples showed no signs of injury nor was there any odor of alcohol perceptible in the chambers. Also, the fact that the carbon dioxide production at 1.2 per cent. oxygen was considerably lower than it was at 2.1 per cent. indicates that at a temperature of 10° C. the extinction point of N R lies close to 1.2 per cent. oxygen or even lower.

SPINACH

The respiration rates of spinach held for three days at a temperature of 20° C. were measured at three levels of oxygen. The results are expressed graphically in figure 4. Obviously, the number of points definitely located is too small to show more than a general trend in the slope of the curves. It is apparent, however, that changes in the oxygen concentration above five per cent. had little effect on carbon dioxide production. Only at an oxygen level of 0.8 per cent. was a significant reduction in respiration

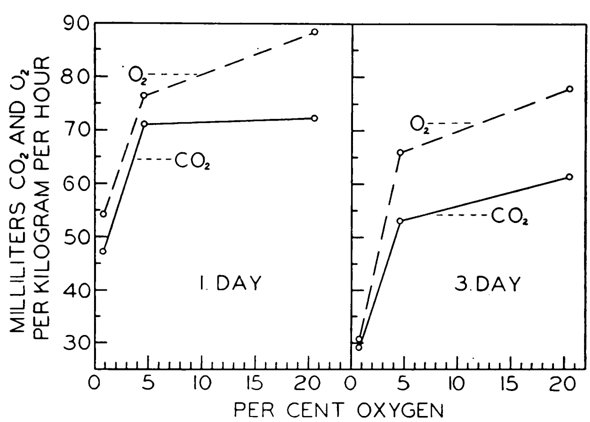

FIG. 4. Rates of oxygen consumption and carbon dioxide production of spinach at three levels of oxygen during the first and third day of storage.

rate obtained. At that concentration, carbon dioxide output had decreased to 65 per cent. on the first, and to 48 per cent. on the third day of storage. In no instance did carbon dioxide production exceed oxygen consumption, although the respiratory quotient showed a tendency to become larger at lower levels of oxygen.

Spinach in normal air has an unusually low respiratory quotient. This may be due to the continuous formation of oxalic acid or other organic compounds of high oxygen content or it may be caused by the decomposition of proteins and their utilization as substrate in respiration. Whatever the reaction involved may be, a lowering of the oxygen content of the storage atmosphere seems to inhibit that process. It is of practical significance that an oxygen concentration of 0.8 per cent. reduced respiration to nearly one-half its normal rate, but was sufficient to maintain normal aerobic respiration. The sample held in that particular gas mixture showed no signs of injury; in fact, it was definitely superior in appearance and taste to that stored in normal air.

Snap beans

As shown in figure 5, the response of snap beans to low concentrations of

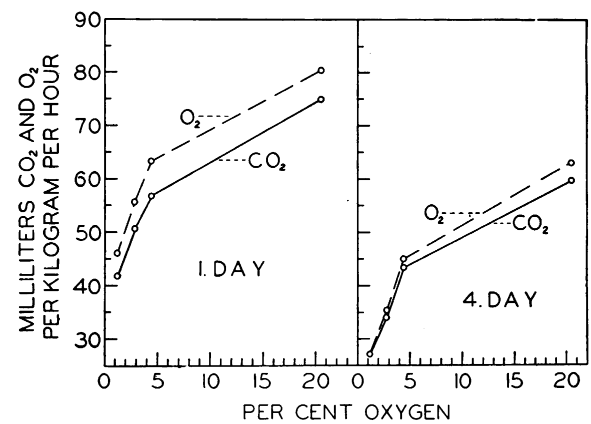

Fig. 5. Rates of oxygen consumption and carbon dioxide production of snap beans at four levels of atmospheric oxygen during the first and fourth day of storage.

oxygen at a temperature of 20° C. was similar to that of spinach. Reducing the oxygen content of the air to 4.4 per cent. had little effect; but at a concentration of 1.2 per cent. the average carbon dioxide evolution during the four-day period was only about 50 per cent. of that which was produced in normal air. Within the experimental range of oxygen concentrations, the respiratory quotient always remained below unity, and this is in accord with the fact that none of the samples developed symptoms of injury which could be traced to anaerobic respiration.

Shelled peas

The respiration curves for shelled peas at a temperature of 20° C. differed in several respects from those of other vegetables. Figure 6 shows

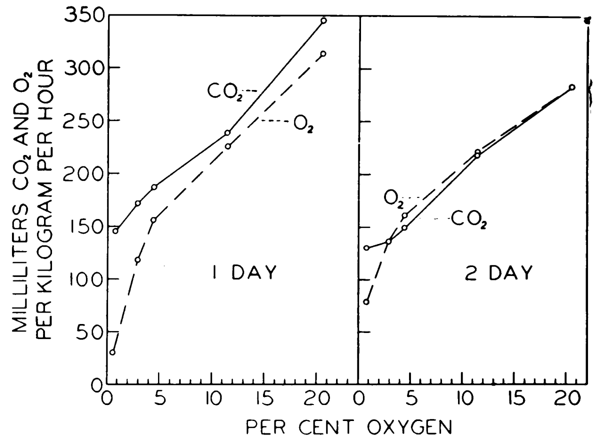

FIG. 6. Rates of oxygen consumption and carbon dioxide production of shelled peas at five levels of oxygen during the first and second day of storage.

that within the experimental range a nearly linear relationship existed between carbon dioxide production and the oxygen content of the air. The respiratory quotient was well above 1.0 at all concentrations during the first day but dropped to a level close to unity a day later. Only at the lowest oxygen level did carbon dioxide production exceed oxygen consumption consistently.

Fermentation occurred in the samples held at oxygen concentrations of 0.8 and 2.8 per cent. This was evident from the strong alcoholic odor of these particular samples and from the pronounced off-flavor before and after cooking. Moreover, the surface of these peas showed a brown discoloration, and the seed coat of some had burst. Although there can be no doubt that in these samples fermentation occurred simultaneously with aerobic respiration, the combined production of carbon dioxide from these two processes did not cause a secondary rise in carbon dioxide output at extremely low oxygen levels as had been observed in asparagus. It is almost impossible, therefore,

TABLE III

EFFECT OF OXYGEN CONCENTRATION IN THE ATMOSPHERE ON TOTAL SUGARS OF SHELLED PEAS HELD AT 20° C. DATA ARE EXPRESSED ON THE BASIS OF ORIGINAL FRESH WEIGHT

OXYGEN CONTENT OF THE STORAGE ATMOSPHERE	STORAGE PERIOD	TOTAL SUGARS	SUGAR RETAINED*
%	*days*	%	%
....	0	6.43	100.0
20.5	2	1.76	27.4
11.4	2	3.09	48.1
4.4	2	4.46	69.4
2.9	2	4.44	69.1

* Percentage of original.

to establish the exact location of the extinction point of N R from inspection of the respiration curves alone.

In commercial practice beneficial results can be expected from storing peas under low oxygen tension, provided the concentration remains sufficiently high to prevent fermentation. At a temperature of 20° C., the best results were obtained at an oxygen level of 4.4 per cent. At this concentration, the average carbon dioxide production was reduced 56 per cent. The degree to which sugar losses were inhibited was even more pronounced than the respiration data would indicate. As shown in table III, the control lot had retained only 27 per cent. of its original sugar content while 69 per cent., that is, more than 2½ times as much, was retained in the sample kept at 4.4 per cent. oxygen.

Carrots

The respiratory behavior of carrot roots, illustrated in figure 7, changed considerably during the six-day storage period. The maximum reduction

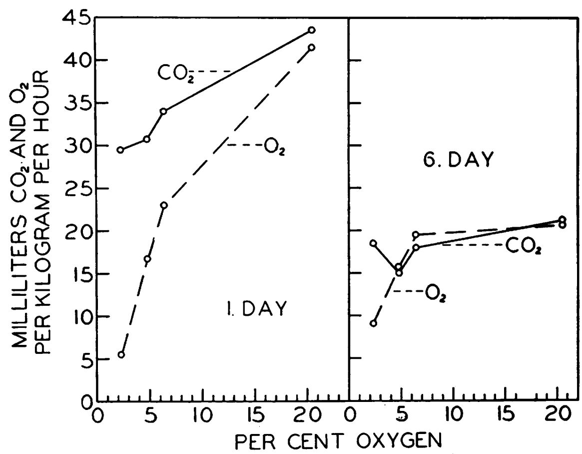

FIG. 7. Rates of oxygen consumption and carbon dioxide production of carrots at four levels of oxygen during the first and sixth day of storage.

in carbon dioxide production observed within the experimental range remained close to 30 per cent. regardless of the fact that the respiratory intensity of all samples declined steadily as time progressed. In the beginning, the respiratory quotient ranged from 1.05 in normal air to 5.8 at 2.3 per cent. oxygen. Gradually the respiratory quotient became smaller, and on the sixth day, two of the samples had reached values slightly below unity. Only at the lowest oxygen concentration did the quotient remain above 2.0 at all times. After the first day, a secondary rise in carbon dioxide production was observed at oxygen levels below 4.8 per cent. This rise persisted; in fact, it became more pronounced during the latter part of the storage period.

Only the sample held at an oxygen concentration of 2.3 per cent. appeared to be permanently injured by toxic end-products of anaerobic respiration. This particular sample had lost its turgor and showed all the other symptoms of injury from an insufficient oxygen supply. The carrots kept at an oxygen level of 4.8 per cent., the next higher concentration employed, remained in sound condition in spite of the fact that the initial respiratory quotient was as high as 1.8.

In this connection, it should be mentioned that in another experiment carrots were kept in excellent condition for six months when stored at a temperature of 2° C. in an atmosphere containing one to two per cent. oxygen. This serves as additional proof that the danger of injury from anaerobic respiration is lessened as the storage temperature is lowered.

Discussion

In analyzing the results of respiration experiments, one must keep in mind that the measured rate of gas exchange deals only with two compounds of the entire chain of reactions that make up the complex process of respiration. Without quantitative chemical analyses showing which organic constituents serve as substrates and which compounds are formed as intermediate and end products, it is impossible to gain a clear understanding of the mechanism of plant respiration. Even if data of such a detailed study were available for one kind of plant tissue, it would be a fallacy to assume that different species or different organs of the same plant have the same respiratory mechanism. Moreover, there is sufficient evidence to show that the course of respiration of any one tissue may change materially with variations in temperature and other environmental conditions. Interpretations of the experimental data of this study are made with these limitations in mind.

An examination of the data on oxygen absorption shows that within the experimental range any decrease in the concentration of atmospheric oxygen produced a corresponding drop in the rate at which oxygen was consumed. This relationship was by no means a linear one. An increment in the oxygen content of the air caused a greater increase in oxygen consumption at low levels of oxygen than it did at levels close to normal. Also, the response to changes in oxygen concentration was more pronounced in the beginning of the storage period than later. Finally, the magnitude of the response varied with different types of tissue.

These observations lead to the conclusion that in the five vegetables examined, oxygen becomes a limiting factor of respiration whenever its concentration drops below that of normal air; and the extent to which the utilization of oxygen is reduced depends on the partial pressure of the gas in the air, the relative respiratory intensity in normal air, and possibly to the permeability of the tissue to oxygen.

The data for carbon dioxide production can be interpreted correctly only if the corresponding values of oxygen are taken into account. The rôle of oxygen in respiration is two-fold: It is a reactant in normal aerobic respiration, and it inhibits anaerobic anabolism. The second function of oxygen is known as the PASTEUR effect. As defined by DIXON (**4**) it is the action of oxygen on living cells which reduces carbohydrate destruction and suppresses or diminishes the accumulation of the products of anaerobic metabolism. The PASTEUR effect comes into play whenever the storage atmosphere contains small quantities of oxygen but complete depression of anaerobic respiration is not attained until a certain threshold concentration is reached. BLACKMAN (**2**) has called this threshold concentration the extinction point of N R, that is the concentration of oxygen at which the course of respiration followed in an atmosphere of pure nitrogen ceases to exist. Below the extinction point, carbon dioxide production, as measured experimentally, consists of the combined gaseous end products of aerobic and anaerobic respiration. Depending on the intensity of anaerobic respiration, the values for total carbon dioxide output may actually increase below the extinction point. This was found to be true in asparagus during the first and second day and in carrots after the first day of storage. A similar secondary rise below the extinction point was observed by BLACKMAN (**2**) in apples held at low concentrations of oxygen. In these tissues the extinction point of N R is obviously close to the oxygen concentration at which total carbon dioxide production is at a minimum.

It is more difficult to determine the position of the extinction point in plant tissues which fail to show a secondary rise in carbon dioxide production. A sudden increase in the respiratory quotient may indicate the beginning of anaerobic respiration, but it must be remembered that a quotient above unity in itself cannot be taken as evidence that fermentation is taking place. The respiratory curves of shelled peas, for instance, show a respiratory quotient considerably higher than unity at all concentrations within the experimental range; but injury from anaerobic respiration was apparent only in the samples held at oxygen levels of less than three per cent. It is evident, therefore, that the exact location of the extinction point cannot always be determined by inspection of the respiration data. In fact, for practical purposes the appearance of symptoms of injury and the presence of an alcoholic odor in the chamber seem to be a safer and more sensitive index of how far the oxygen content of the storage atmosphere can be lowered without harmful effects.

Important is the fact that different plant tissues vary considerably in their tolerance to low levels of oxygen in the atmosphere. Oxygen concentrations of less than one per cent. were sufficient to maintain normal aerobic respiration in spinach and snap beans while shelled peas did not tolerate levels below four per cent. Also, there was evidence that the tolerance to low oxygen increases with the aging of the tissue or with a lowering of the storage temperature.

The degree to which the rate of respiration could be reduced varied with different vegetables. In some, the reduction exceeded fifty per cent.; in others it was barely forty per cent. for the entire storage period. Certainly, these results conflict with the statement commonly made that the oxygen content of the air has little influence on the respiratory rate of plant tissue. In fact, the magnitude of the effect of low oxygen storage on respiration suggests that the benefit from modified atmosphere storage, in which part of the oxygen is replaced by carbon dioxide, is due chiefly to the limited oxygen supply rather than to the presence of carbon dioxide. Additional experimental data are needed to determine quantitatively the effect that these two gases have on the respiration rate of various fruits and vegetables.

On the basis of results obtained thus far, it appears that holding fruits and vegetables in an atmosphere of low oxygen content offers possibilities as a practical method of storage. It has been shown that in some vegetables the retention of sugars is even greater than could be expected from the respiration data. Moreover, recent unpublished data have demonstrated that low oxygen is equally effective in retarding the destruction of ascorbic acid.

Several limitations and technical difficulties must be recognized. Aside from the fact that low oxygen storage requires gas-tight storage rooms, provisions have to be made for the continuous removal of carbon dioxide. In order to avoid injury from anaerobic respiration and to obtain maximum benefits, the oxygen concentration in the atmosphere must be maintained within a narrow range, the exact range being specific for each crop and each temperature. It also should be pointed out that many fruits and vegetables spoil because of storage diseases long before an appreciable loss in carbohydrates has occurred. In the course of recent experiments, it was frequently observed that molds and bacteria grow equally well at an oxygen concentration of one per cent. as in normal air. Even the presence of 20 per cent. carbon dioxide in the atmosphere was ineffective in controlling the spread of storage diseases. Consequently, beneficial results from low oxygen storage can be expected only for those crops which are highly perishable because rapid respiration or oxidation of ascorbic acid are important factors in deterioration.

Summary

Five vegetables, asparagus, spinach, snap beans, shelled peas, and carrots were held in respiration chambers in which part of the oxygen was replaced by nitrogen. A definite concentration of oxygen within the range of 0.8 to 20.5 per cent. was maintained in each chamber. Average daily rates of oxygen consumption and carbon dioxide production were determined.

The critical oxygen concentration below which the tissue was injured by anaerobic respiration (extinction point of N R) was about one per cent. for spinach and snap beans, 2.5 per cent. for asparagus, and four per cent. for peas and carrots when held for several days at 20° C. There was evidence that the tissue became more tolerant to low oxygen with aging and with a lowering of the storage temperature.

By choosing the most effective oxygen concentration, the respiration rate as measured by carbon dioxide production could be reduced about 50 per

cent. At the most effective oxygen level, the respiration rate of asparagus was 40, and that of carrots 65, per cent. of the rate in normal air.

Sugar losses occurring in the course of respiration were determined for asparagus and peas. At the most effective levels of oxygen, asparagus retained eight times and peas two and one-half times as much sugar as comparable samples in normal air. It was shown that in asparagus proteins furnish about one-third of the substrate of respiration.

CORNELL UNIVERSITY
ITHACA, NEW YORK

LITERATURE CITED

1. ASSOCIATION OF OFFICIAL AGRICULTURAL CHEMISTS. Official and tentative methods of analysis. Washington, D. C. 1935.
2. BLACKMAN, F. F. Analytical studies in plant respiration. III. Formulation of a catalytic system for the respiration of apples and its relation to oxygen. Proc. Roy. Soc. (London) **103B**: 491–523. 1928.
3. CHOUDHURY, J. K. Researches on plant respiration. V. On the respiration of some storage organs in different oxygen concentrations. Proc. Roy. Soc. (London) **127B**: 238–257. 1939.
4. DIXON, KENDAL CARTWRIGHT. The Pasteur effect and its mechanism. Biol. Rev. **12**: 431–460. 1937.
5. MACK, W. B. The relation of temperature and the partial pressure of oxygen to respiration and growth in germinating wheat. Plant Physiol. **5**: 1–68. 1930.
6. PARIJA, P. Analytical studies in plant respiration. II. The respiration of apples in nitrogen and its relation to respiration in air. Proc. Roy. Soc. (London) **103B**: 446–490. 1928.
7. PLATENIUS, HANS. Effect of temperature on the respiration rate and the respiratory quotient of some vegetables. Plant Physiol. **17**: 179–197. 1942.
8. STEWARD, F. C., BERRY, W. E., and BROYER, T. C. The absorption and accumulation of solutes by living plant cells. VIII. The effect of oxygen upon respiration and salt accumulation. Ann. Bot. **50**: 345–366. 1936.
9. THORNTON, NORWOOD C. Carbon dioxide storage. III. The influence of carbon dioxide on the oxygen uptake by fruits and vegetables. Contrib. Boyce Thompson Inst. **5**: 371–402. 1933.